

The “Mammalian Species” Paper: *Equus caballus*

by Deb Bennett and Robert S. Hoffmann

Introductory Note to Readers: The following article reproduces the text of this paper exactly as it was printed, with the addition of a few more recent references. Due to constraints of space and budget, only four illustrations, all in black and white, appeared in the original publication. In PDF format we fortunately have no such limitations, and so the distribution maps have been rendered much more clearly and usefully in color, and other helpful illustrations have been added. The figure numbering has been changed accordingly.

One aspect of this paper is now in need of revision: in the years since 1999, we have received the unfortunate news that the radiocarbon dates for the Dereivka archaeological site discussed in the “Remarks” section are in error; the site is about 1500 years younger than we report here.

It is my hope that the majority of visitors to this website, who are not professional paleontologists, mammalogists, or biologists, will nevertheless find that they can read and benefit from this “technical” publication. It contains a wealth of facts about horses in condensed form, and is followed by a very useful list of references.

For those who may not be familiar with the term, the “synonymy” section traces all the valid and invalid references to the species *Equus caballus* that have appeared in the technical literature since it was named by Linnaeus in the eighteenth century. Tracking down all the references proved to be by far the most difficult and time-consuming part of this paper, requiring hours (actually amounting to years) of search through proverbially dusty and crumbling tomes.

For those of you who do not know my co-author, Robert Hoffmann was (until his recent retirement) the Assistant Secretary for Research at the Smithsonian Institution, and before that the Director of the U.S. National Museum of Natural History. He is a past president, and continues to be a guiding force, in the American Society of Mammalogists, and is a world traveller, having been on expedition many times to China, Russia, the Arctic, and other far-flung parts of the world. Bob’s special fields of expertise are trans-Beringian studies in general and marmot biology, speciation, and distribution in particular. I think of Bob, however, simply as one of my favorite teachers – I first met him in 1976 when I took his graduate course in Mammalogy at the University of Kansas, where, in fact, the research that informs this paper was also first begun. He has been friend, colleague, and mentor ever since, and it’s a privilege for me to present this collaborative piece of work.

I would like to take this opportunity to thank the American Society of Mammalogists and the editors of “Mammalian Species”, Elaine Anderson, Leslie Carraway, Karl Koopman, James A. Lackey and Barbara H. Blake, along with my friend and colleague Robert Timm (currently President of the ASM), whose perspicacity and generosity made the original publication possible.

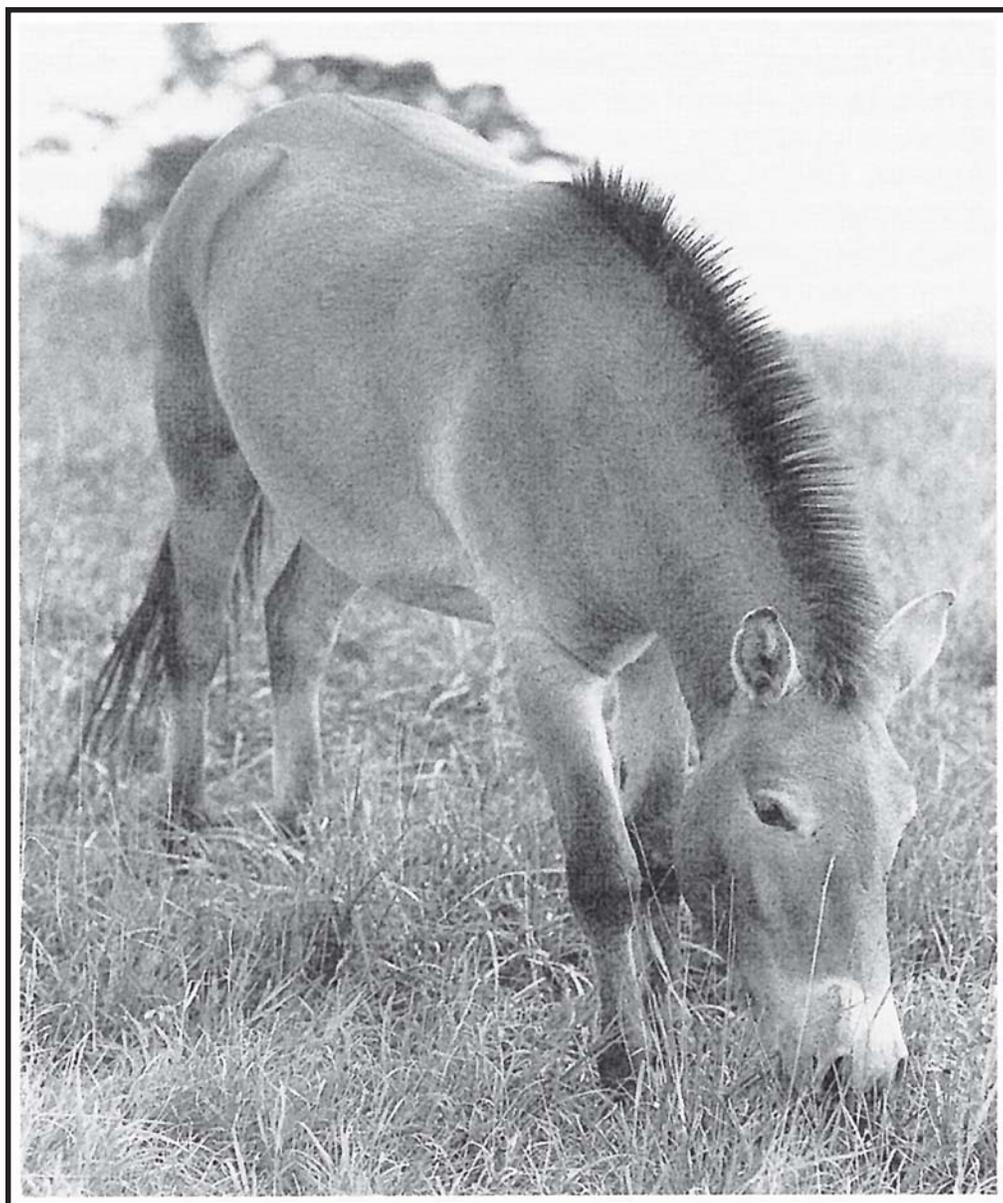


Fig. 1. Adult female Mongolian wild horse (*Equus caballus przewalskii*) in Conservation Research Center, National Zoological Park, Smithsonian Institution, Front Royal, Virginia, 6 September 1984. Photograph by Jessie Cohen.

Equus caballus Linnaeus, 1758

Horse

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Originally published in: **Mammalian Species** (Official Publication of the American Society of Mammalogists), no. 628, pp. 1-14. Published 3 December, 1999 by the American Society of Mammalogists.

Section I: Synonymy

Equus caballus Linnaeus, 1758:73. Type locality “in Europa.” Restricted by Linnaeus (1761:16) to “Scania and Gottlandia” [southern Sweden](domestic horse).

Equus ferus Boddaert, 1785:159. Type locality “...Woronesk, Russia” [Chichonko, 45 verst [48 km] from Bobrovsk, Voronezh district]. From Groves, 1986.

Equus sylvestris Brincken, 1828:49. Type locality “la forêt impériale de Bialowieza en Lithuanie” [Bialovezha Forest, Poland].

Equus przewalskii Polyakov, 1881:1. Type locality “Peski Khanobo (Kanobo) okolo 250 km k yugovostoku ot Zaisanskovo posta (pribilizitel’no ha 46° C. sh. K yugu ot oz. Ulyungur); tsentral’naya Dzungariya.” [Kanobo (Kanabo) sands, about 250 km SE Zaisan Post (ca. 46° N lat. South of Lake Ulyungur), central Dzungaria = Xinjiang Province, China]. From Heptner et al., 1961.

Equus mosbachensis Reichenau, 1903:54. Type locality “Mosbach”, near Wiesbaden, Germany. Pleistocene.

Equus hagenbecki Matschie, 1903:583. Type locality “der Quelle Ebi aus der Wuste Gobi in der Nahe der Strasse von Kobdo nach Barkul.” Ebi Spring, Gobi Desert, Mongolia.

Equus caballus pumpelli Duerst, 1908:397. Type locality “Anau, Turkestan” [ca 20 km SE Ashkhabad, Turkmenia]. This form was considered a hemione by Lundholm (1949) and Davis (1980), but affirmed as a horse by Willoughby (in Groves, 1986). Pleistocene. However, if it is a hemione, then the next available name for this taxon is *algericus* Bagtache et al., 1984.

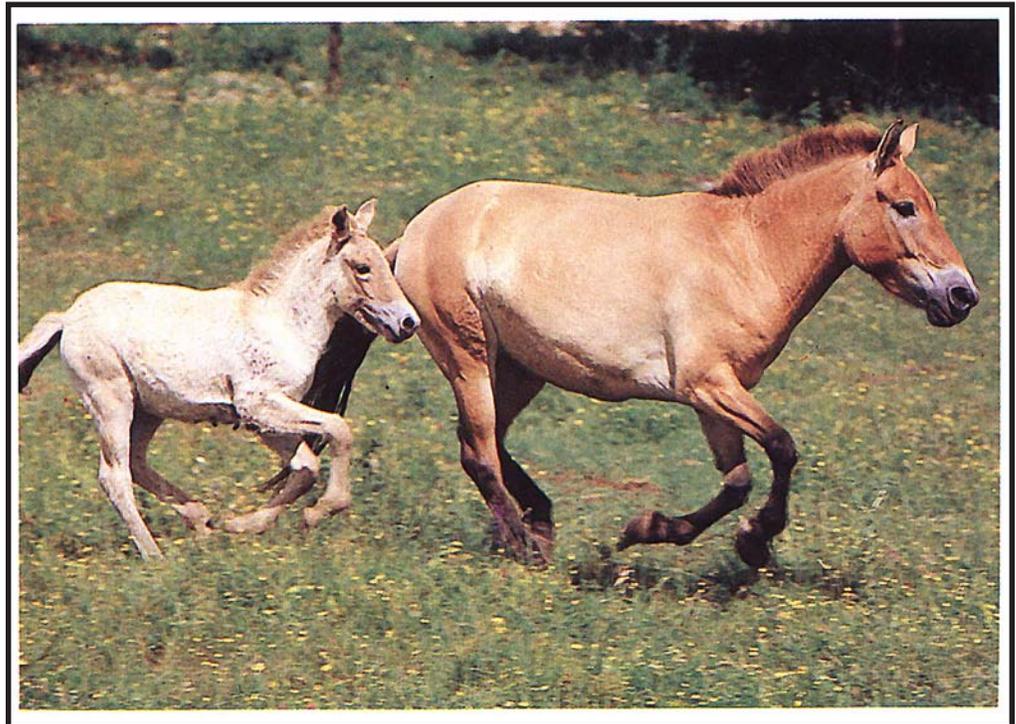


Fig. 2. Adult female *Equus caballus przewalskii* and her foal about one month old. The foal is larger relative to its mother's size and noticeably stouter in build than in many domestic horses (compare to Fig. 18).

