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A novel examination of the preorbital fossae of Equidae (Perissodactyla, Mammalia)

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ABSTRACT - The soft anatomy and skull of the extant Equus *(Equidae, Mammalia) help in the understanding of the preorbital fossa (POF) of extinct Equidae. The preorbital fossae which are prevalent in the extinct species are reduced but not absent in* Equus*. None of the facial muscles of* Equus *coincide with their facial fossae. The nasolabialis muscle is situated over the shallow preorbital fossa not the levator labii superioris. The levator labii superioris is closer to the orbit; its tendon is supported by a special fascial sling of the nasolabialis. Although the preorbital fossa in the modern horse is externally shallow, it is present as folded bone within that bony fossa. It is also present internally and therefore is not lost. The tholos, the murus reticulatus and the pontis are internal structures of the paranasal sinuses of* Equus *and may represent parts of the original preorbital fossa. The preorbital fossae in extinct equids are probably independent of the nasolabialis and levator labii superioris muscles. They simply coincide in space and may be functionally unrelated structures. These muscles were most likely attaching on taut membranes that covered the preorbital fossae in extinct taxa. Micro CTs of* Merychippus *reveal that the floor of the fossa is an extremely thin bone (0.3 mm) and unlikely suitable for muscle support. The nasolacrimal duct disappears in the fossa area. Embryology of mammals supports that the fossa is the duct wide open. Rostral to the fossa, the duct is reconstituted. In other words, it is reassembled. The fossae could contain glands or a sound-producing structure. Fossae most likely were derived from embryonic placodes. Membranes may have covered the fossae. The extinct equids were grazing less than* Equus*; the fossae are reduced in* Equus *probably because of its extreme grazing. Apparently, the maxillae are better in supporting the high force and grazing functions than the nasal capsule. In* Equus*, parts of the fossae are relocated in the paranasal sinuses (e.g., tholos, murus reticulatus). The internal nasal cavity of* Merychippus *reveals structures homologous to those observed in* Equus*.*

INTRODUCTION

The preorbital fossa (POF) is a depression in front of the orbit in most extinct Equidae. The fossa has a caudal and dorsal sharp and continuous margin, and it is usually a deep depression. The POF is widespread in the Equinae of the Miocene and much interest has been placed in this structure. *Merychippus* Leidy, 1857 possesses such a typical deep fossa. Hulbert & MacFadden (1991) and MacFadden (2005) showed that *Merychippus* is central in the evolutionary branching of Mio-Pliocene Equidae. We use *Merychippus* and *Equus* Linnaeus, 1758 as templates to understand the POF. Many genera phylogenetically near *Hipparion* de Christol, 1832 also possess preorbital fossae. The preorbital fossa has been used in systematics by many researchers (e.g., Gregory, 1920; Zhegallo, 1978; Bernor et al., 1980, 1989, 1990, 1997, 2021; MacFadden, 1994, 2005; Woodburne 2007, 2009; and others). These authors characterize or describe the preorbital fossa using the fossils and their research is paleontological. Yet, there is no deeper anatomical examination of the POF: there are no micro-CT examination or dissections of fossils and the modern horse to relate and connect the various morphological characters. In addition, there are other facial fossae in certain equids; for example, in *Protohippus* Leidy, 1858 and *Pliohippus* Marsh, 1874 a second large fossa (the malar) is situated closer to the zygomatic arch and the orbit. Some equid genera also have a buccinator fossa. These additional facial fossae have not been studied as much. Almost all equids are now extinct, except for *Equus*, the only living genus that represents the Equidae. *Equus* evolved from *Dinohippus* Quinn, 1955. In *Equus* however, the preorbital fossa is clearly reduced and the literature points this out in many studies. For example, MacFadden (1994, p. 104) reports: "There is no homologous structure in living horses". We do not agree with this assertion. The fossa of *Equus* is truly reduced in depth and the margins are smooth, but it is not lost. The reduction of the preorbital fossa is a perplexing change from the norm, since the norm is for horses to have one or more preorbital fossae, which is many species with one or more preorbital fossae. For the extinct species, we only have the bony skull to study, no soft tissues. This way, a study is limited. For the domesticated *Equus*, we have the skull, soft tissue anatomy, fetal specimens, and embryos. The soft anatomy is highly relevant to the fossae and the extinct taxa. The present study is of paleontological value although it is mainly based on the detailed examination of the soft anatomy in *Equus*. Clearly, a comparison of extant and extinct taxa is necessary. Comparisons with rabbits are also essential and our research shows that it explains better the observed anatomy of equids.

In our study we describe the preorbital fossa of the domesticated horse and its associated soft anatomy and ontogenetic development. We will also be discussing external to the skull and internal structures related to the facial fossae (POF, malar and buccinator). Part of the depth of preorbital fossa in *Equus* is concealed. The fossa appears shallow but the floor of the fossa bone is folded multiple times (within the bone) revealing a deeper POF

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(like wrinkling a piece of paper). A second part of the POF has migrated caudally and is positioned internally in the paranasal sinuses. The fetal development of the fossa is also examined. We relate the fossa to the nasolacrimal duct. We also describe a selected group of fossae from extinct species with an emphasis on *Merychippus insignis* Leidy, 1857, *Pliohippus mirabilis* (Leidy, 1858), and *Protohippus pernix* (Marsh, 1874).

Equids have a notably rich record in N. America (Osborn, 1918; Matthew & Chubb, 1921; Matthew, 1926; MacFadden, 1994; Mihlbachler et al., 2011; Bernor et al., 2021). There have been numerous species through time from 55 Ma to the Late Pleistocene when the last remaining horse, *Equus*, became extinct in North America. Many species coexisted in North America, especially during the Miocene. A few also migrated to Eurasia and Africa (hipparions, *Equus*, and others). Cirilli & Bernor (2025) address newer information on the complexity in morphology and adaptive radiations of hipparions.

MATERIAL AND METHODS

We dissected twelve heads of horses, which were donated by the University of Pennsylvania Veterinary School and the Bolton Equine Center; Perry Habecker helped us in obtaining the specimens. We used specimens of domesticated *Equus caballus* Linnaeus, 1758 in the NS collection, namely: NS 8, NS 10, NS 99, NS 100, NS 103, NS 104, NS 105. Fetuses from Wards Biological Supply were: NS 4, 200, 201, and 202 (donkey). The specimens are numbered in our lab (NS numbers) but will be donated to the American Museum of Natural History (Paleontology). Horse adult skulls were sectioned coronally and longitudinally with a bandsaw. We also used many specimens in the osteology collection of the American Museum of Natural History Department of Mammalogy. At the AMNH, we examined the preorbital fossae of extinct horses. *Merychippus insignis* AMNH 78002 was selected as an ideal representative species of the preorbital fossa – it is a small animal and part of the skull would fit in the micro CT chamber. In AMNH 78002 the internal anatomy is visible (we had the sediment removed professionally). This species is known from many specimens at the AMNH, especially from the Echo Quarry of the Olcott Formation in Nebraska (Woodburne, 2007). We also examined *Pliohippus mirabilis* and *Protohippus pernix*. *Merychippus* AMNH 78002 was micro CT scanned by Kelsi Hubble at NYITCOM to see the internal structure of the fossa and the nasolacrimal bony tube. *Merychippus* AMNH 87003 was scanned in a larger scanner at St Barnabas Hospital.

We have also begun to study the rabbit *Silvylagus* sp. to clarify certain issues about its preorbital fossa (NS 500, 501 and 502). NS 501 was micro CT scanned. NS 502 was preserved in formalin and injected with (red plastic) arteries and (blue plastic) veins. This head was sectioned with a carpenter's bandsaw. In order to increase clarity, the sectioned head was scanned under water on a typical flatbed scanner at 900 dpi, after constructing a well with clay on the glass of the scanner. We also dissected a chacma baboon, *Papio ursinus* (Kerr, 1792); all *Papio* have a preorbital fossa. We have observed the baboons in the New York Zoological Society and have examined skulls at the AMNH.

Anatomical terms employed (Solounias, 2024)

Bone spicules: cover the external floor of the preorbital fossa (POF).

Diverticularis muscle: a thin muscle forming the inner floor of the nasal diverticulum.

Fascial sling of levator labii superioris: supports the levator labii superioris (LLS) muscle from the nasolabialis.

Fibrofatty cushions: located deep in the buccinator fossa, attaching onto the base of the nasalis ventralis muscles.

Murus reticulatus: the "decorated wall" in the paranasal sinuses.

Nasalis dorsalis muscle: originates from the external nasal surface and attaches onto the ventral concha.

Nasalis ventralis anterior and posterior muscles: originate from the buccinator fossa and attach to the sigmoid cartilage.

Nasolacrimal bony tube: the bony tube that encloses the nasolacrimal duct and accompanying arteries.

Nasolacrimal lake: an expansion of the nasolacrimal duct located beneath the sigmoid cartilage.

Pillars: fibrous structures connecting the membrane of the preorbital fossa (POF) to trabecular bone; surrounded by blood.

Pontis: a bony bridge in the nasal cavity.

Preorbital fossa membrane and pillars: embryonic membrane forming the unossified floor of the POF.

Red hue in the bone of the POF: the bone of the POF is often stained red due to internal blood.

Sigmoid cartilage: also called sigmoid by Schmaltz (1905-1929) or medial accessory nasal cartilage (sensu Nickel et al., 1986); located lateral to the nasal septum, connecting to the external nostrils and nasalis ventralis muscles, and lying over the nasolacrimal lake.

Suturiscus: a small suture located within a single bone.

Tholos: a dome-like bony structure found in the paranasal sinuses.

Abbreviations

AMNH, American Museum of Natural History; LLS, Levator labii superioris; Ma, Mega annum - million years ago; NHMBe, Naturhistorisches Museum Bern; NS, Nikos Solounias collection at NYIT COM; NYIT COM, New York Institute of Technology College of Osteopathic Medicine; POF, Preorbital fossa.

RESULTS

The study presents the facial fossae as distinct. This is a preliminary approach that helps in focusing on the structures of each fossa (Solounias, 2024). However, examination of numerous species suggests that the buccinator, POF and the malar fossae may all be just one structure expressed in different ways in the plethora of taxa. The first chapter in a book recently published by the senior author covers the preorbital fossa as it was understood roughly ten years ago (Solounias, 2024). The current study brings the relevant anatomy into a new focus.

Equus caballus*, the domesticated horse*

The preorbital fossa is complicated as it has external and internal structures.

External fossa structure in *Equus* - What are the contents of the *Equus* preorbital fossa? The superficial POF of the modern horse is clearly reduced, but it is present - unlike the common belief that is totally lost (MacFadden, 1994). It is, however, not as deep and does not have sharp edge margins unlike the other extinct taxa. The horse's superficial preorbital fossa is approximately 12 mm deep from the higher external surface (NS 10, NS 100). The maxilla and the nasal bones connect by a simple suture in the center of the fossa. The area of the fossa is half in the nasal and half is in the maxilla. The fossa is at the level of P4-M1.