Equus gmelini Antonius, 1912:516. Type locality “...Sagradoffschen Steppe des Gouvernements Cherson...”[Zagradov Steppe, right [W.] bank, Dnepr River, near Kherson, Ukraine].

Equus niobrarensis alaskae Hay, 1913:2,3. Type locality “...near Tofty, Alaska...on Sullivan’s Creek.” Pleistocene.

Equus mexicanus Hibbard, 1955:66. Type locality “...Tajo de Tequixquiac, Estado de Mexico.” Pleistocene. Since its description, this form has been considered an ass, but is allocated to *E. caballus* (as a synonym of *laurentius* Hay, 1913) by Azzaroli (1995).

Equus midlandensis Quinn, 1957:24. Type locality “Scharbauer ranch, 8 miles southwest of Midland, Midland County, Texas.” Pleistocene. The name *laurentius* Hay 1913 has in the past been used for this taxon (Winans, 1989), but the holotype dates to recent historic times (R. Graham, in lit.).

Equus algericus Bagtache, Hadjouis and Eisenmann, 1984:609. Type locality “Allobroges, Algerie.” Pleistocene.

Groves (1986) has proposed *E. ferus* to replace *E. caballus*, because Linnaeus’ type was a domestic horse; guidelines are recommended by Corbet and Clutton-Brock (1984). We choose instead to follow Wilson and Reeder (1993), using the scientific name of the domesticated form (if older) to refer to both conspecific domesticates and their wild ancestors. Azzaroli (1995), Eisenmann and Turlot (1978), Groves (1986), Groves and Willoughby (1981), Heptner et al. (1961), Kurtén and Anderson (1980), and Skorkowski (1938) provide taxonomies and reviews of species.

Section II: Context and Content

Order Perissodactyla, Suborder Hippomorpha, Family Equidae, Subfamily Equinae, Genus *Equus*, Subgenus *Equus*. Following Trumler (1961), we recognize seven living or recently extinct subspecies, listed below (Bennett, 1992b). These are delimited, and their characters inferred, from the morphology and distribution of late Pleistocene to early Holocene fossils, historical descriptions of Eurasian wild horses, and finally, the characters of the early breeds of domesticated horses. Genetic analysis based on chromosome differences (Benirschke et al., 1965) and mitochondrial genes both indicate significant genetic divergence among the several forms of wild *E. caballus* as early as 200,000 – 300,000 years ago, long before domestication (George and Ryder, 1986). Thus, these diverging ecomorphotypes were, in various parts of Europe, domesticated in parallel; for example, the tarpan (*E. c. ferus*) in the steppe region of eastern Europe, and the warmblood (*E. c. mosbachensis*) in central Europe (Azzaroli, 1990).

Breeds established prior to 1500 exhibit a pattern of geographic distribution and morphological stability that is the result of conservative breeding based on the “native broodmare.” The different domestic breeds of horse are each originally derived from different wild populations distributed from Europe to the Middle East. Given the multiple origins of early breeds (“coldblood,” “Afro-Turkic,” “warmblood,” “konik,” or “tarpan”), and subsequent conservative breeding, it is possible to infer the general characters of now-extinct wild populations from the conserved characters of their descendants (Bennett, 1992b; Eisenmann, 1986; Trumler, 1961). Therefore, we recognize three forms in Europe (coldblood, warmblood, and tarpan) and one from North Africa to the Middle East (Afro-Turkic), all of which survive only as domesticates, being now extinct in the wild. All four contributed to the gene pool of

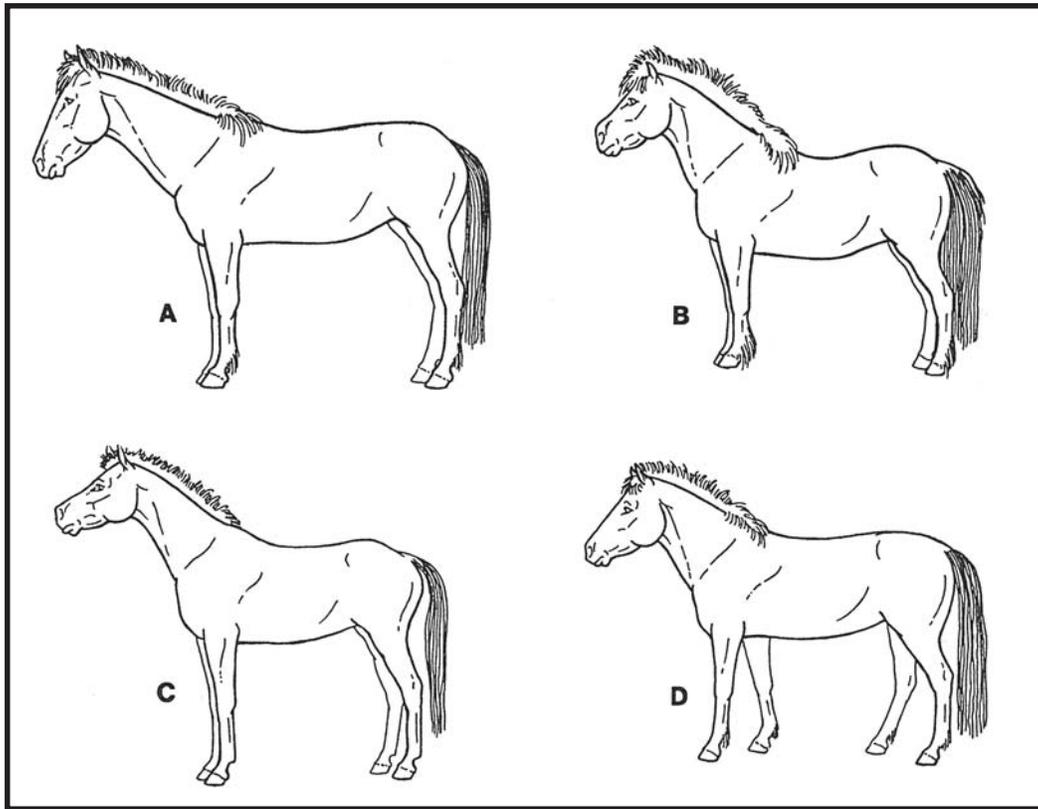


Fig. 3. Reconstructions of four subspecies of *Equus caballus*, based on fossil remains, old photographs, and appearance of probable domestic descendants from the same geographic areas (Bennett, 1992b, modified from Trumler, 1961). A. Central European horse (*E. c. mosbachensis*); B. Northwestern European horse (*E. c. caballus* — the dwarfed insular pony is illustrated); C. Afro-Turkic horse (*E. c. pumpelli*); D. Tarpan (*E. c. ferus*). For reconstruction of the Beringian horse (*E. c. alaskae*) see Strelkov (1977). The American Periglacial Horse (*E. c. mexicanus*) is not illustrated but probably most closely resembled the Beringian and Mongolian wild horses (Figs. 1, 2). See also Fig. 19.

domestic horses and are inferred to have 64 diploid chromosomes, as do all breeds of domestic (including feral) horses that have been studied (Ryder et al., 1978). In addition, we recognize three forms of wild horse from Asia, Beringia, and North America, *przewalskii*, *alaskae*, and *mexicanus*, respectively. These subspecies, inferred (on the basis of living *przewalskii*) to have 66 diploid chromosomes, appear to have contributed little or nothing to domesticated breeds, although Volf (1996) believes that “Das Mongolische Hauspferd ist ein direkter Nachkomme des Przewalskipferdes” [The Mongol domestic horse is a direct descendant of the Przewalski horse]. The distinctive phenotype (Figs. 1, 2) of these three closely related ecomorphotypes largely developed in response to late Pleistocene steppe and steppe-tundra conditions (Bennett, 1992b). A similar scheme was advanced by Groves (1986), although he used different nomenclature.

List of recognized subspecies:

E. c. alaskae Hay, 1913:2,3, see above. Lamut, or Beringian Horse.

E. c. caballus Linnaeus, 1758:73, see above. Northwestern European Horse [c.f. “Draft” in other works of Bennett, “coldblood” in preceding discussion].

E. c. ferus Boddaert, 1785:159, see above. Tarpan (*gmelini* Antonius, *sylvestris* Brinken are synonyms).

E. c. mexicanus Hibbard, 1955, see above. American Periglacial Horse (*laurentius* Hay, *midlandensis* Quinn are synonyms).

E. c. mosbachensis von Reichenau, 1903:583, see above. Central European Horse [c.f. “Warmblood” in other works of Bennett, and in preceding discussion].

E. c. przewalskii Polyakov, 1881:1, see above. Przewalskii Horse, Mongolian Wild Horse (*hagenbecki* Matschie a synonym).

E. c. pumpelli Duerst, 1908:397, see above. Afro-turkic Horse [c.f. “Oriental” in other works of Bennett]. The assignment of this name to *E. caballus* remains controversial. If it is not, then *algericus* Bagtache, Hadjouis and Eisenmann 1984 is the available name.

There are a very large number of names that have been given to mid- to late-Pleistocene horses which we do not attempt to evaluate. Kurtén (1968:149 commented “...it is most improbable that all or even a majority of them will turn out to be valid.” However, many are likely to be assignable to *E. caballus* (Azzaroli, 1988).

Section III: Diagnosis

Equus caballus has, on average, the heaviest body build, the widest and deepest head, and the heaviest limbs of any of the six to eight living and one recently extinct (*E. quagga*) species in the genus (Figs. 1, 3). However, there is great variation in size and proportions among domesticates. The skull is elongated (>500 mm); orbits large and oriented dorsolaterally; molar row long (>80 mm); and incisor region broad (Fig. 2; Osborn, 1912). Upper cheek-teeth large, usually with long, bipartite protocones connected to the protoloph; hypoconal groove deep (Quinn, 1957). Edges of pre- and post-fossettes more intensely folded than in congeners (McGrew, 1944). The lower cheekteeth are characterized, as in other caballoid horses, by a U-shaped entoflexid between the metaconid and metastylid, in contrast to stenoconids, which have a V-shaped entoflexid (Forstén, 1988a). The coat is usually unmarked, sometimes spotted or incompletely striped, but never “zebra-striped”: venter is never much lighter than the dorsum. The most widely occurring pigmentation pattern is solid body color with dark points. Hooves rounder, ears shorter (<20cm), and tail much more fully haired than in congeners (Figs. 2, 18; Willoughby, 1974).

Section IV: General Characters

True wild horses (not feral domestic “mustangs”) show little inflation of the frontal sinuses; domestic forms often show more (Edinger, 1950). Cranial flexion ranges from slightly positive (“ram-nosed or “convex-headed” forms) to negative (“dished face”; Bennett, 1992a). Auditory meatus does not project beyond the shelflike squama temporalis and is not visible from above (Fig. 5; Heptner et al., 1961). Cranium “unfolded” anteroposteriorly as well as laterally broadened compared with fossil and living congeners (Fig. 4, 6, 10; Groves, 1986). Inferior teeth large and straight with oval metaconid-metastylid columns widely separated; molars usually lacking true isthmuses (Fig. 8A; Skinner and Hibbard, 1972).

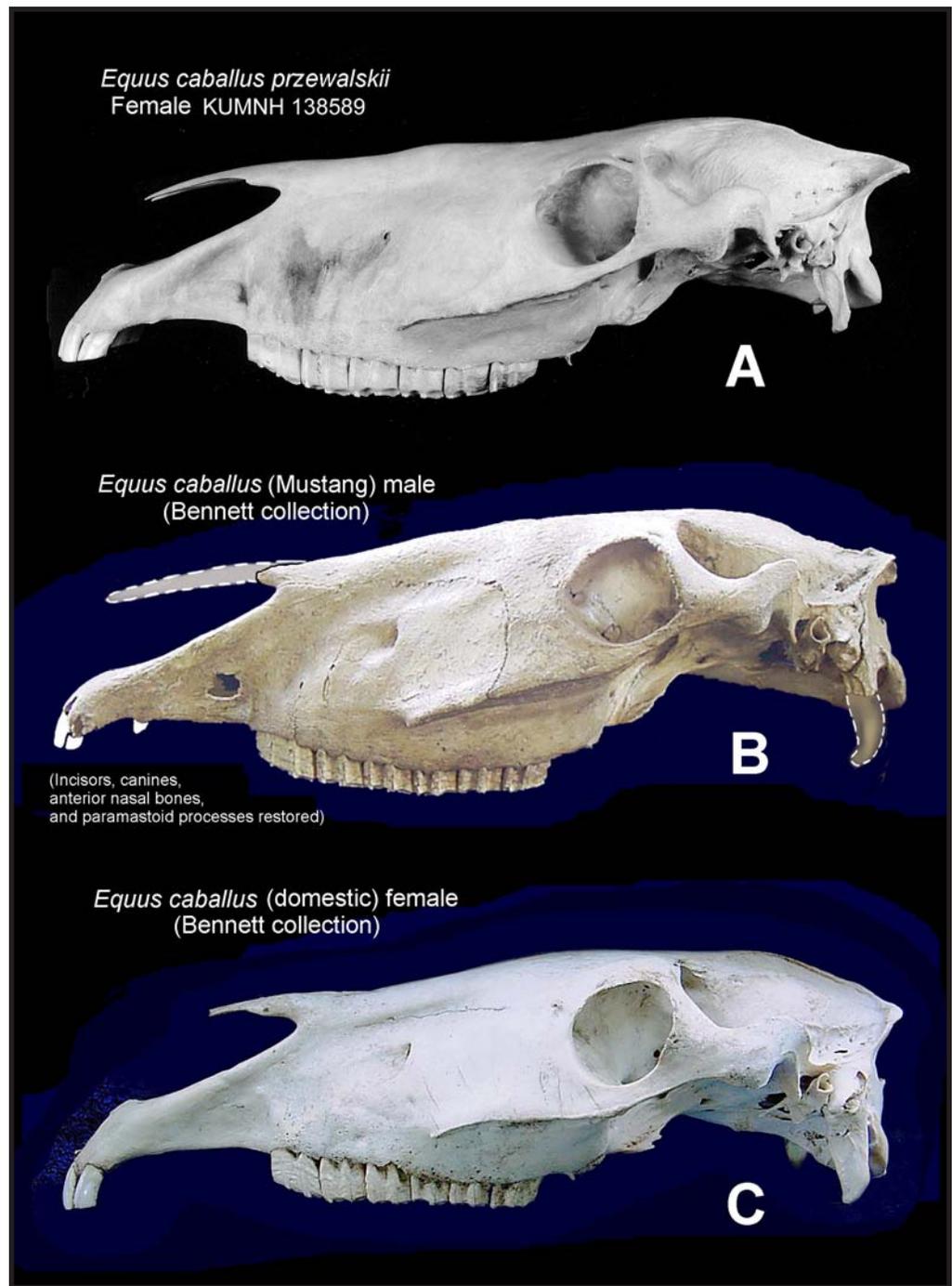
Mid-dorsal stripe always present in wild horses and very common in domestic ones (Salensky, 1907; Sponenberg, 2003). Shoulder, ankle, and wrist stripes occasionally present in both wild and domestic

Fig. 4. Lateral views of crania of adult *Equus caballus*. All skulls in this figure and Figs. 5, 6 have been reduced to the same length to facilitate comparison of proportions. Note differences in facial profile, placement and shape of orbit, and overall robustness of skulls.

A. Mongolian Wild Horse, *E. c. przewalskii*, female. Museum of Natural History, University of Kansas (KU 138589). Greatest length of skull is 52.7 cm.

B. Domestic horse, Mustang from Pryor Mountain herd, northern Wyoming, male. Greatest length of skull is 54.1 cm. (Incisors, canines, distal portion of nasal bone, and paramastoid process restored).