Figure 1 shows only the relevant structures of the study and Fig. 2 outlines the location of the fossae on the skull of three taxa. From our dissections of *Equus caballus* (12 heads dissected over several years) no muscle corresponds in location to any of the preorbital fossae. The muscle which overlays the POF but does not attach at the POF is the nasolabialis. It spans and covers the POF but does not attach there; it attaches at the median dorsal suture of the two nasals. The prevailing view in the literature considers the levator labii superioris (LLS) as the muscle of the preorbital fossa. In contrast, Schmaltz (1929) figures the origin of the LLS correctly. That muscle sometimes has its own very shallow fossa caudally to the preorbital fossa and close to the orbit (Figs 1, 2a) (Solounias, 2024, fig. 15). The origin is a small region of the dorsal-most part of the malar fossa but never covers the entire malar fossa. This origin is the topographic location of the LLS. In many specimens there is no fossa at all for the LLS. The LLS is a face muscle and all face muscles attach to the deep membranous lamina and not to the bones of the face (Solounias & Colalillo, 2024). Next to the origin of the LLS is the malaris muscle that has its origin on the cranial edge of the most rostral part of the zygomatic arch. The muscle belly is over the LLS and connects with the orbicularis oculi. From the zygoma to the orbicularis oculi is a thin tendon. Both of these muscles lie over the LLS which is deeper. The malaris is unrelated to the malar fossa.

The buccinator is also not in the buccinator fossa. That fossa is for the two nasalis ventralis muscles, as shown by Solounias (2024), who also discusses the connecting cushions of these muscles.

In mid-term and later fetuses there are two ridges on the skin of the face. They are directed rostrally from the orbital area. One ridge is dorsal to where the POF would be and one ridge is ventral to where the POF and malar would be. Specimens NS 4, 200, 201, 202 and 204 have these two dermal ridges (they are late fetuses). The bone deep to the ridges does not show any ridges. In early embryos these ridges are absent. The ridges outline the location of fossae in newborns (POF and malar combined).

Coronal cross sections of horse skulls reveal an interesting pattern. Caudal to the preorbital fossa, the bone, in a cross section, is thin (3.76 mm) and simple. Proceeding into the shallow fossa, in the center of the fossa, the bone is thicker (12.04 mm) and is full of numerous bony infoldings and twisting of bone. Rostral to the fossa, the bone is again thin and simple in a cross section (3.7 mm). These bony infoldings within the POF vary in magnitude in different specimens but are always present. If unfolded, a thought experiment, the resulting POF would be large and deep.

Two muscles are in this region of the skull: the nasolabialis and the levator labii superioris (Fig. 1) (Ellenberger & Baum, 1894; Boas & Paulli, 1908; Schmaltz, 1929; Ellenberger et al., 1956; Popesko, 1990; Solounias, 2024). The nasolabialis begins at the dorsal margin of the preorbital fossa on the nasal, spans the fossa, and descends rostrally to the lips. It is obliquely directed across the face of the horse. Distally, the nasolabialis splits, and the inferior limb attaches to the upper lip, whereas the superior limb attaches to the nostril. The caninus muscle passes through the split of the nasolabialis (Ellenberger & Baum, 1894; Schmaltz, 1929; Ellenberger et al., 1956; Popesko, 1990; and other veterinary anatomy books). The nasolabialis pulls the angle (corner of the upper lip) and upper lip up and back. The zygomaticus passes parallel

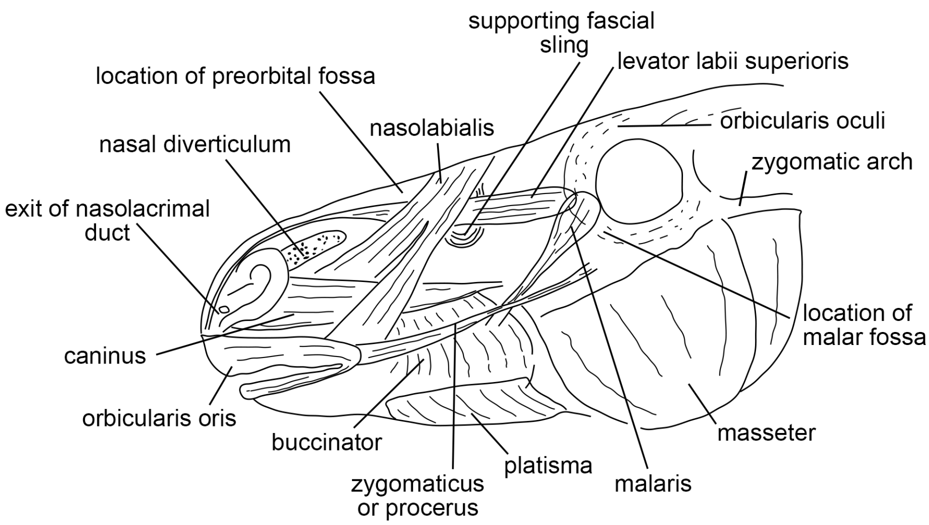
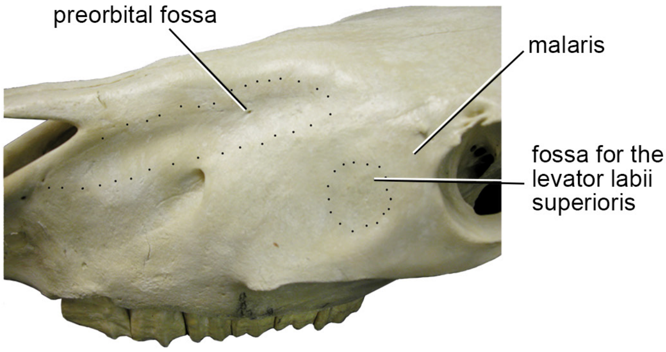


Fig. 1 - A schematic of a horse head showing the position of muscles relevant to the study.

a



b

c

Fig. 2 - (color online) a) A typical *Equus caballus* skull showing the remnant preorbital fossa and the fossa of the levator labii superioris (dotted areas). b) The holotype of *Cremohipparion proboscideum* from Samos (NHMBe 5019); the POF is double and large. c) *Pliohippus pernix* (AMNH 60800), Burge Member, Nebraska; the malar and preorbital fossae are well-developed.

to the nasolabialis and also attaches at the angle of the lip. The zygomaticus or procerus is very weak and as in many mammals pulls the angle (corner) of the lip and nostril back.

Herein, we add new information on the external structures of the preorbital fossae of *Equus*. In the preorbital fossa there are fibrous fasciae which emanate forming a loop and are connected to the nasolabialis externally and the bony floor of the POF internally. The fasciae descend and form a sling (a loop) (Fig. 1). The levator labii superioris tendon passes through that sling and is clearly supported by it. The sling is similar to that used for an arm break, that typically wraps around the neck. The levator labii superioris tendon freely moves and slides back and forth within the sling like a piston. The muscle tendon is long and a supporting sling makes sense.

The levator labii superioris begins (i.e., its origin is) well caudal to the preorbital fossa by the orbital rim at the dorsal region of the malar fossa. It is paired with a supporting muscle called the malaris. The malaris is external to the LLS and it has its origin on the rostral edge of the zygomatic bone. It has a long thin tendon that passes over the malar fossa and it attaches at the orbicularis oculi (Solounias, 2024, fig. 14). Both may form their own shallow and small circular fossa which is 3 mm deep and clearly distinct from the classic preorbital fossa of the extinct equids. This small fossa is for the levator labii superioris close to the orbital rim. Being almost perfectly circular (Fig. 2a), this fossa (35 mm × 23 mm from specimen NS 10) is congruent to the shape of the origin of the levator labii superioris, whereas the preorbital fossa is not circular: it is long and oval and thus does not match the shape of the levator labii superioris (139 mm × 81 mm from specimen NS 10). We clarify: the POF is not of a circular origin, and it is distinct from the origin of the levator labii superioris (Fig. 2a).

The levator labii superioris is horizontally oriented and proceeds rostrally to the upper lip of the horse. It passes through the fascial sling of the nasolabialis. Rostrally, the levator labii superioris becomes very thin and tendinous, there are no muscle fibers there. It inserts on the inner margin of the upper lip and raises it. The two (the left and right levators) merge at the median margin of the lip with a common terminating Y-shaped tendon. The two levators labii superiores work together to move the upper lip laterally and up. The horse does movements of the upper lip as two horses greet each other, and as they graze, during the flehmen response and more. The upper lip is flexible like a short proboscis and very similar in function to that of the black rhinoceros. There is no reason to assume other functions and other locations of the levator labii superioris in the extinct equids.

The preorbital fossa of *Equus* is not reduced despite what paleontologists believe (Zhegallo, 1978; Bernor et al., 1990; Woodburne, 2007). Examination of *Equus* skulls in coronal cross sections revealed an interesting structure. In the area where the fossa is reduced, the bone is folded over and over like a pastry of phyllo (Fig. 3a2). The structure of the bone resembles nappes of strata in the Alps. Multiple layers of bone are compressed in there, folded, contorted and twisted. Rostral and caudal to the fossa the cross section of the bone is simple. It is only the reduced fossa area that shows this contorted infolding bone. This observation suggests that the fossa is externally present and large and the reduction is only superficial; the result of this is the infolding of the bone. This fossa would have been large and deep but concealed by the folding (folding internal to the bone).

The floor of the POF in fresh unpreserved horse specimens is always distinct as the bone has a pink-red hue from blood and probably other substances (fluids from the Harderian gland and possibly hormones). The blood is contained in the bone (maxilla and nasal). The hue stops at the border of the fossa. Outside the POF, the bone is typical white.

In the orbit, there is a tube from the lacrimal gland (above the eye) and a tube from the Harderian gland (below the eye) (Rehorek, 1997) (Fig. 4). The Harderian gland was first described in 1694 by Johann Jacob Harder (1656-1711); it opens at the nictitating membrane of the eye (Santillo et al., 2020). Two small muscles (lacrimalis) aid the passage of fluids from the ducts into the nasolacrimal sac and the nasal cavity. Microscopic examination of the floor of the fossa reveals a scatter of bone spicules throughout the surface. The spicules are separate from the bone surface (Fig. S1 of Supplementary Online Material [SOM]). They range from 0.22 to 0.24 mm. They may be related to the origin of the fascial sling previously described.

Internal structures in *Equus* - The bones of the external fossa are the nasal and the maxilla. In addition, there is a thick inner surface from the ossified nasal capsule in the adult (see Fig. 3). In the coronal section the thicknesses are: nasal capsule, 1.61 mm; folded bone, 6.27 mm; external maxilla, 2.68 mm (Solounias, 2024, figs 17, 18). The nasal capsule is internal and fused to the surface bones (nasal, lacrimal, maxilla, frontal). In the POF region, the nasal capsule is fused to the maxilla and the nasal. The capsule extends internally rostrally all the way to the premaxilla.