C. Domestic horse, Thoroughbred breed, Idaho, female. Greatest length of skull is 57.3 cm.



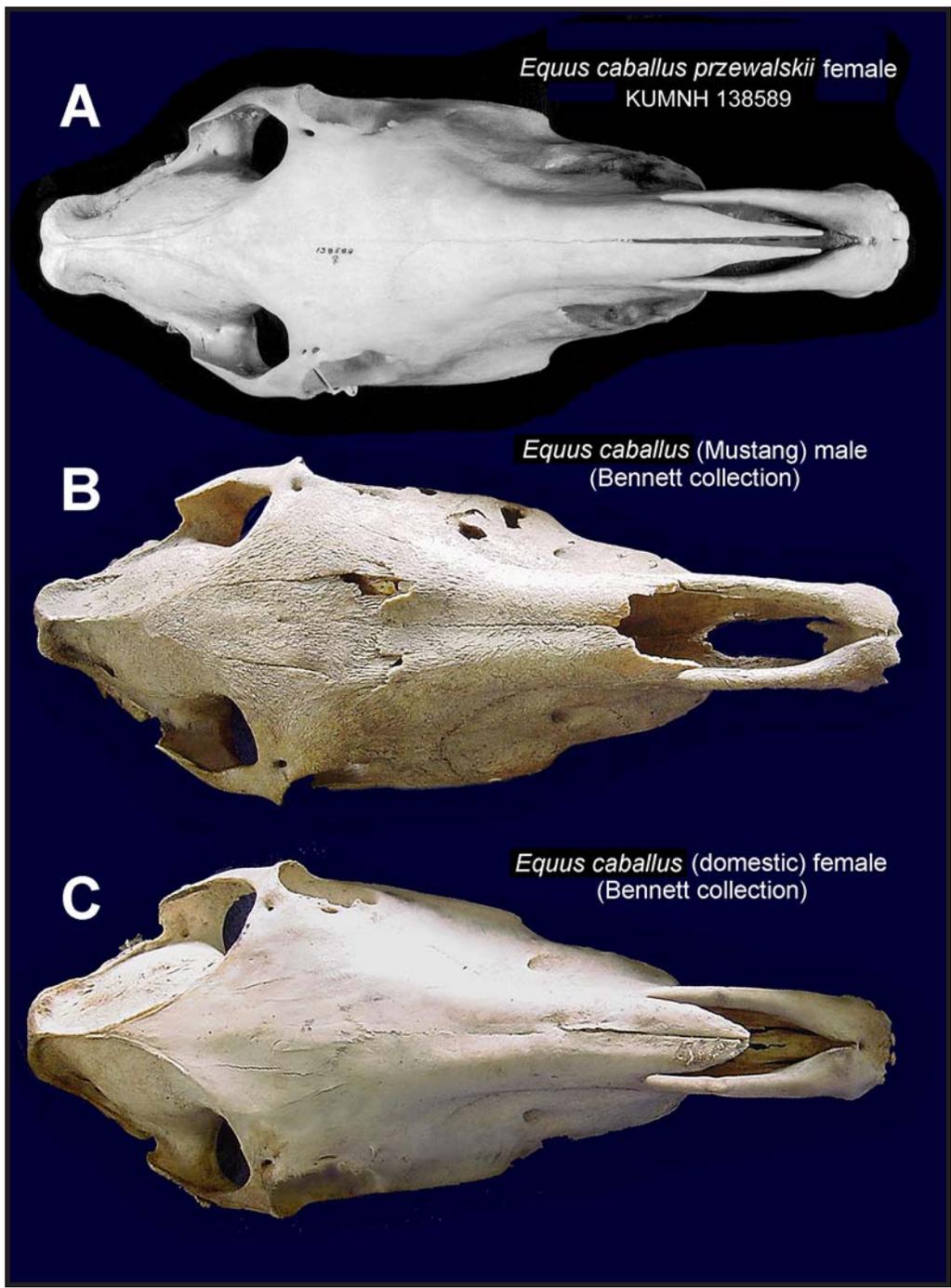


Fig. 5. Dorsal views of crania of adult *Equus caballus*. All skulls in this figure and Figs. 4, 6 have been reduced to the same length to facilitate comparison of proportions. Note differences in skull breadth across lambdoidal crest, orbits, cheekbones, and muzzle. Nasal bones in B and C partially broken away.

A. Mongolian Wild Horse, *E. c. przewalskii*, female. Museum of Natural History, University of Kansas (KU 138589).

B. Domestic horse, Mustang from Pryor Mountain herd, northern Wyoming, male. (Nasal bones and part of palate broken away).

C. Domestic horse, Thoroughbred breed, Idaho, female.

Fig. 6. Ventral views of crania of adult *Equus caballus*. All skulls in this figure and Figs. 4, 5 have been reduced to the same length to facilitate comparison of proportions. Note differences in skull breadth across palate, cheekbones, muzzle, and ear region, and compare length of cheek tooth row and diastema.

A. Mongolian Wild Horse, *E. c. przewalskii*, female. Museum of Natural History, University of Kansas (KU 138589).

B. Domestic horse, Mustang from Pryor Mountain herd, northern Wyoming, male (anterior dentition and paramastoid processes largely broken away).

C. Domestic horse, Thoroughbred breed, Idaho, female.

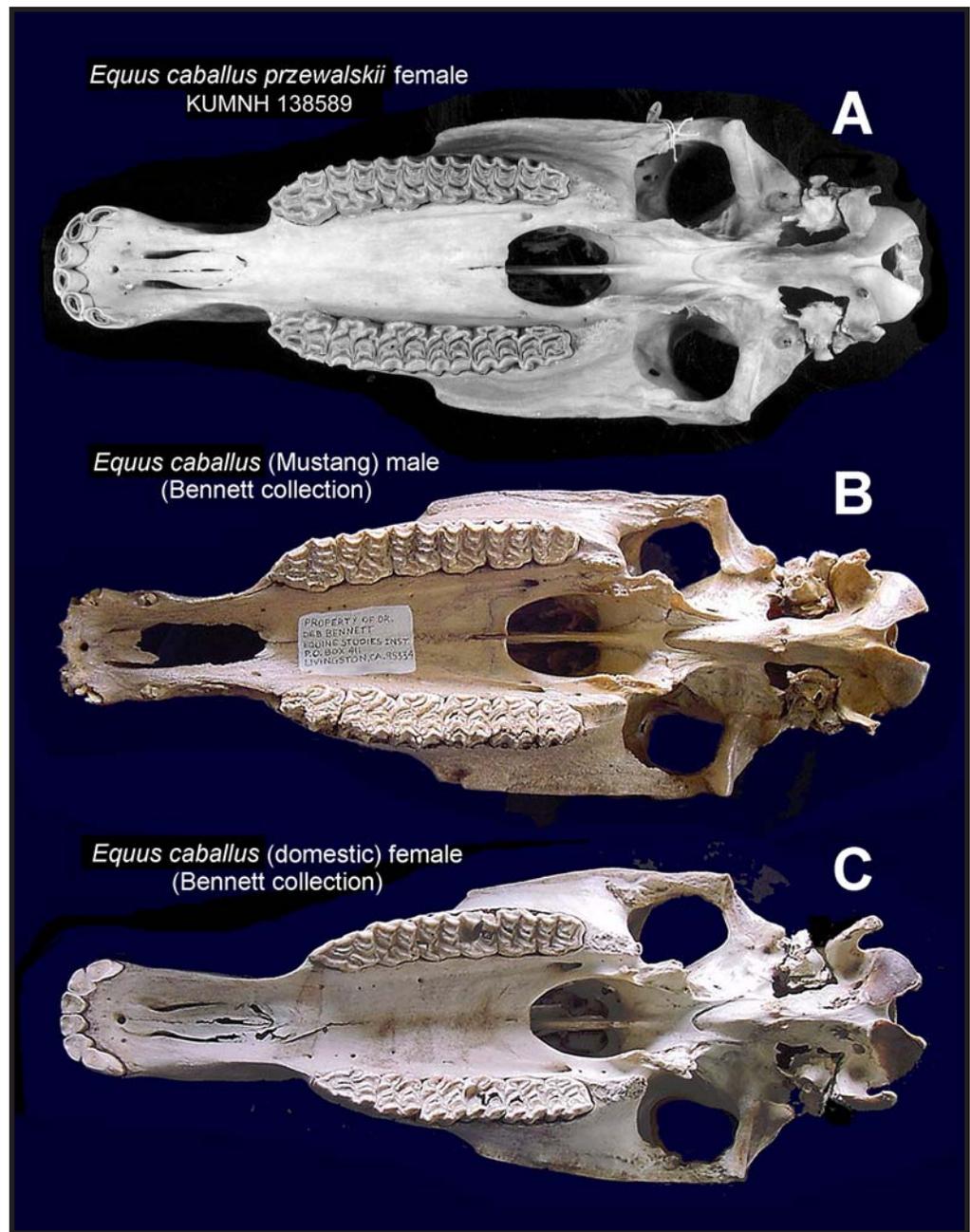
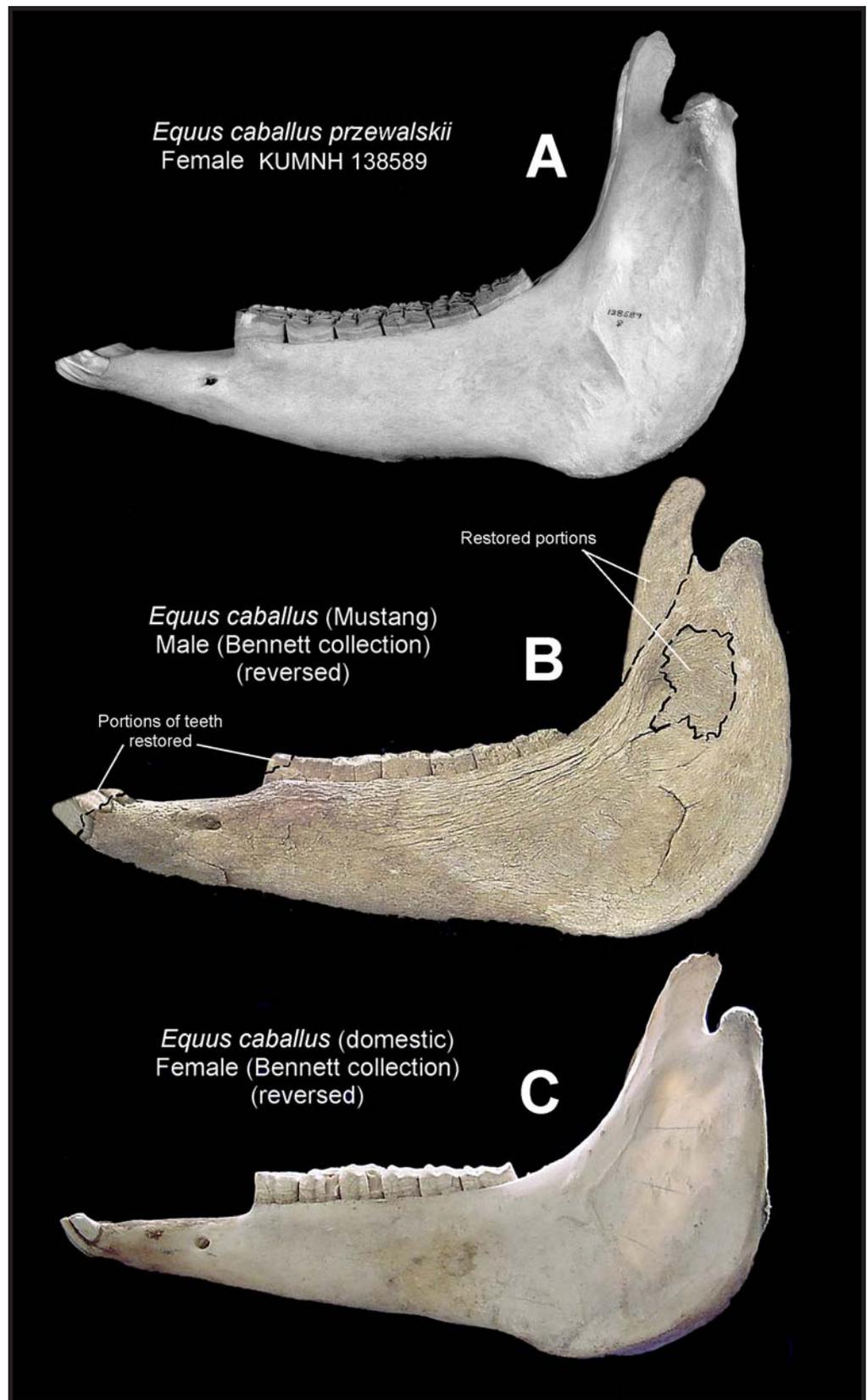


Fig. 7. Left mandibles of of adult *Equus caballus*, lateral view. All mandibles in this figure have been reduced to the same length to facilitate comparison of proportions. Note differences in diastema length, cheek tooth row length and curvature, and overall robustness of the bone.