The nasolacrimal tube, that begins in the orbital rim, enters the nasal cavity. In the orbit there is a tube from the lacrimal gland (above the eye) and a tube from the Harderian gland (below the eye) (Rehorek, 1997) (Fig. 4). The tears and other fluids pass into the duct at the orbital rim. This bony tube terminates in the inner nasal cavity in all mammals. In cross sections of a horse and a rabbit (NS 502) the nasolacrimal tube is surrounded by at least 16 arteries and no veins (Fig. S1a). The rabbit also has spicules embedded in the membrane that covers the fossa. These are much larger than those of the horse (ranging from about 0.31 mm to 0.71 mm) (Fig. S1b). The appearance of the arteries surrounding the duct superficially resembles the pancreatic acini cells surrounding an islet. We see no veins there and we know this as the injected plastic was red for the arterial system of the rabbit. The arteries surround the tube and are all enclosed in a more external tube which is contained in the nasolacrimal bony tube. In the rabbit, we see bony spicules externally that are part of the fossa. The dermal ridge of the horse is external and it is assumed to be a remnant of the preorbital fossa (Fig. S1c). The ridge is near the nasolacrimal duct seen in this cross section.

Internally, in *Equus*, a bony dome, the tholos (dome in Greek) is dorsal to the nasolacrimal duct (Fig. 5a). The tholos is the result of two overlapping bones, one dorsally and one ventrally. These bones connect to the adjacent nasal cavity and the conchae but are totally avascular. The tholos is separated from the conchae by well-defined sutures. The tholos resembles the dorsal margin of the preorbital fossae of *Merychippus*, *Protohippus*, *Cormohipparion occidentale* Skinner & MacFadden, 1977 (see also Woodburne, 2007) and *Cremohipparion proboscideum* (Studer, 1911) (see also Qiu et al., 1987). We assume that the tholos is an inner expression of the caudal preorbital fossae, i.e., a remnant of the POF. The nasolacrimal duct passes next to a very thin wall of bone. This is the murus reticulatus (decorated wall; Fig. 5b1) (Solounias, 2024, fig. 21). It is an internal thin wall of bone (0.3 mm thick) made of a mesh of spicules in *Equus*. This wall is avascular and it is situated medial to the nasolacrimal bony tube. Externally, the lacrimal/maxillary bones are located external to the nasolacrimal duct. The bare nasolacrimal duct (uncovered by the bony tube) passes lateral to the murus reticulatus deep to the lacrimal bone.

Anterior to the murus reticulatus, the duct passes under a bony bridge (the pontis, small bridge) which is a distinct ossification in the nasal cavity (Fig. 5b2). The duct continues rostrally and passes under the sigmoid cartilage (Solounias, 2024, figs 2, 10, 11). The pontis is located at the level of P4-M1, there is a robust thickening of a separate ossification that is derived from the embryonic nasal capsule which is well-fused to the inner wall of the maxilla. The structure provides a passage in the center for the nasolacrimal duct which is reconstituted as it passes through it. We term this the pontis (Fig. 5b2) (Solounias, 2024, figs 12, 21). The pontis has bony extensions like roots (supporting extensions) which attach to the inner side of the nasal cavity. Dissections reveal that the bone of the pontis is full of blood as is the bony floor of the POF; the blood is probably derived from the arteries surrounding the nasolacrimal duct. The duct and the surrounding arteries

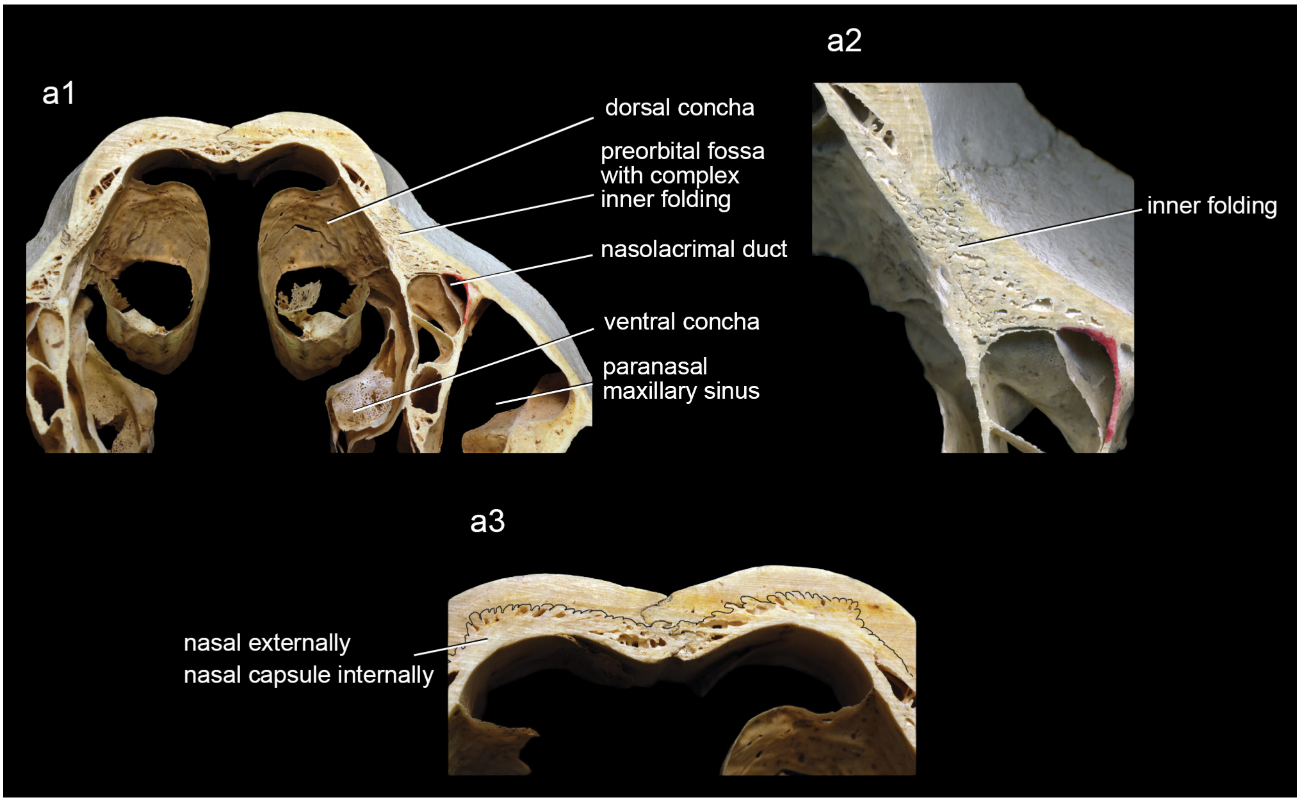


Fig. 3 - (color online) A cross section at the area of the preorbital fossa of *Equus caballus* (NS 100). a1) Magnified area showring the folding of the bone within the fossa. a2) Magnified fossa to see the complex inner folding. a3) The dorsal area of the nasals showing the fusion of the nasal capsule internally to the nasals externally.

enter the bone of the pontis and the POF. The bone takes usually a pink hue. This hue is visible internally and externally. Fig. 5 shows the tholos, the murus reticulatus, and the pontis.

Under the sigmoid cartilage, the duct enlarges and forms a lake (an expansion of the duct). The duct becomes narrow again anterior to the sigmoid cartilage and exits the nasal cavity. The exit opening is exactly at the edge of the nostril (Fig. 1). It is exactly next to the opening of the nasal diverticulum of the nostril (a blind sac). The nasolacrimal tube of *Equus*, unlike in other mammals, drains at the very edge of the nostril. This external drainage is exceptional and we know no other mammal like this.

The nasal diverticulum is a conical blind sac opening at the nostril (Solounias, 2024, figs 5, 6). It is situated at the nasal notch. The cone extends back from the nostril to the nasal bony notch. The inner surface of the nasal diverticulum is lined with fur (hair) and pigmented dark. A muscle, the diverticularis, covers the outer surface of the diverticulum. This muscle is involved in the snorting behavior (Solounias, 2024). When the horse blows air out of the nostril, the nasal diverticulum and nostril vibrate.

In human development, the best-known development, the nasolacrimal duct begins as an external trough on the surface. We believe that it is a placode (Hinrichsen, 1985; Steding, 2009, p. 33; Solounias, 2024). It spans the distance from the nostril's edge to the orbit. The trough sinks into the head, as all placodes do, first rostrally and later towards the eye. In a 20 mm horse embryo donated by the Cornell Veterinary School, the head was 18.6 mm and the nasolacrimal duct (placode) was already sunk in the head.

Medially and caudally to the tholos is a gap with no structures (Fig. 4b) which separates the tholos from the ethmoids. This is termed the fronto-maxillary aperture (Nickel et al., 1986, fig. 288) or Oberkieferhöhle (i.e., hole of the upper jaw) (Schmaltz, 1929, pl. 139). Examination of early equids suggests that later equids expanded that region elongating the skull. The ethmoids did not expand but the structures cranial to the ethmoids did.

The nasal diverticulum - It is a blind sac in the shape of a cone opening at the nostril of *Equus* (Fig. 1). Internally it is covered with black pigmented fur (hair). It is surrounded by a thin muscle (the diverticularis) and it is probably involved in the typical snorting of the horse. In terms of size it fits perfectly in the nasal bony notch. It has been suggested that the nasal diverticulum was lager and was placed in the preorbital fossae of extinct equids (Gregory, 1920). We propose that air from exhalation enters the nasal diverticulum and exits forming air currents and eddies. These currents would spray the fluids of the nasolacrimal duct in the environment (Solounias, 2024, figs 5, 6).

The buccinator fossa - The buccinator fossa is deep and situated in the diastema caudal to the canine in the maxilla in *Equus*. The buccinator muscle is external to that but it is not part of the fossa. The fossa contains, instead of the buccinator, two large nasalis muscles which enter the nasal cavity and attach on the sigmoid cartilage (medial accessory nasal cartilage). The buccinator is external to these and appears not to be related to the fossa which carries its name (Fig. 1) (Solounias, 2024, figs 4, 8, 10).

The lower malar fossa - The POF and the malar fossae of *Pliohippus mirabilis* and *Protohippus pernix* are two and they are deep. The malar fossa is located close to the upper molars and the zygomatic bone (Figs 2c, 7). In the modern *Equus caballus* this malar fossa is clearly the same and visible inside the paranasal sinuses. It is identical to the extinct taxa but internal (Fig. 6c). It is termed crista semilunaris (because of its new location and as it is a bony crest in the shape of a half-moon) (Solounias, 2024, fig. 23a). It is internal and it is certainly the malar fossa relocated. Rostrally it is straighter and termed the oblique septum. It is situated ventral to the nasolacrimal bony tube in the paranasal sinuses. In *Pliohippus* and *Protohippus* it is external (Fig. 6).

The reduced POF of *Equus* contains small bony spicules on its external surface (Fig. S2 of SOM). They are fixed onto the surface of the nasal and maxilla. They are similar to the spicules of the murus reticulatus (Fig. 5b1).

The embryonic nasal capsule - The internal nasal cavity in mammals is derived from an oval melon-like (American football ball-like) cartilaginous cluster (e.g., de Beer, 1937; Grassé, 1967, p. 421; Smith & Rossie, 2008, fig. 3; Solounias & Colalillo, 2024). The nasal capsule is endochondral. It is thin rostrally where it meets the nostrils and also thin caudally where it meets the ethmoids. In the center, it is thick and internally forms the nasal septum and the conchae. The adult nostrils and nasal cartilages form from the nasal sac (rostral part of the nasal fossa). The nasal capsule caudally is constricted and connects with the neurocranium (again endochondral) (Grassé, 1967; Klima, 1999). We show the nasal capsule of *Oryctolagus* Dice, 1917 (capsule nasale in Grassé, 1967, fig. 12a), *Lepus* Linnaeus, 1758 (de Beer, 1937, fig. 12b), and the horse (de Beer, 1937, fig. 12c) (Fig. S3 of SOM). The nasal capsule fuses with the surface intramembranous bones in the adult (Fig. 3a3). The fusion of the two layers is often obliterated in adults. In the adult, the fusion cannot always be observed and looks like a single layer.

The two layers can be observed in Fig. 3a3. In the horse and probably other mammals, the inner wall of the nasal cavity is also formed by the nasal capsule. Structures in the nasal cavity are formed in part by the nasal capsule. Two rabbits (*Oryctolagus* and *Lepus*; Fig. S3) show that the nasal capsule is dorsally domed (full); however, in the same figure we see that the horse's nasal capsule has a concave dorsal dip. This dip is also present in the ossified skull of the more developed horse embryo (Barreto et al., 2016). This dip in the bone structure lines up with the location of the preorbital fossa. We hypothesize that the POF is related to the space ventral to the cartilage termed tectum nasi (Solounias, 2024, fig. 45). As the horse and other mammals develop, the inner wall of the nasal cavity becomes lined by the nasal capsule. We hypothesize that the malar fossa is related to the space between the

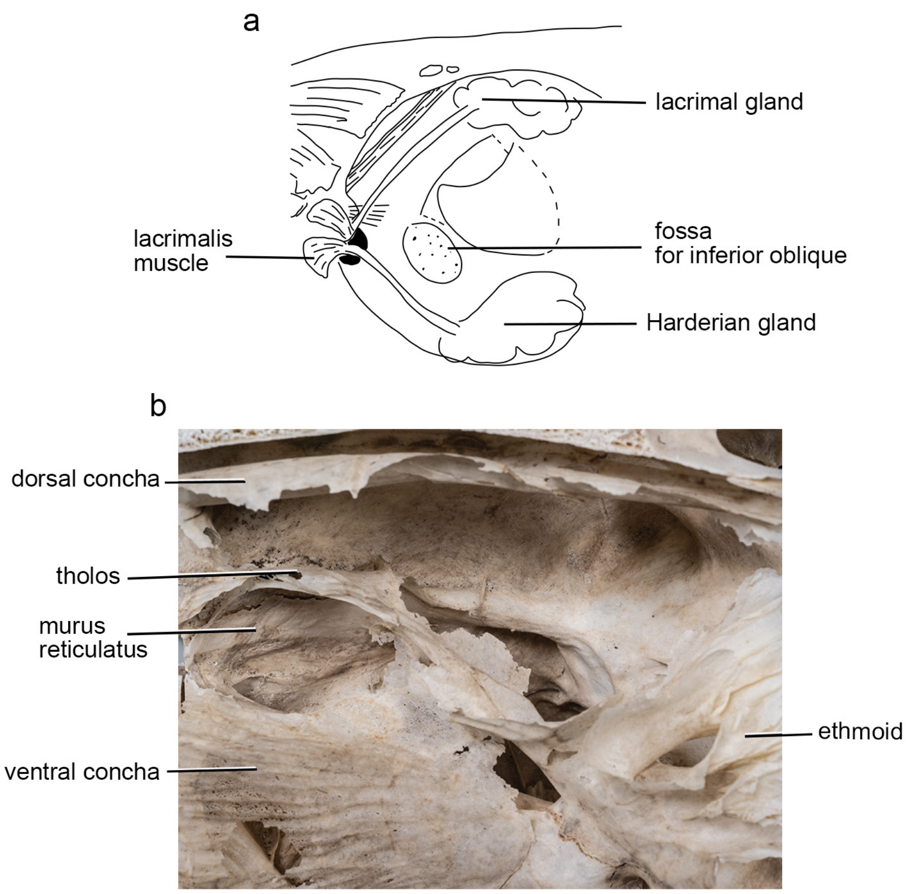


Fig. 4 - (color online) a) Orbital area of *Equus* and the two ducts entering the nasolacrimal tube. The lacrimal duct is located dorsally and the Harderian gland duct ventrally. b) Rostral region to the left. The dorsal concha has been removed. The tholos and the murus reticulatus are visible, orbit and the nasolacrimal tube are visible.

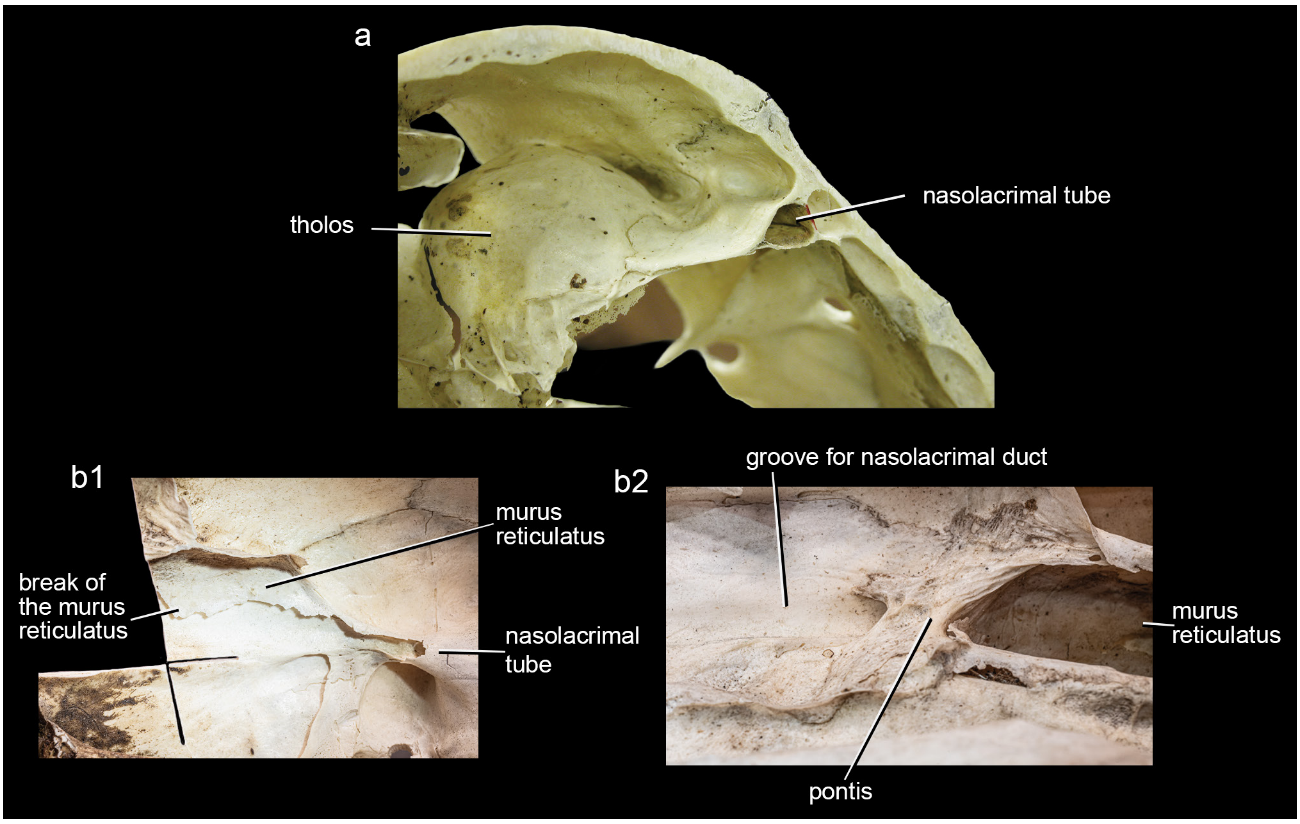


Fig. 5 - (color online) a) *Equus caballus* tholos and the bony tube of the nasolacrimal duct (NS 100). b1) Murus reticulatus - broken surface (NS 10) (rostrum to the left). b2) The pontis and passage for the nasolacrimal duct (NS 10).

pares nasi cartilage of the nasal capsule and the anterior transverse lamina cartilage of the nasal capsule (Solounias, 2024, fig. 45). The nasal capsule is likely the floors of the POF in *Equus* (Klima, 1999, figs 6, 19, 36).

A special specimen of *Equus* - This specimen (NS 103) is most likely a donkey (it has large ears and head). The length of the late fetus is 70 cm (from head to base of tail). The bone of the fossa has a sharp dorsal edge as in extinct taxa (Solounias, 2024, figs 47-49). This fossa is situated near the orbital rim. The observed fossa is the POF or the malar or both. There is a taut membrane spanning the entire fossa area. The membrane terminates at the alveoli of the upper molars. The levator labii superioris and the fibro-fatty material attach on the external surface of the membrane are structured as in all dissected *Equus* specimens. The fossa is very shallow (4 mm). The bone deep to the fossa has no cortex (surface); it is just medulla. Deep to the membrane, there are small pillars (hundreds of them) that connect the membrane to the medullary bone below. The empty spaces between the pillars is full of loose flowing blood. Eventually the membrane will ossify and the adult fossa will be reduced or obliterated. The nasolacrimal duct is present in the bone deep to the fossa. Within the fossa was the foramen for cranial nerve V2 (Fig. S4 of SOM).

Merychippus insignis *from the Olcott Formation and other extinct species*

Merychippus insignis is known from many specimens at the AMNH. We selected AMNH 78002 (Olcott Formation, Echo Quarry; Barstovian, 14.5 Ma) for description and study (Figs 7, S5, S6 of SOM). The fossa is deep with sharp margins dorsally and caudally. The ventral and rostral edges are less sharp and blend with the surrounding external bones. This is a typical POF. The opening in the orbital rim for the nasolacrimal duct is also typical. There are also numerous very small foramina in the caudal wall of the fossa that may be connecting to the main nasolacrimal duct and the arteries surrounding it (Solounias, 2024, fig. 34).