A. Mongolian Wild Horse, *E. c. przewalskii*, female. Museum of Natural History, University of Kansas (KU 138589).

B. Domestic horse, Mustang from Pryor Mountain herd, northern Wyoming, male (incisors, part of P/2, coronoid process, and area of ascending ramus within black dashed line restored).

C. Domestic horse, Thoroughbred breed, Idaho, female.



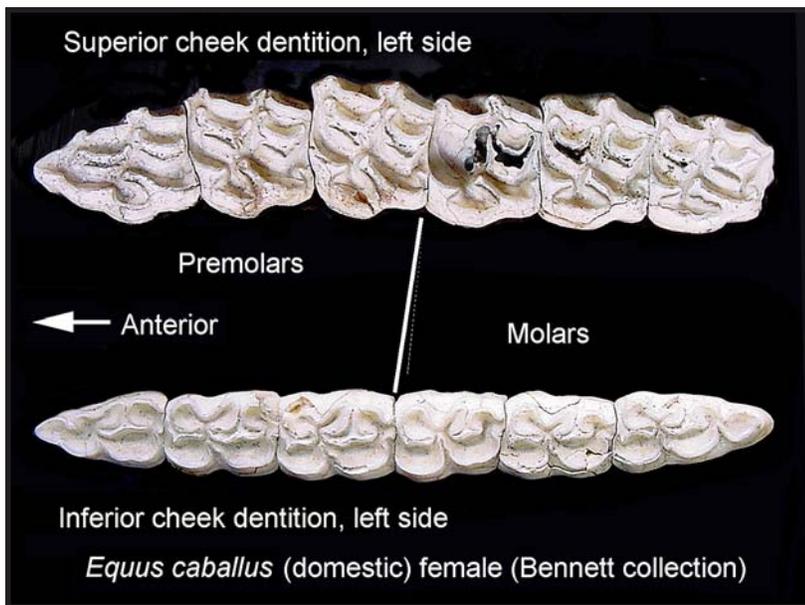


Fig. 8A. Cheek dentition in *Equus caballus* (domestic). This is a mare of about 12 years of age. Note the complexity and characteristic shape of the occlusal enamel pattern. There are two fossettes completely ringed by enamel in each superior tooth, and the protocones are connected to the hypoloph. In the inferior teeth, the metaconid and metastylid loops are well-inflated while the ectoflexid penetrates far medially, creating a short isthmus. Note the loss of intra-infundibular cementum (or failure of its original deposition) in all three superior molars, and the large dental caries in the anterior half of M1/. Dental caries are extremely rare in fossil, wild, or feral *E. caballus*, but common in domestic horses.

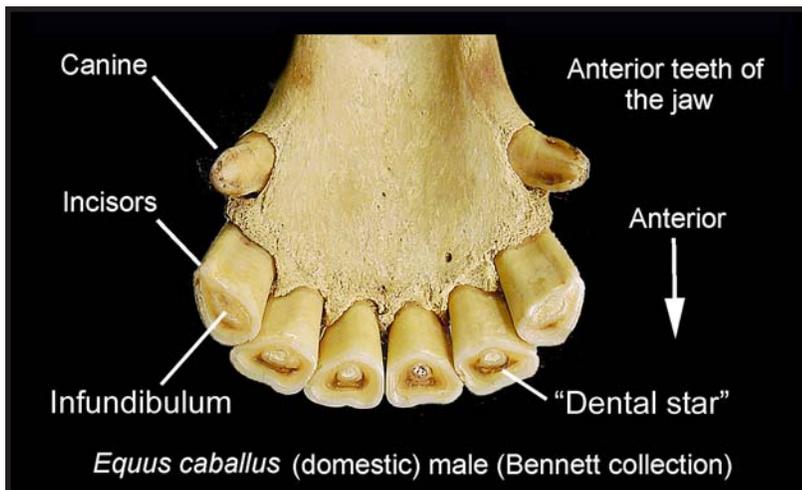


Fig. 8B. Anterior dentition in *Equus caballus* (domestic). This is a male horse of about 7 years of age. Note the characteristically anterior position of the canines. In young males the anterior and posterior edges of the canines are bladed; the sharp edge gradually becomes blunted. Note the infundibula, ringed by enamel, in all incisor teeth. The dark mark anterior to the infundibulum in each tooth is the "dental star", the distal portion of the embryonic pulp cavity.

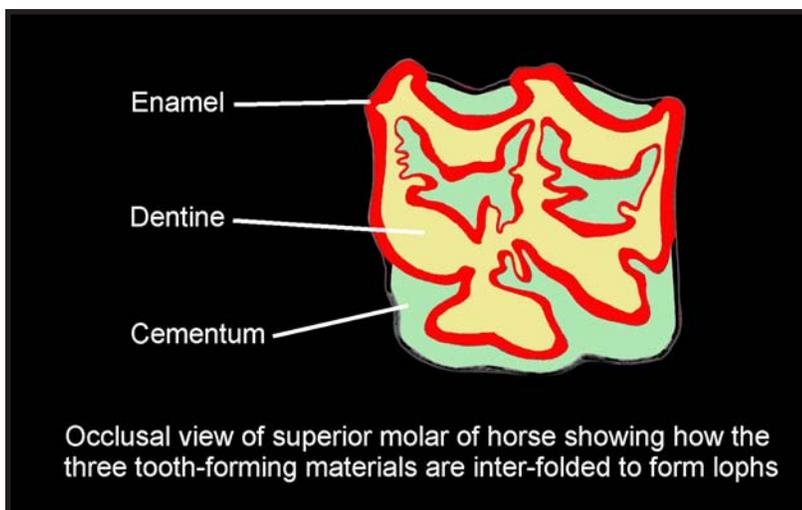


Fig. 8C. The lophodont cheek teeth of horses are composed of three mineralized biogenic substances, enamel, dentine, and cementum. Since these substances differ in hardness, their alternation on the occlusal plane of the teeth creates a self-renewing surface ideal for milling grass. The chewing stroke in horses drags the mandibular cheek teeth across the superior cheek teeth from the lateral to the medial side.

forms. Shanks, center of mane and tail, tips of ears, and margins of mouth and nostrils black in wild and many domestic horses (Figs. 1, 2).

Interruptions of pigmentation on the face and legs, which evidence themselves as irregular white markings, are common in domestic horses but are rare in the wild horse (Mohr and Volf, 1984; Willoughby, 1974). A white or lighter-colored border around the eyes, muzzle, mane, dorsal stripe, and root of the tail is usual in the species (Groves, 1974; Sponenberg, 2003). Basic coat-color ranges from white (so-called “partial albino”) through cremello, palomino, and isabella (clear shades of yellow) to buckskin, dun, and reddish dun (the latter colors displayed by *przewalskii*), to chestnut (reddish brown to brick red), brown (a rich sienna in shades nearly to black), liver (flat brown), mouse-gray (was characteristic of *ferus*), and black. Agouti coloration (called “grulla” if on mouse-gray hair and “dun,” “dusty,” or “smutty” if on yellow or reddish-yellow hair) also is common (Campbell and Lasley, 1975; Heptner et al., 1961; Sponenberg, 2003).