In AMNH 78002 the internal anatomy is visible (Fig. 7). The conchae are exposed and an inner view of the preorbital fossa is clearly visible. The bony tube for the nasolacrimal duct connects the orbital wall to the POF. At the posterior margin of the fossa the two structures are merged. The nasolacrimal duct is not present deep to the fossa as an independent structure. The rostral region of the tube connects to an expanded and thickened bony region, i.e., the pontis. It forms the caudal margin of the POF. The bony region has two extensions, like tree roots adhering to the external bones (nasal, lacrimal and maxilla). The dorsal extension forms the margin of the preorbital fossa and then extends caudally inside the lacrimal bone. The more horizontal ventral extension forms the ventral margin of the preorbital fossa. The nasolacrimal duct, after exiting the nasolacrimal bony tube, enters the pontis and the POF (Figs S5, S6). In Fig. S5 one can see the thick internal structure of the pontis. The opening of the duct is covered with a small mesh of structures of unknown function. They may be vascular or glands. Next to it, in the pontis there are two more tubes even more invaded with a mesh. In summary, the pontis, the nasolacrimal duct and the caudal part of the fossa are one structure.

In the micro CT scans (Fig. S6a-f) the tube contains a smaller tube within and other structures interpreted as bony walls of arteries. The artery interpretation is based on coronal sections of *Equus* and *Silvylagus* (Fig. 8). Figure S6a shows the duct approaching the pontis at the caudal aspect of the fossa. Some arteries surrounding the duct are visible. Figure S6b is the duct which is situated closer to the pontis and multiple vessels are developed adjacent to it. Figure S6c is the duct and other structures merge into the pontis. Vertical ridges are visible which are found in many equids in the deepest part of the fossae. Figure S6d is the deepest part of the POF which appears as a notch. It is adjacent to the pontis and duct (ventral to the POF). Within the pontis three oval clusters of trabecular bone separated by ridges have formed. These have been observed also in other specimens from the Echo Quarry. Figure S6e shows the main POF, the floor of which is a notably thin surface of bone (0.3 mm). The bony nasolacrimal tube of the duct is not observed in the POF. The tube fades into the fossa and becomes the fossa (the open fossa is basically an open nasolacrimal duct) and it is externally open as in the typical embryonic condition in mammals. The fossa is an open nasolacrimal duct. Ventral to the POF is the space for cranial nerve V2. Figure S6f shows that the fossa is enlarging (widens) cranially and forms a bony ridge at the dorsal edge of the fossa. The nasolacrimal duct re-emerges internally.

Figure S5 is a magnified region of the duct entering the fossa as in Fig. S6d. The duct and the passage for V2 nerve are medial to the deepest part of the POF. Three oval structures of unknown explanation appear ventral to the duct within the thick margin of the POF. The structures may contain vascular or gland tissue.

Rostral to the fossa and the conchae there are two bony grooves (impressions) inside the nasal cavity for ducts. We hypothesize that they are both part of the nasolacrimal system. They appear to exit near the nostril in a manner similar to *Equus*. We do not know about the presence of a sigmoid cartilage or a duct lake.

The main conchae of *Merychippus* are two as in *Equus*. The dorsal is situated at the superior margin of the fossa; it is long straight and tubular. The ventral concha is larger and it covers the entire preorbital fossa region. The nasal notch is small and plesiomorphic with a large contact at the notch with the premaxilla. The nasal notch is different from that of *Equus* (Solounias, 2024, fig. 7).

In *Lepus*, many arteries surround the nasolacrimal duct. We know they are arteries as the veins were injected with blue plastic. The spicules are larger than in *Equus*. In *Equus* in the coronal section one can see dermal ridges. They outline the POF but the bone deep to them is not ridged (Fig. S1).

Observed differences between *Equus* NS 10 and *Merychippus* AMNH 78002 - Structures are in different positions in the two genera. 1) In *Merychippus* the pontis is part of the caudal inner wall of the preorbital fossa. The pontis is caudal to the POF. It forms its caudal edge. The tholos is also where the preorbital fossa is located in *Merychippus*. It forms the dorsal margin of the fossa of *Merychippus*. The murus reticulatus is probably the inner surface of the fossa. 2) In *Equus* the tholos is not exactly internal to the surficial reduced preorbital fossa but rather caudal to it by 80 mm. Clearly, movement of

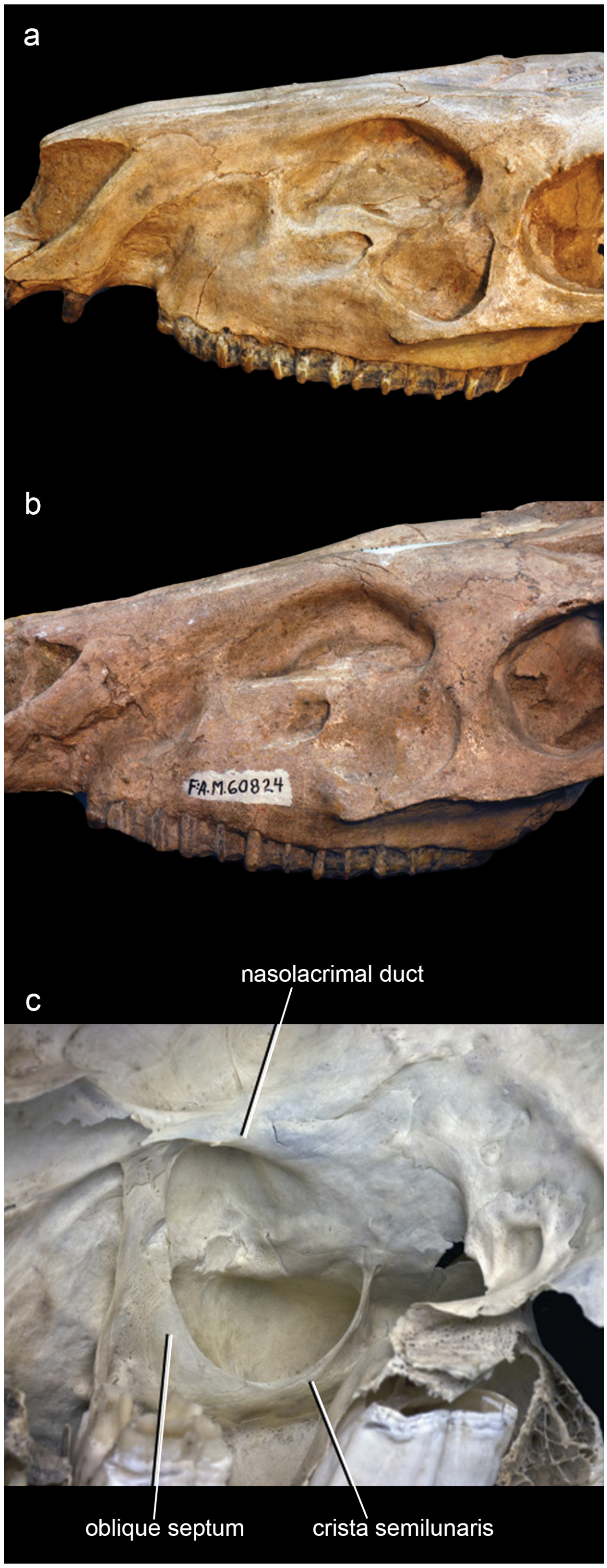


Fig. 6 - (color online) a) *Pliohippus mirabilis* AMNH 60810. b) *Protohippus pernix* AMNH 60824. c) *Equus caballus* NS 10. These figures show examples of the malar fossa. In *Equus caballus* the malar fossa is identical to the fossil specimens but internal.

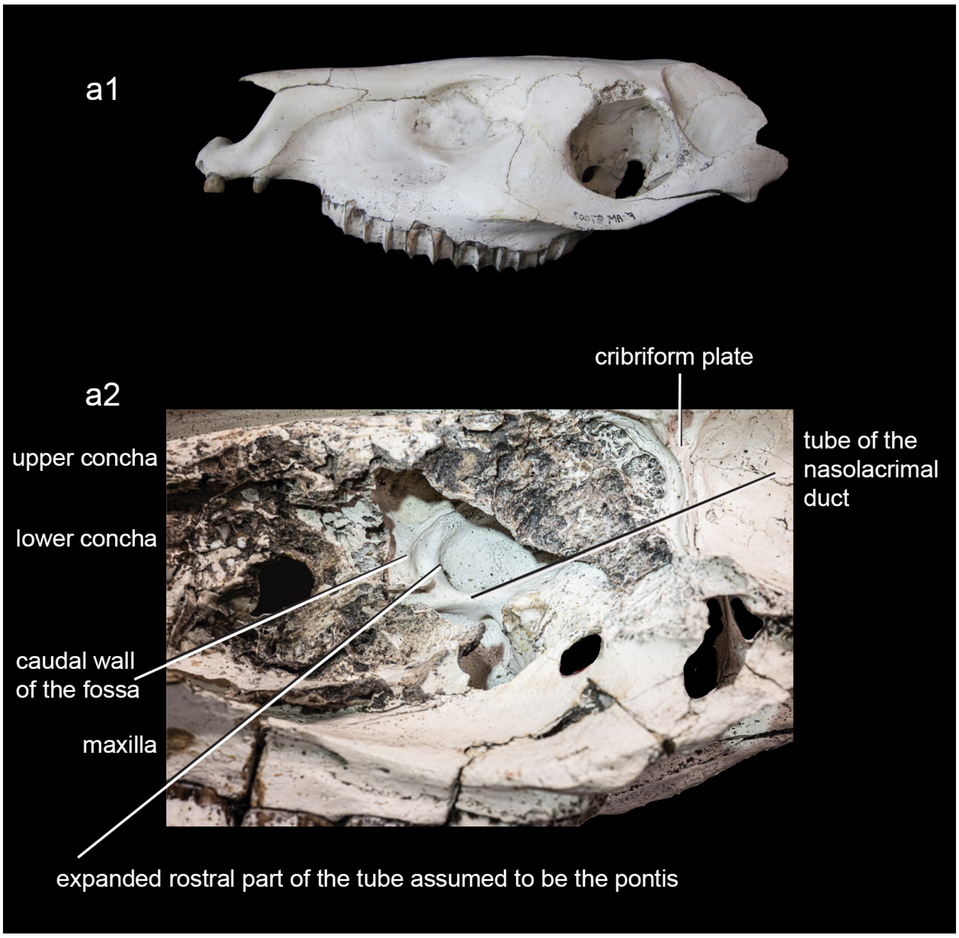


Fig. 7 - (color online) *Merychippus insignis* from the Olcott Formation, Echo Quarry (Woodburne, 2007), AMNH 78002 in outer (a1) (a reversed image flipped to look like a left side with a minor digital repair of a hole in the preorbital fossa) and inner (a2) views.

certain structures during development has taken place. The pontis is rostral to the murus reticulatus and the tholos in *Equus*. It appears that structures have moved as in transform faults of geology. This movement may relate to the elongation of the face in *Equus* and the fact that the fossa moves inward from its original position (Fig. 8). We have not done metrics but we know from observation that hypsodont teeth of *Equus* fit well below the fossa in extinct equids. Thus, the height of the molars is not constrained by the fossa which is the current scientific belief (Bernor et al., 1990). An alternative hypothesis is that the external reduced POF of *Equus* is a different structure from the POF of *Merychippus*. In this hypothesis, little movement of structures would have taken place.