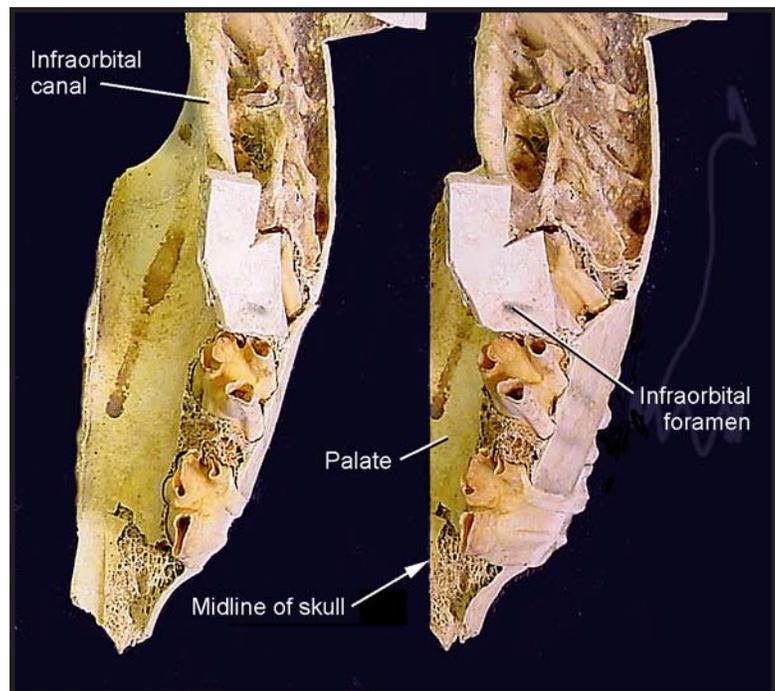
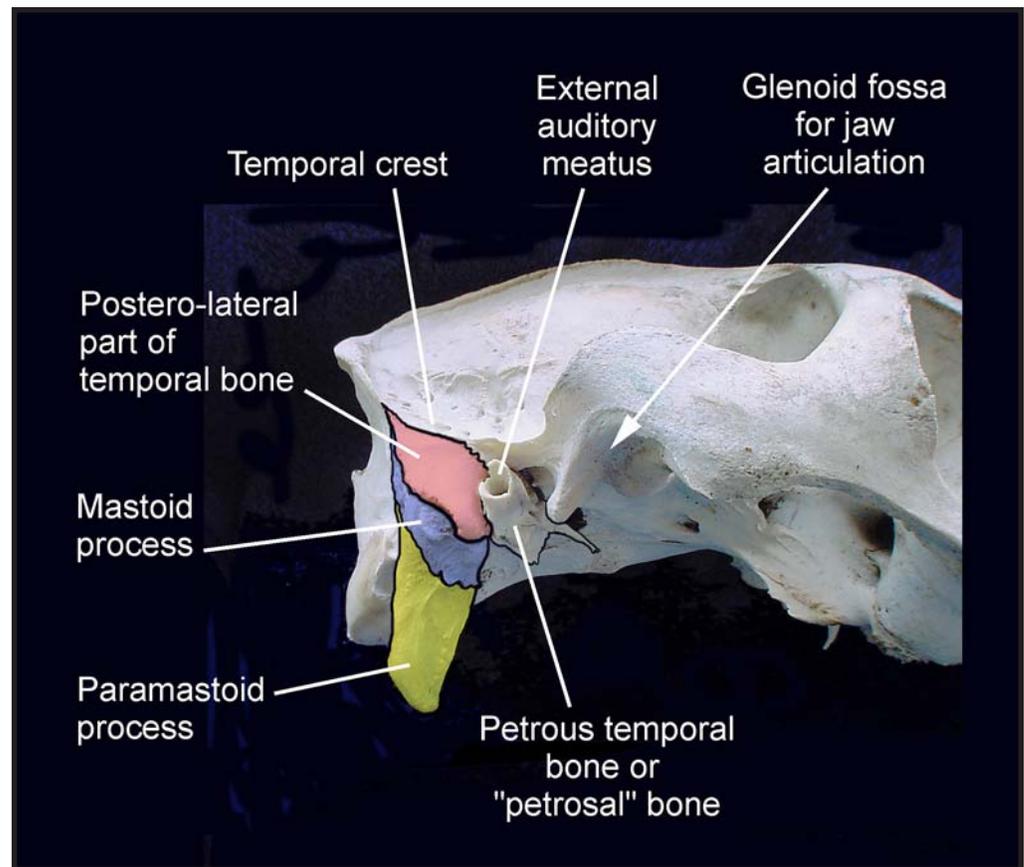


Fig. 9. Left maxillary region of partially dissected horse skull in dorsal view, showing how the roots and reserve crowns of the long (hypsodont) cheek teeth project upwards into the large, hollow, and specially adapted maxillary sinus. This is a horse of about 9 years; the longest cheek tooth visible here measures about 11 cm. The roots of the cheek teeth remain open and the pulp chambers continue to receive a full blood supply until the teeth are nearly worn out, generally between ages 15 and 25. The infraorbital artery and nerve, which course through the tubelike infraorbital canal, supply the superior dentition.

Hooves round in contrast to congeners which have narrower, oval hooves (Willoughby, 1974). Ears short, pointed, and pricked (Bennett, 1992a). A tuft composed of short hairs is present at the top of the tail in the winter coat of the wild horse and in many domestic horses (Groves, 1974). The mane is composed of coarse hairs. In surviving wild horses, the short mane is upright (Figs. 1, 2), but in extant domestic forms, it grows longer and “falls” (Fig. 18, 19). The wild tarpan of eastern Europe, *E. c. ferus*, showed an intermediate, “partly falling” mane. Extant wild horses are stocky animals with relatively very short ears and large, deep heads (Figs. 1, 2; Groves, 1974). Domestic forms descended from other subspecies have been considerably changed through contact with humans, who have consistently selected taller individuals with shorter heads, finer muzzles, broader foreheads, and higher “withers” (neural spines of anterior thoracic vertebrae; Zeuner, 1963; Fig. 18, 19). Nevertheless, both wild and domestic horses are readily distinguishable from congeners on the basis of many skeletal measurements.

Equus caballus is the largest species in the genus (Willoughby, 1974). External measurements (in cm) of *E. c. przewalskii* (Klimov and Orlov, 1982; Xiao and Qiu, 1990) are as follows: length of body, 220-280; length of tail including hair, 99-111; without hair, 38-60; length of ear, 14-18; and height at withers,

Fig. 10. Closeup of the ear region of the skull of a domestic horse, right lateral view. The "open fan" formed by the squamous temporal bone, mastoid process, and paramastoid process is diagnostic of the species. An "open fan" gives the occiput a slight to moderate posterior slant. A reliable method for distinguishing the skulls of domestic or Mongolian Wild horses (*E. caballus*) from those of mules (*E. caballus* X *E. asinus*), asses (*E. asinus*), or any other equine, is to set the skull on its occiput upon a level surface. If the skull balances solidly and remains upright, it is that of a horse. If it falls over to the front, it is not *E. caballus*.



120-146. Adult mass is 200-300 kg. Cranial measurements of adults (older than four years), in mm: mean \pm SE:range) for four wild-caught animals are the following: basal length of skull, 482 ± 3.9 (471 – 489); greatest maxillary width, 132.7 ± 0.47 (132 – 134); mastoid width, 105.5 ± 2.62 (100-110); width of interorbital constriction, 87.5 ± 0.95 (86 – 90); length of nasal, 255.7 ± 1.37 (253-259); height of maxillary above P2, 96.7 ± 2.13 (91-100); length of upper tooth row, 184.2 ± 2.09 (180 – 190); length of premolar row, 104.7 ± 2.49 (98 – 109); length of molar row, 83.0 ± 1.87 (79 – 88); length of mandibular ramus, 411.7 ± 1.87 (402 – 422); greatest length of jaw, 428.8 ± 4.15 (420 – 440); depth of jaw in front of p2, 52.2 ± 0.85 (50-54); depth of jaw at rear of m3, 114.0 ± 4.45 (107 – 127); length of alveolar row, 191 ± 1.29 (188 – 194); alveolar width of lower incisors, 65.7 ± 1.31 (62 – 68); least width of mandibles, 43.5 ± 1.19 (42 – 47); and length of mandibular diastema, 77.2 ± 3.25 (68 – 83).

Geographic variation in wild horses was principally in size, skull shape, limb length and color. The only surviving wild subspecies, *przewalskii*, which until recently ranged from Siberia through Mongolia, is of moderate size with a relatively large head and thick neck, yellowish dun in color, erect mane, and with dark mid-dorsal stripe poorly expressed and clearly evident only in summer pelage (Fig. 1, 2). The molariform teeth are large, and the profile of the nasal bones straight to slightly concave (Fig. 4; Mohr and Volf, 1984). To the north and east of the Przewalski horse, the Beringian wild horse (*alaskae*) ranged along the arctic border of Siberia and eastward beyond Alaska (Fig. 12, 13). It was similar to the

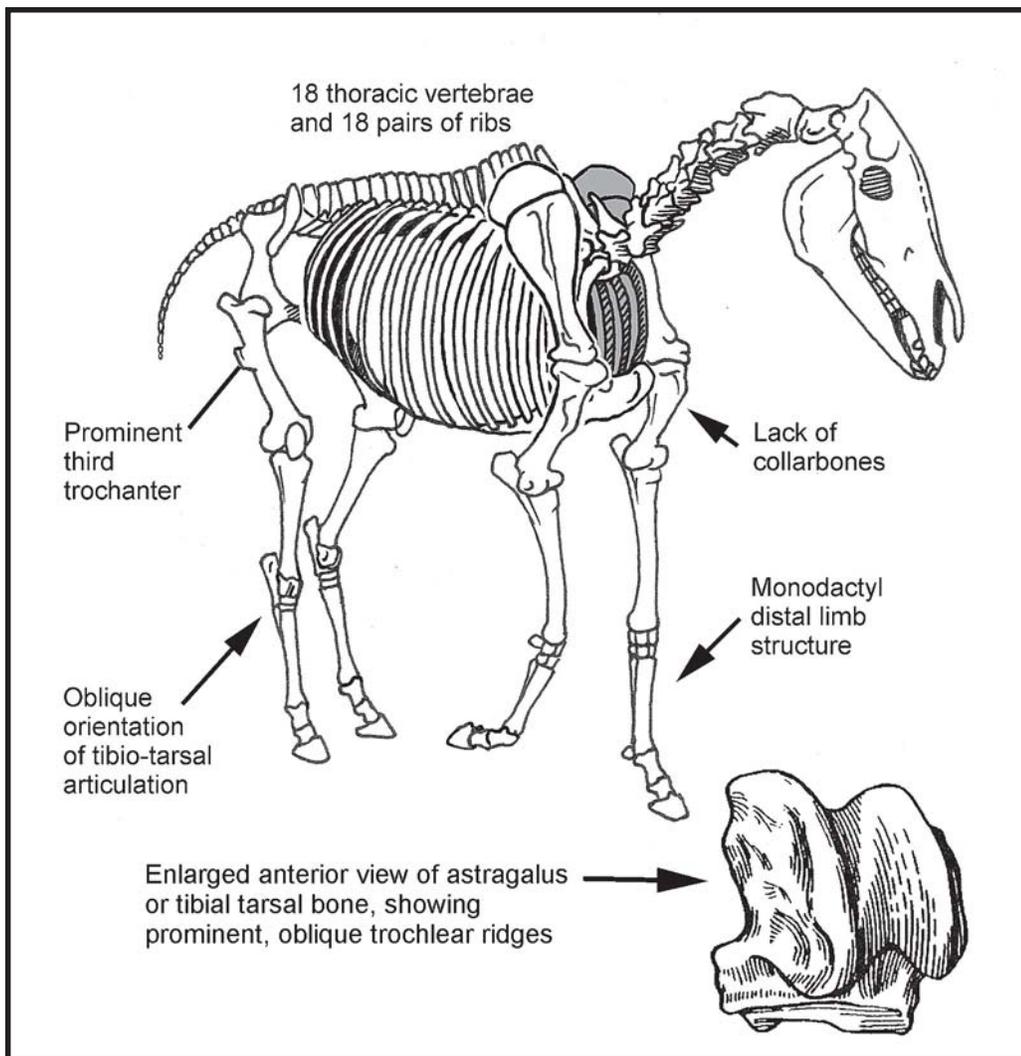


Fig. 11. Skeleton of domestic horse in anterior oblique view. The complete vertebral formula in the Mongolian Wild Horse, *E. c. przewalskii*, is: 7 cervical, 18 thoracic, 6 lumbar, 5 sacral, and about 12 caudal. In domestic horses, there can be fusion of lumbar 5 and 6 or complete loss of the most posterior lumbar. Rarely, there may be 19 thoracics, or 4 sacrals.