Humans

The nasolacrimal duct enters the maxilla at the end of week 7 of the embryo. The duct is widely exposed during the early part of week 7 and before that (Hamilton & Mossman, 1972, fig. 249; Steding, 2009, p. 33). During week 8 the duct is submerged in the nasal cavity except for a small 20% portion near the orbital edge. In this condition, the duct resembles that of Cervidae and of *Cynthiacetus* (Cetacea; Martínez-Cáceres et al., 2017). We do not have early embryonic horse data for this duct. In one specimen donated from the Cornell Veterinary College in Ithaca NY, a 20.6 mm horse embryo has the duct already submerged.

Rabbits

In *Silvylagus* the fossa is deep and extensive. It is covered by a membrane. On the membrane there are large bony spicules which cover the entire fossa; the larger ones are 1.28 mm, the smaller ones are 0.8 mm. The spicules are interconnected and fused together in what appears to be a disorganized fashion (Fig. S1).

Baboon

The preorbital fossa of the baboon *Papio* is large. It forms a lateral pouch. The bony floor of the POF is thicker than in equids. In this taxon, it appears that the floor of the fossa is the maxilla. The results of the dissection revealed the cheeks are more expanded over the fossa. That includes the integument, buccinator and masseter muscles. There are folds of additional skin caudal to the fossa. The folds expand to make the pouch even larger. Inserting a finger under the skin orally shows that the entire area is expandable. Air from the mouth will enter the fossa and pouch. The buccinator contacts and makes noise (as observed in videos). The clicking noise is produced. Videos of the baboons show how they use the sound for appeasement of females and the young.

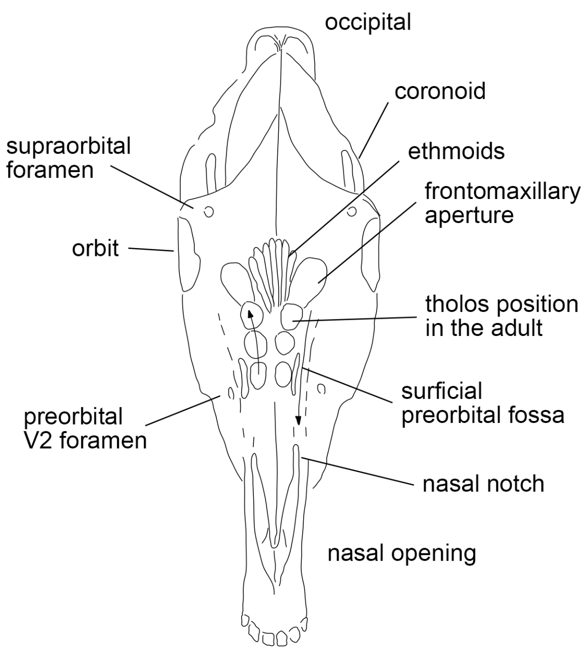


Fig. 8 - *Equus caballus* in dorsal view to show the probable migration of the tholos caudally. The preorbital fossa is rather rostral. Arrows show a hypothetical differential motion of structures.

DISCUSSION

Although the horse is one of the most anatomically well-known species (e.g., Schmaltz, 1905-1929), the soft anatomy structures relating to the preorbital fossa were unexplored. In contrast, the fossae in extinct taxa are well studied. The three key fossae (POF, malar and buccinator) are probably expressions of one basic fossa, but, for the time being, it is convenient to treat them separately until we understand more. The variation of the preorbital fossa's structure and appearance throughout evolution, as well as the reason behind morphological differences across different species of horses needs more study. An initial exploration is delivered from the current study and in a book on the horse (Solounias, 2024).

The dermal ridges in fetal horses are interesting because they resemble in general the sharp rims of the POF of the extinct equids. We provide an example that seems to parallel these ridges as an explanation. In the cow front limbs there are two floating small hooves. It is clear that these are remnants of hooves which included bones and other elements internally. Now they are just keratinous remnants free floating on the skin without any internal structures. We hypothesize that the ridges in fetal *Equus* are remnants of the preorbital fossa on the skin. Deep to them the bone does not have a fossa.

In most *Equus* skulls one can see the fossae. The preorbital is shallow without sharp margins. The malar is very shallow to absent but fully formed internally. The relevant muscles are the nasolabialis, the levator labii superioris, and the malaris. The buccinator fossa is deep. It houses expandable cushions and two nasalis muscles and not the buccinator.

There are two prevalent hypotheses about the function of the preorbital fossa. The POF is for muscles or a large nasal diverticulum: Gregory (1920) proposed that a large nasal diverticulum could be situated in the fossa of many extinct taxa. A large diverticulum is a plausible explanation of the POF. The baboon example shows how this would produce sounds. Gregory (1920) also suggested that muscles were possibly related to the fossa. Since then, many others have suggested that the levator labii superioris is the muscle that attaches inside the POF (e.g., Zhegallo, 1978; MacFadden, 1994; Woodburne, 2007, 2009). The relationship of the LLS and the POF are the prevalent view. In the dissections we find no exact relationship of the fossae to nasolabialis, the levator labii superioris, and the malaris.

The information on *Equus* reveals a shallow elongated external preorbital fossa and several apparently related structures internally. In *Merychippus* and *Cremohipparion* one encounters POF. The current anatomy of the POF in *Equus* is connected slightly to the nasolabialis and not to the levator labii superioris. The fascial sling emanates from the POF and it is connected to the overlying nasolabialis. The sling aids the levator labii superioris to function as it is rather long and horizontal and it slides through the sling as a piston. Dual or multiple functions of a biological structure are common. For example, thorns protect the plants and still have functioning cells with chlorophyll, since they evolved as rolled leaves. The POF could act as a support of the fascial sling and also may house a gland. The red bony matrix of the floor of the fossa in *Equus* does indeed suggest a within the bone-gland. Preliminary data from rabbits and a donkey fetus suggest that the preorbital fossae may have had a membrane covering their openings. Our dissection of the fetal donkey showed that it did have a membrane over the blood-filled fossa. If that were the case in extinct taxa, then the muscles in question were attaching on that membrane never entering the fossa. This is the case with the obturator internus and externus muscles which attach to a membrane. There is, in rabbits, a bony lattice which is most likely a partially ossified membrane or a membrane with large spicules. The fossa in rabbits is deep to the spicules and the membrane. The muscles attach on the membrane and the bony spicules. The POF is deep and appears to be empty. In *Equus*, the spicules are in the floor of the fossa. This suggests that the bony floor of the fossa is an ossified membrane. That would be a different membrane from the surface one.

The floor of the POF is bone that is folded multiple times in most *Equus* specimens. This reduces the depth of the POF but in reality, it would be a deep POF in *Equus* if the bone were unfolded. Unfolding that, a thought experiment, would make a large fossa cavity. The pink-red hue from blood within the bone of the fossa could be a gland, a bone gland.

The gland hypothesis

There may have been glands in the fossa as well. These glands of *Equus* are within the bone of the POF and are not clearly known. Bone tissue was essentially considered as a mechanical structure. In addition, bone functions as an endocrine gland producing osteocalcin, which in turn interacts with other tissues, such as fat, pancreas and gastrointestinal tract (Zárate et al., 2010; Guntur & Rosen, 2012). As a consequence, osteocalcin intervenes into glucose metabolism, peripheral insulin sensitivity and inflammatory process. Bone may be accepted as an endocrine gland (Guntur & Rosen, 2012). All the species of *Equus* are adapted for extreme grazing on grasses (Mihlbachler et al., 2011). As grazers, sugars hurt their digestive system and may result in laminitis. Laminitis is pathology of detaching the hoof keratin from the dermal papillae resulting in distortion of the bones and hooves (Zárate et al., 2010; Pollitt, 2016).

The gland hypothesis would make the fossa similar to those of artiodactyls which often have preorbital glands in preorbital fossae. Several preorbital fossae of Equinae have small foramina on the ventral or caudal wall (Solounias, 2024, fig. 39). The foramina may have had a probable connection to the adjacent nasolacrimal system. It should be remembered that the nasolacrimal duct is situated internally to the preorbital fossa and in proximity to these foramina. We find in *Merychippus* that the bony tube of the nasolacrimal duct has foramina connecting to the POF (Solounias, 2024, fig. 34). This would make the preorbital fossa similar to the fossae in artiodactyls where these types of glands are lodged in preorbital fossae. Dual or multiple functions are common in nature. In this scenario, it would be 1) a gland in the fossa plus 2) the fascia sling supporting the long tendon of the levator labii superioris, and 3) a sound-producing organ. It is also important to point out that in general muscles do not make fossae on the various bones. So, the muscle hypothesis as a sole contributor to fossae is weak. The thin floor of the fossa reinforces that.

The Harderian gland was first described in 1694 by Johann Jacob Harder (1656-1711) (Santillo et al., 2020). In the horse we suspect that the fluids merge with the lacrimal fluids, pass through the nasal cavity, and are secreted externally at the nostril. The orbital foramen is surrounded by two lacrimalis muscles. Humans have these as well. They contract and aid the transmission of fluids into the nasolacrimal duct. There is no clear explanation for bony spicules of the floor of the POF. They may relate to the blood contained in the bones of the POF as part of an endocrine gland (Santillo et al., 2020). In rabbits the spicules are larger and cover the POF.

The murus reticulatus of *Equus* has been described (Solounias, 2024), but its function is unknown. It may be a remnant of spicules from a today non-existing caudal fossa in *Equus*. Anatomically, there is a location problem. The murus reticulatus is medial to the nasolacrimal duct in *Equus* and caudal. If the murus reticulatus were part of a fossa, one would expect the duct to be medial to the murus not lateral. But in *Equus* structures may have moved internally and caudally making their exact interpretation to those of *Merychippus* difficult.

The pontis is clearly the caudal margin of the POF as observed in *Merychippus*. It actually forms the most caudal part of the POF. Solounias (2024, fig. 43), in describing the pontis of *Equus*, hypothesized it to be rostral to the fossa where there is a thickening in *Merychippus*. The newly interpreted position explains the pontis in *Merychippus* as the place where the nasolacrimal duct becomes wide open as the POF.

In *Equus* the pontis is more caudal than the POF; it has shifted.

The sigmoid cartilage (also known as the medial accessory nasal cartilage; Schummer et al., 1979) is described in detail in Solounias (2024, figs 11, 12). It is a widespread cartilage in ungulates and other mammals such as carnivores and insectivores. When compressed, it creates a seal onto the nasolacrimal duct in *Equus*. When pulled up by the nasalis ventralis muscles and their fibrofatty cushions, it dilates the nasolacrimal duct allowing fluids to pass through and out at the exit of the duct.

During development, the nasolacrimal duct of *Equus* sinks into the head rostrally and caudally but not in the center of the duct. Importantly, in the center the duct probably remains on the surface as an open trough which widens in time forming the preorbital fossa. This hypothesis is based on information from *Merychippus*. The nasolacrimal duct is like the old polio vaccine which started as a scratch and then widened forming the characteristic scar on the arm.

There are three septa which probably help the mixing of the nasolacrimal and Harderian fluids within the lacrimal lake (Solounias, 2024, fig. 12). The inner structure of the lacrimal lake resembles a lymph node.

The nasolacrimal duct exits at the edge of the nostril in *Equus*. At the edge of the nostril, air currents from the blind sac of the nasal diverticulum probably help to spray the fluids exiting the duct as a mist to the environment. Other horses would smell these mists which occur during the snorting behavior. The nasolacrimal duct is the most critical part of interpreting the function of the POF in *Merychippus*. The duct is most likely a placode (Solounias, 2024): it fits all requirements to be a placode. Most placodes are oval discs. This placode is rather long and probably that is why it was not recognized by embryologists as a placode. It is embryologically an external wide-open elongated trough (Hinrichsen, 1985). We hypothesize that the placode forms the floor of the POF. In embryos these structures are membranous. Thus, the retention of a thin bony floor of the POF is reminiscent of the membranous origins.

The tholos is another new structure in the paranasal sinuses. It is a dome and resembles the dorso-caudal part of preorbital fossae. It is avascular. We hypothesize that the tholos is part of the POF. However, its position is about 8 cm caudal to the POF of *Equus*. This implies two events: the sinking into the nasal cavity of the dorso-caudal part of preorbital fossa and the migration caudally. This hypothesis explains why *Equus* does not have sharp margins on the external fossa; they are still sharp but are now internal as the tholos.

The frontomaxillary aperture is just a space rostral and lateral to the ethmoids. Nothing passes through this space. It may relate of the allometric elongation of the head from primitive equids (Radinsky, 1984).

The taut membrane is an interesting feature observed in the fetal donkey. It spans the area of the POF. Externally muscles attach onto the membrane. The inner side of the membrane was full of blood which suggests a similarity to the *Equus caballus* specimens where the floor of the POF is red from blood. Deep to that is a network of pillars attaching onto the medullary bone. These structures are clearly a stage in the embryonic POF retained in the young specimen. Their biological functions are unknown.

Communication by chemicals and/or sound

As the horse snorts, eddies of air enter and exit the nasal diverticulum which is a blind sac. These eddies will definitely spread a mist of the fluids from the nasolacrimal duct to the space next to the horse. Note that the exit of the nasolacrimal duct is unusual in draining outside the nose: this is another feature where *Equus* is unusual. Herding individuals would benefit by smelling these mists. Gregory (1920) writes that perissodactyls (horses, tapirs and rhinos) do not have facial glands in their face; artiodactyls do. Maybe these perissodactyl glands are more plesiomorphic and have not been recognized. Gregory (1920), MacFadden (1994), Hulbert & MacFadden (1991), and others focused on the idea that the fossa housed soft anatomy (perhaps a diverticulum) that enabled the various species of equids make different sounds (an adaptation for phonation), each species with its own unique sound signature. The snorting of the horse may be a remnant of a more elaborate sound, where the preorbital fossa was involved. The diverticulum could be used for phonation and communication. However, multiple functions occur in living organisms and thus, this hypothesis does not exclude other functions. It is possible that the equids had a fossa similar to that of the baboon or the saiga. It would produce sounds and it would be separate from the nasal diverticulum. The baboon also makes communication noise with its POF. We consider the sound hypothesis as highly plausible.

Large noses in mammals are not rare and multiple functions exist. The bovid takin and the cervid moose have typical large noses; however, these large noses are not for sound. In the dik-dik, a constant motion of the nose helps collect moisture from the air; rabbits do this as well. In saiga, the nose is a sex display. In tapirs the POF relate to the proboscis and the meatal diverticulum. In bats and whales nasal complexity relates to sounds and sonar.

The *Equus* buccinator fossa is misunderstood. It is believed that it houses the buccinator muscle: that is why it is called the buccinator fossa (Zhegallo, 1978; Bernor et al., 1990; Woodburne, 2007). It is true that the buccinator muscle spans a little of the external surface of the fossa. However, deep to that muscle, there are two fibrous cushions attaching onto the bony floor of the buccinator fossa and two large muscles nasalis ventralis anterior and posterior are lodged in the fossa. They enter the nasal notch and attach onto the sigmoid cartilage and clearly lift the cartilage when contracting. The cushions are fibrous full of air spaces and possibly add elasticity to the system. They are also possibly for vibration. The buccinator is not even in the fossa. Clearly, all these functions are not related to the buccinator. The crista semilunaris is the internal expression of the malar fossa in *Equus*. It is interesting that this structure is identical to the external malar fossa best observed in *Protohippus.* No muscles seem to be affected by this inward migration. Then why would muscles attach in the malar fossa in the first place as it is theorized for *Protohippus*? It is more logical that the muscles acted independently to the malar fossa. They may have attached onto a membrane over the malar fossa. The malaris muscle begins on the zygomatic arch and attaches onto the orbicularis oculi. Thus, ironically it is also independent of the malar fossa.

In *Pseudoryx* (the rare bovid saola) and the muntjac, they possess large glands in the preorbital fossae. Other cervids and bovids also have glands in the fossae. We have found evidence that the nasolacrimal gland was part of the fossa in *Merychippus* and *Equus*. The bony surface of the fossa in *Equus* is reddish and the bone of the fossa bone is full of blood. This blood filled-surface could be some type of a gland within the bone. In *Merychippus*, the nasolacrimal duct is wide open as the floor of the POF. Thus, the POF of *Merychippus* is a wide-open nasolacrimal duct. In extinct equids, we think the nasal diverticulum was not situated in the fossa. It is a rostral structure. But we leave the question open as to whether the nasal diverticulum could be involved with the gland and therefore the POF.

The muscle attachment hypothesis is basically from Gregory (1920), Zhegallo (1978), and Woodburne (2007, 2009). They suggested the muscles or the nasal diverticulum as possible soft structures of the preorbital fossae. There are over 600 muscles in the mammalian body. If a fossa was an integral part of a muscle attachment (in this case the origin), we would see evidence of numerous fossae throughout the skeleton in connection with each muscle – which we do not. Many bones are quite smooth where muscles originate or have a slight bone tuberosity, not depressions. The nasal area of mammals often does not show muscle attachments. One of the best examples of this is the trunk of the elephant. Scientists have said numerous times that if the elephants were extinct today, we would not know that they had a proboscis, because there are no clear markings on the base nasal aperture to indicate the presence of a trunk. Proboscidea go back in time to 45 million years. In this case, they might be reconstructed like a more typical looking mammal: without the trunk. Tapirs and the moose have complex noses with no fossae for muscles (Witmer et al., 1999; Clifford, 2004).

Clearly, the facial fossae and the face muscles have different developmental histories – although they coincide in location. In *Equus* the fossae are reduced but the muscles (nasolabialis and levator labii superioris) are not reduced. Is more logical to assume that the muscles can exist there independently of the fossa. What is complicated is that fossae and muscles are in the same general area. The muscle becomes forced to occupy the space of the fossa. In other words, the formation of the preorbital fossa may have nothing to do with these muscles. This is a novel idea verified by the membrane seen in the donkey over the POF, the thin floor of the fossa in *Merychippus* and the muscle positions in *Equus*. A good example is the levator labii superioris of *Equus*. It hardly has a fossa so why would the same muscle create a fossa in the extinct taxa?

The membrane that we see overlying the pillars in the donkey specimen is also seen in the skull of the rabbit. Pillars could be the spicules. Therefore, we can use the rabbit as a model to explore the function of this membrane and its associated pillars. The muscles lie external to the membrane, attaching there instead of inside the bony fossa. It is possible that extinct species of equids also had a similar membrane overlying the fossa. We hypothesize that the developmental starting point for the preorbital fossa –prior to ossification– is this spiculated membrane as in rabbits.

The thin bony surfaces of the floor preorbital fossa of *Merychippus* and other equids is a strong additional proof that muscles would not be supported there. The extremely thin floor of the membrane and the involvement of the nasolacrimal duct and arteries are suggestive of some function relating to a gland in the POF or within the bone.

The nasolacrimal duct - The duct is surrounded by sixteen or more arteries and no veins in proximal end. The appearance is not dissimilar to the exocrine cells of the pancreas. This is unprecedented in any other duct that we know of. This finding leads us to believe that the duct has more functions in horses and rabbits than just a tear transmission. The Harderian gland is also involved in this anatomy. The murus reticulatus is also constructed by bony spicules. It may be a remnant of another more caudal fossa that has disappeared.

The placode hypothesis

The nasolacrimal duct is undoubtedly a placode, as clearly revealed by human embryology. As such, it originates on the surface as an elongated groove and then sinks into the nasal cavity. The rostral part of the duct sinks in earlier than the caudal near the eye. As the duct is a placode, then the fossa which is derived from the duct is also a placode (e.g., Hinrichsen, 1985; Steding, 2009). As a placode, the duct may sink in as in *Equus* or may stay on the surface as in *Merychippus*.

Migration of structures

We propose that structures move relative to each other as an individual grows. It is common knowledge that as a young horse ages, its face elongates, and brings internal and external structures that were more caudal into a more rostral position (Radinsky, 1984). There are many structures within the mammalian body that migrate as growth takes place from an initial position to a different adult position. This type of localized movement is relative and it can be traced because the surrounding structures do not move in the same manner. In humans, nasolacrimal duct (ectodermal) moves inward into mesoderm via the nasomaxillary groove (Hamilton & Mossman, 1972; Hinrichsen, 1985). This migration phenomena are part of the foundation to the method that we propose to explain the difference between the fossa in extinct species of horses and the modern horse. The preorbital fossae of *Pliohippus mirabilis* and *Protohippus pernix* possess a second deep fossa close to the upper molars (the malar). This fossa seems to enter the nasal cavity directly in the same position it was on the surface. It is located right above the molars on the paranasal sinuses in *Equus*. We hypothesize that there are relative movements of the tholos as the horse grows up. The preorbital fossa is in part in the paranasal sinuses in *Equus*. Differential movement and snout elongation, as the horse grows, would also relocate certain internal structures. This is a hypothesis. The differential movement may be the result of gazing, hypsodonty and the elongation of the horse's face (Radinsky, 1984). In the newborn horse specimen (NS 99), the tholos is developing in the same position to the faint external preorbital fossa. It is in the original location of the tholos but as the horse grows older, the tholos moves caudally. We do not have a series of specimens to trace that movement as the horse grows.

Merychippus*,* Protohippus *and* Pliohippus

Merychippus, a representative species of the extinct Equini, possesses a deep preorbital fossa and a small to absent malar fossa. The dorsal and caudal margins of the POF are very sharp and well-defined. As shown in specimen AMNH 78002, the nasal cavity is open, and the nasolacrimal bony tube terminates on the back wall of the preorbital fossa. There is a thickening there that resembles the pontis of the modern horse. We hypothesize that this is indeed homologous to the *Equus* pontis. Specimens *Merychippus insignis* AMNH 87003 and AMNH 87004 clearly have a distinct bony plate surrounded by sutures inside the external preorbital fossa. The origin of this small bone is unknown. It is not present in every specimen. This is a small example that preorbital fossae (except for the hipparions) have not been studied in detail. In addition, the nasal bone appears to be expanding above the orbit. When a bone is expanded, a suture can form within that bone during development – which we see in several examined specimens of *Merychippus*. These partial sutures have been termed suturiscus (little suture in Greek ending) by Solounias (2024). There are also very small and numerous foramina in the caudal wall of the fossa of *Merychippus* that may be related to the nasolacrimal duct which is immediately adjacent and internal to this area of the POF. These foramina could also be related to a gland situated in the preorbital fossa that may also be related to the function of the nasolacrimal duct.