Przewalski horse, but its coloration was probably much lighter, in dilute shades of dun in summer pelage to nearly white in winter (Zeuner, 1963). South of the Wisconsinan glacial margin of the Great Plains, and elsewhere in North America, the American Periglacial horse (*mexicanus*) developed in parallel. *E. c. mexicanus* possessed a skull and dentition similar to that of *alaskae* and *przewalskii*, but was larger, with a longer head and concave facial profile (Hibbard, 1955).

The tarpan (*E. c. ferus*) of the western Eurasian steppe and forest-steppe zone (Fig. 13) averaged smaller, ca. 130 cm high at the withers. It was mouse-gray in color, with a well-developed black mid-dorsal stripe, partly falling mane, slightly smaller molariform teeth, a more pointed muzzle, and a slightly concave facial profile (Fig. 3). The northwestern European subspecies, *caballus*, averaged larger than *ferus* or *przewalskii*, but dwarfed insular populations ("island ponies") also occur (Short, 1975). *E. c. caballus* was distinguished by large, round feet and a straight or undulating facial profile. The body build was stocky or even bulky, with a heavy neck and steep pelvic angle (Fig. 3, 19). Judging from domestic descendants, the pelage was long and thick, with a tendency for the growth of long hairs ("feathers") from the posterolateral surfaces of the metapodials; the mane was probably long and falling. In contrast to *caballus* to the northwest, the Central European horse (*E. c. mosbachensis*) had a long narrow head in which the eye was placed fairly high, with a straight to convex nasal profile. Taller than any other wild forms of the horse, *mosbachensis* possessed a shallow torso, long flat neck, and long,

sturdy legs (Fig. 3, 19). The guard hairs of the coat of its domestic descendants grow long in winter pelage, but lack the thick undercoat grown by its more northern neighbors, producing a shaggy, rather than a woolly appearance. The southernmost subspecies, *E. c. pumpelli* (Fig. 3, 19), was small in size but had relatively the longest, slenderest legs and ears. The facial profile was straight or concave (“dished”), due to a combination of negative cranial flexion and tendency for inflation of the frontal sinuses. As in *mosbachensis*, the cross section of the thorax was a flattened oval, not rounded as in *caballus*, *ferus*, and *przewalskii*. There was a tendency to shorten the lumbar span by the loss or fusion of the posterior lumbar vertebrae (Fig. 16). Domestic Afro-Turkic horses are always less hirsute than other forms, and in the wild state probably possessed a short, scant, erect mane (Bennett, 1992b; Trumler, 1961).

Section V: Distribution

The known distribution (Fig. 12, 13) in Late Glacial time (*sensu* Graham and Lundelius, 1994) of wild *E. caballus* included Europe (except the extreme north) as far south as the Iberian Peninsula (Uerpmann, 1976). Eastward, it ranged across the steppe and forest steppe zone of Belarus, Ukraine, Russia, and Kazakhstan to western China and Mongolia. Several taxa of Late Glacial *Equus* have been described from China and Japan (Olsen, 1988; Shikama and Onuki, 1962), and *E. caballus* occurred in the northern and eastern provinces of China. Whether the wild horse was in Tibet is unclear (Smith, 1845).

Wild horses also occurred in the steppe-tundra of the northern Palearctic and Beringia, from the Yamal Peninsula eastward to the Kolyma region (Lazarev, 1980) and across Beringia to Alaska and the northern Yukon (Schweger et al., 1982). They survived in the Yukon until at least 13,000 years ago (Morlan and Cinq-Mars, 1982), and there is some evidence for survival of a relict population of wild horses in northern Yakutiya (Russia) until historic times (Vereschagin and Barishnikov, 1982). In North America, populations occurred south of the glacial margin in suitable habitat from the confluence of the Mississippi and Ohio rivers northwest along the Missouri to Wyoming and Idaho, and southwest in the Great Plains and suitable valleys to California, Nevada, Texas, and Mexico, and probably elsewhere (Arroyo-Cabrales et al., 1993; Bennett, 1992b; Graham and Lundelius, 1994; Winans, 1989). It probably did not inhabit the boreal taiga that Martin and Neuner (1978) termed the *Symbos-Cervalces* faunal province in the northeastern United States.

In Africa and southern Eurasia, the species may have occurred north of the Atlas Mountains from east of the Tangiers to the Tunisian peninsulae, but only one specimen is known, from Algeria (Bagtache et al., 1984). In the Near East, the horse was probably found in Egypt (Boessneck, 1970), along a narrow strip up the Levant coast on the eastern end of the Mediterranean (Davis, 1980), and perhaps south for an undetermined distance along the east coast of the Red Sea. To the north, its distribution broadened to include the hills and plains of Anatolia (Boessneck and von den Driesch, 1976), through Iraq (Turnbull, 1986) and Iran (Firouz, 1973), as far north as the Cis- and Trans-Caucasus, where the tarpan and “Southwest Asian” (Afro-Turkic, “Oriental”) horse occurred, respectively (Vereschagin, 1959); thence eastward through Turkmenia (Duerst, 1908) and Uzbekistan to the Syr Darya River (Smith, 1845) and north-central Afghanistan (Uerpmann, 1987). It was apparently absent from the taiga that developed in the Late Glacial in the West Siberian Lowlands and eastward to the lower Amur basin (Markova et al., 1995; Moreau, 1955). (Causes of extinction are discussed under Conservation Status).

HOLARCTIC DISTRIBUTION OF *Equus caballus* 9,500 - 15,000 YEARS AGO

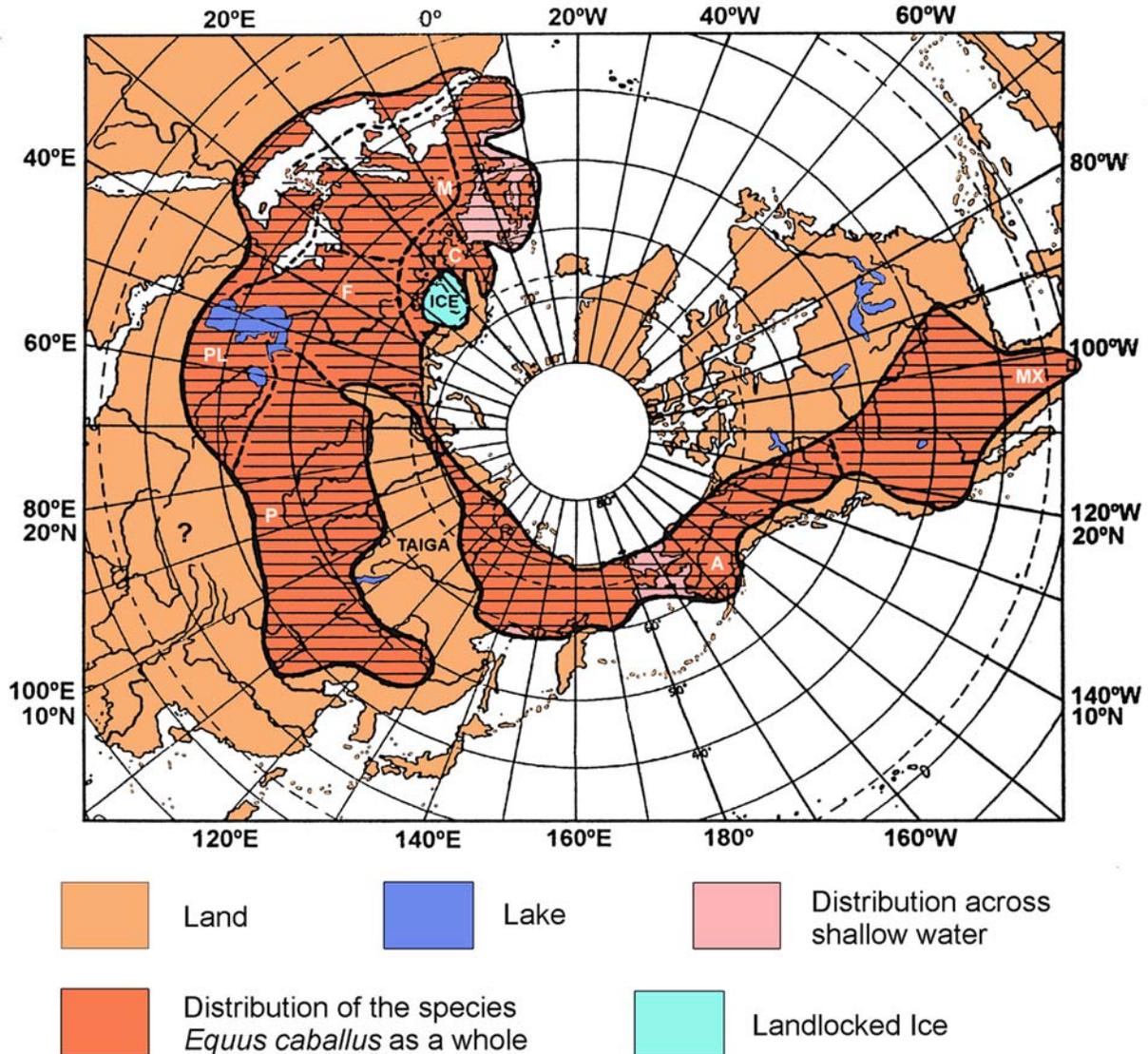


Fig. 12. Distribution of *Equus caballus* during the Late Glacial, 9,500-15,000 years ago, when melting glacial ice still remained in some places, restricting its range (Markova et al., 1995). Exposed land along continental margins occupied by the horse, as well as Bering land bridge, are shown. Type localities of recognized subspecies indicated by letters: A, *alaskae*; C, *caballus*; F, *ferus*; MX, *mexicanus*; M, *mosbachensis*; P, *przewalskii*; PL, *pumpelli*. Dashed lines indicate boundaries between subspecies. For reconstruction of historic range in former USSR, see Heptner et al. (1961). Possible former occurrence in Tibet is indicated by question mark.