Using *Equus* and *Silvylagus*, it is very likely that the fossa was covered externally by a membrane. The muscles in question would attach on the membrane. In *Silvylagus*, the membrane is clearly present deep the bony spicules and external to the fossa. In *Equus*, the membrane covered the entire fossa. The pillars are the spicules (Fig. S4).

In *Merychippus*, the surface of the fossa, the floor, is notably thin bone (0.3 mm). This thin surface could not support muscles. The gland hypothesis is very strong; a gland within the bone as in *Equus*. Using the *Equus* as a reference, the gland is probably embedded in the bones of the POF. Therefore Gregory (1920) may have been wrong assuming that there were no preorbital glands in perissodactyls, but he may have been right that the nasal diverticulum reaches the fossa area. That hypothesis would not counter our observations. Using *Silvylagus* as a model, the muscles originate from a thick membrane and from the bone spicules which cover the fossa. Using *Equus*, a membrane initially covers the fossa and it later ossifies. Gregory was not that interested in the fossa and these mammals: he was simply working for Osborn. Gregory's real interests were fish skulls, *Notharctus*, and humans.

In *Merychippus*, there is no tholos which makes sense as we hypothesize that the tholos is the dorsal-rostral part of the preorbital fossa. In other extinct equid taxa, there are one or more foramina within the fossa. Thus, the nasolacrimal duct may have different glands and functions there. The face muscles are more external (superficial) and maybe independent of the POF, even if the location of the two coincides.

In *Protohippus* and *Pliohippus* a second large fossa (malar) is located externally and is the same with the one internal in *Equus* (same location and size). In these examples, the malar fossa also appears to have penetrated the nasal cavity and remained as large as before and in the same position but within the paranasal sinuses. The internal bony structures in *Equus* are avascular and have been named crista semilunaris and oblique septum (Solounias, 2024).

The interplay of intramembranous and endochondral components of the skull

The mammalian skull is formed by the interaction of intramembranous and endochondral structures (de Beer, 1937; Roux, 1947). The nasal capsule is internal and is endochondral. The external skull face is intramembranous. In the adult, these two structures fuse. The fusion is commonly complete, and one cannot distinguish the two layers in sections in adult specimens. Sometimes, however, it is possible to see the two layers. *Equus* NS 100 is one example of this where the layers are readily visible (Fig. 3a3). De Beer (1985, p. 394) describes the nasal capsule. His whole book covers numerous nasal capsules. Grassé (1967, p. 421) shows a wonderful image of the nasal capsule in *Oryctolagus* surrounded by intramembranous dermal surface bones. The bottom line is that the adult cartilaginous nasal capsule fuses and interacts with the external to it intramembranous bones. The nasal capsule acts as a scaffolding for the formation of the external intramembranous bones or the opposite. This interaction is largely unexplored. The preorbital and malar fossae have components from the nasolacrimal duct, the nasal capsule and the maxilla and the nasal bone.

The internal nasal cavity is derived from the embryonic nasal capsule, including the conchae and the nasal septum. The nasal capsule also covers the inner lateral walls of the nasal cavity. Before the fusion occurs, as the fetal horse develops, we theorize that the relative movement of structures (tholos and pontis) takes place, and the two layers slide past each other, much like a geologic transform fault (Fig. 8). Therefore, the internal fossa of the modern adult horse (the tholos) is approximately 80 mm caudal to the external surface of the POF. This can be attributed to the movement of these structures during early development. In humans, for example, this fusion of the intramembranous and endochondral layers occurs after the fetus reaches 60 mm in length (Williams, 1995, fig. 3-146c, p. 287). In *Equus* it is not known exactly as to when the tholos is in its original position. Newborn specimens at the AMNH suggest the movement of the tholos occurs after birth, possibly the second year of the baby horse. The nasal capsule has been illustrated by Roux (1947, figs 9, 40), Reinbach (1952, fig. 13), Klima (1999, figs 6, 19, 36), and Maier (2002, fig. 10).

Why is the fossa reduced in Equus*?*

The presence of a membrane in the fetal horse and the pillars suggest that the fossa is derived from a placode. Structures move internally reducing the size of the fossae externally. Placodes form complex structures and, in this case, it could originally be some type of a support for a gland; a gland that received fluids from the nasolacrimal duct. A new hypothesis is that hard grass grazing increased with the origin of *Equus* (Mihlbachler et al., 2011). Older taxa were apparently grazing less (Solounias, 2024). Many equids had the nasolabialis and the levator labii superioris attached on the membranes covering the fossae. As *Equus* gazed heavily, the fossae were interfering (a hypothesis). Structures moved inward in the paranasal sinuses. The maxilla and nasal became involved with supporting the face muscles more efficiently than the previous membranes. The rabbit exhibits this, with the muscles attaching to the spicules and membrane. Similarly, the *Equus* preorbital fossa still has small bony spicules. No muscles attach there now. Therefore, the reduction of the fossa is probably multifactorial – due to a change in diet, crown height, gland structure, as well as increasing the efficiency of muscles related to grazing. Examination of the hypsodont teeth below the POF shows no problem with space. Thus, the fossa of extinct taxa does not prevent hypsodonty. Hypsodont teeth act as roots embedded in the bone for the attritional and abrasive stresses from the vegetation (Solounias et al., 2019).

Internal nasal anatomy and the preorbital fossa - We propose that the tholos is the rostral-dorsal side of the POF. The pontis is the original brace, as in *Merychippus*, of the rostral and ventral side of the preorbital fossa. The stretching of the area may form a murus reticulatus. The avascularity of these structures makes them distinct from the highly vascular conchae (Hillenius, 1994).

We compared the bony nasolacrimal tube of the horse with that of sheep, deer, antelope, rabbit, and possum skulls. The ungulates had a similar bony tube to the horse and *Merychippus*. They all had a tube for the nasolacrimal duct except for the racoon and the dog. We hypothesize that the presence of the bony tube is consistent within many primitive mammals (including ungulates), and it is widespread. It is therefore not unique to the horses.

Placodes - The nasolacrimal duct is of a placode origin (Hamilton & Mossman, 1972, fig. 248; Hinrichsen, 1985; Williams, 1995, p. 261; Steding, 2009). There are many images of the duct in Hinrichsen (1985) which show clearly that the nasolacrimal duct is in fact an elongated placode. The embryonic surficial duct is described as "a nasolacrimal furrow" which enters the nasal cavity from the surface. We theorize that the preorbital fossa is also part of the placode system. That is why it forms on the surface in *Merychippus* and later in evolution it sinks into the nasal cavity as in *Equus*.

The vomeronasal organ nostrils and conchae - The vomeronasal organ is a small tube in the nasal cavity next to the bone termed the vomer. It contains endothelium and special cranial nerve fibers for smelling pheromones. This organ is very well developed in fishes, amphibians and reptiles. In many mammals, it is also large. In humans it is very small and some scientists think it is vestigial. In the horse, it is very large and long. We hypothesize that it forms by an elongated placode. The placode sinks into the nasal cavity. The nostrils are derived from the nasal sac, a structure rostral to the nasal capsule (Klima, 1999), they are commonly not ossified but contain cartilages (Schummer et al., 1979, figs 277-281). They contain alar and other cartilages. They are rostral to the nasal capsule. Parts of these structures enter the nasal cavity. The conchae are derived from the inner walls of the nasal capsule. The ethmoids seem to be a separate ossification.

Hypothesis relating to the equid preorbital fossae

The preorbital fossae and contents are the outcome of the interaction of three structures: the nasolacrimal duct resulting from a fossa placode, the maxillary and nasal bones externally, and the nasal capsule internally. In conclusion, the preorbital fossa is the result all of these. Sound production and glands are plausible functions.

CONCLUSIONS

None of the three muscles in question (nasolabialis, LLS, malaris and buccinator) are part of their fossae. It is best to consider the POF and the malar fossa as one. 1) The nasolabialis muscle is situated over the preorbital fossa. 2) The levator labii superioris is not within the fossa, it is closer to the zygomatic and it has its own very faint but circular fossa. 3) The levator labii superioris is supported by a special fascial sling of the nasolabialis as it is long and horizontally positioned. Although the preorbital fossa in the modern horse is externally shallow, it is present internally (tholos and pontis) and therefore is not lost. It is also present as folded bone within the POF. 4) In addition, the tholos, the murus reticulatus and the pontis (terms introduced in Solounias, 2024) are internal structures of the paranasal sinuses and may represent parts of the original preorbital fossa. 5) Part of the preorbital fossa moved internally and migrated caudally. 6) In *Merychippus*, the fossa has a very thin floor. A muscle attaching on such a thin surface of bone is unlikely. There the nasolacrimal duct and numerous surrounding arteries expand into the surface of the fossa; they are the POF. The duct becomes the fossa. More rostrally, the duct is reconstituted but without the surrounding arteries. 7) The preorbital fossa in extinct equids may be independent of the nasolabialis and levator labii superioris muscles. They simply coincide in space but fossae and muscles may be functionally unrelated structures. They are both in the same area, so the muscle becomes forced to occupy the space of the fossa. In other words, the formation of the fossa may have nothing to do with these muscles. Fossae could contain glands and are derived from placodes. 8) The nasal capsule is an embryonic endochondral scaffolding that interacts with the surface bones (intramembranous) in all mammals. It is oval-spherical and has a hinge near the ethmoids. 9) The nasal diverticulum could have been larger and may have produced sounds using the space of the fossa as a sounding chamber. Alternatively, similar sound productions could be produced by cheeks and fossae as in *Papio* baboons. 10) The preorbital fossae are originally developmentally most likely in part placodes. As such they can easily enter the nasal cavity. The placodes lodge on the surface of the bones (maxilla and nasal) and interact with these bones, muscles and with the nasal capsule. 11) In extinct equids the fossae could co-exist with the nasolabialis and levator labii superioris, especially if they were covered by membranes. These geologically older species were grazing less than *Equus*. The fossae may be reduced in *Equus* probably because of the extreme grazing and open habitats. Apparently, the new face surfaces (maxilla and nasal) are better than a membrane in supporting the high force and grazing function required of the nasolabialis and levator labii superioris. 12) There is a notable elongation of the modern horse's nasal cavity and snout in comparison to the *Merychippus* and other extinct horse species. There is a differential movement of the various components of the skull.

SUPPLEMENTARY ONLINE MATERIAL

Supplementary data of this work are available on the BSPI website at: https://www.paleoitalia.it/bollettino-spi/bspi-vol-643/

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