DISTRIBUTION OF SUBSPECIES OF *Equus caballus*

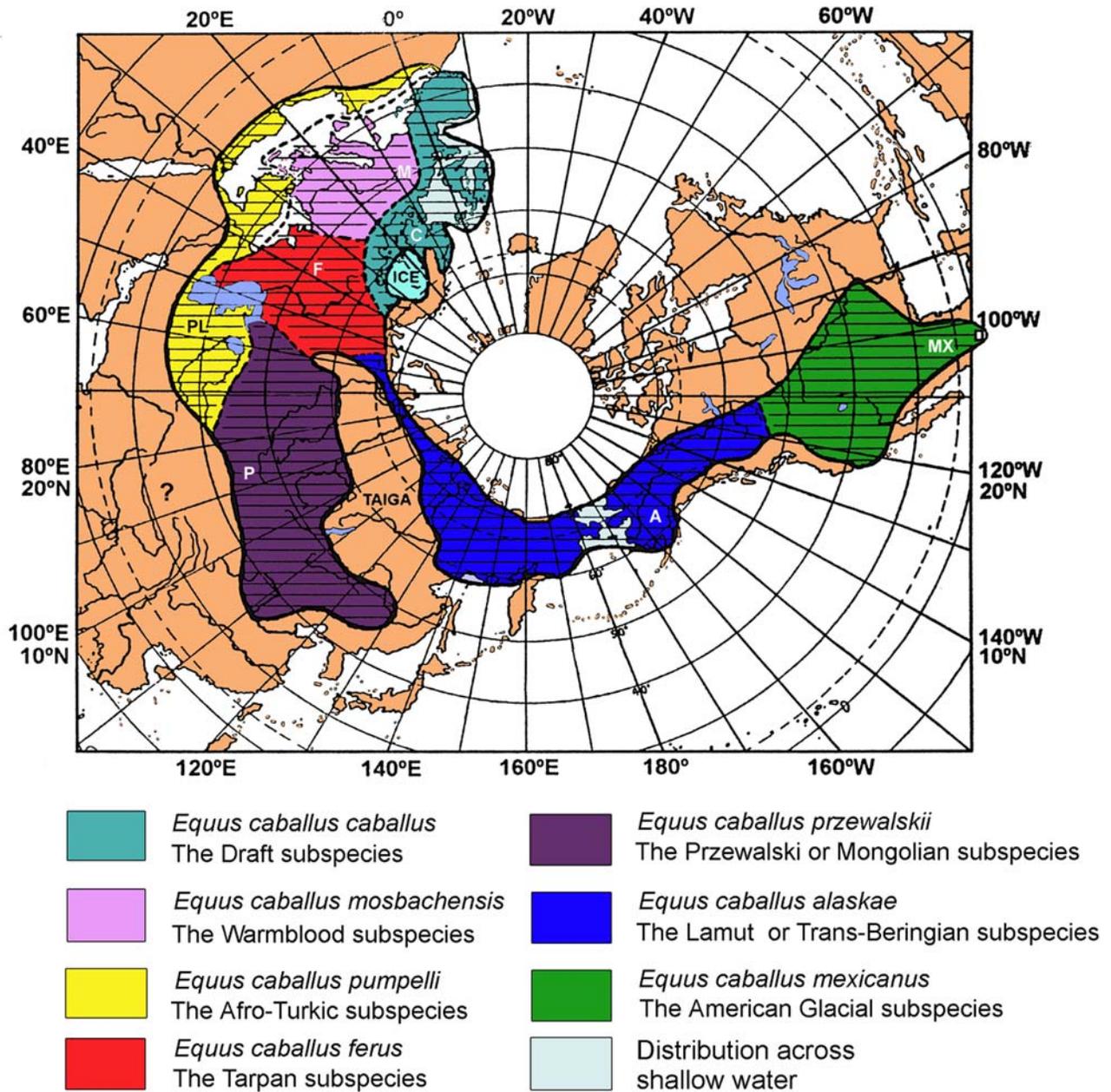


Fig. 13. Distribution of subspecies of *Equus caballus* during the Late Glacial, 9,500 - 15,000 years ago, when melting glacial ice still remained in some places, restricting its range (Markova et al., 1995). Exposed land along continental margins occupied by the horse, as well as Bering land bridge, are shown. Type localities of recognized subspecies indicated by letters: A, *alaskae*; C, *caballus*; F, *ferus*; MX, *mexicanus*; M, *mosbachensis*; P, *przewalskii*; PL, *pumpelli*. Dashed lines indicate boundaries between subspecies. For reconstruction of historic range in former USSR, see Heptner et al. (1961). Possible former occurrence in Tibet indicated by question mark.

Section VI: Fossil Record

Equus, a monophyletic taxon, is derived from the late Miocene *Dinohippus* (Quinn, 1957). The genus evolved during Pliocene (Blancan) time, ca. 4 million years ago in North America (Forstén, 1989), and is first represented in western North America by *E. simplicidens* (syn. *Shoshonensis*; Azzaroli, 1992). This medium-sized equid was directly ancestral in North America, ca. 3 million years ago, to later Blancan species (Azzaroli and Voorhies, 1993). However, about 2.5 million years ago *Equus* also migrated to Eurasia via Beringia (Prat, 1980); the oldest species there is *E. livenzovenssis* (Azzaroli, 1990), which was followed by the “dentally primitive” (Forstén, 1989) stenorid horses, so-called after *E. stenonis*, the most widespread species, which first appeared about 2 million years ago in both Eurasia and North America. Stenorids, which include zebras, survived in the New World until the late Pleistocene (*E. enormis*; Azzaroli, 1995), and persisted in Eurasia until at least 1 million years ago (middle Pleistocene; Azzaroli, 1990; Kurtén, 1968). However, Forstén and Dimitrijevic (1995) argue that *E. hydruntinus* was a stenorid that survived to the end of the Pleistocene.

The origin of “dentally more advanced” caballoid horses is uncertain. Kurtén (1968) suggested that the stenorid *E. bressanus* may have given rise to the oldest caballoid ecomorphotype, *E. c. mosbachensis*, but Azzaroli (1992) believed that another branch from ancestral simplicidens, the late Pliocene *E. idahoensis*, was the source of caballoid horses about 2 million years ago in North America. These then migrated to Eurasia about 1 million years ago (Azzaroli, 1988), leaving others (such as *E. niobrarenensis*) in North America (Azzaroli, 1995). Initially rare, caballoids were associated with stenorids in Eurasia, but over the next half-million years replaced them because of climatic preferences and different niche width (Forstén, 1988a). In North America, isolated lower molar teeth and a mandible from sites of Irvingtonian age (Azzaroli, 1995; Schäfer and Dalquest, 1991) appear to be *E. caballus* morphologically. In the Rancholabrean (Late Pleistocene), much more material is available, but most is assigned to other species; the only North American taxa which can definitely be assigned to *E. caballus* are *alaskae* (Azzaroli, 1995) and *mexicanus* (Winans, 1989, using the name *laurentius*). These may either have derived from *niobrarenensis* (Azzaroli, 1995) or else from Beringian horses crossing over the Bering land bridge from Siberia (Repenning, 1967). A third alternative is that *E. c. alaskae* was descended from Eurasian horses and *E. c. mexicanus* from *niobrarenensis* stock. However, through much of the Pleistocene in North America, the commonest species of *Equus* were not caballines, but rather other lineages resembling zebras, hemiones, and possibly asses (McGrew, 1944; Quinn, 1957).

The horse (*E. caballus*), being very adaptable, has occupied a variety of habitats, from semidesert to steppe-tundra, but has tended to favor cooler, more moist habitats – grassland, open forest and tundra – as opposed to the dry steppe and desert habitat of asses and hemiones, and their Holarctic fossil distribution reflects this (Alberdi et al., 1992; Bennett, 1992b; Heptner et al., 1961). By the late Pleistocene, *E. caballus* occupied suitable periglacial habitats in as nearly a circumpolar distribution as the positions of glacial masses would allow (Guthrie, 1990; Kurtén, 1968; Lazarev, 1980; Markova et al., 1995). Shifts between glacial and interglacial intervals in the late Pleistocene seem to have affected the distributions of forest and steppe/tundra ecomorphs, and during glacial phases of the Würm period, both forest (*caballus*, *mosbachensis*) and steppe (*ferus*) or steppe-tundra (*alaskae*, *przewalskii*) forms were found in Europe (Eisenmann et al., 1985; Forstén, 1986; Zeuner, 1963), although probably not syntopically.

By the early Holocene (8,000-10,000 years ago; Graham and Lundelius, 1994) all North American horses had become extinct. The final date is now considered to be 11,400 years ago, and dates as late as 8,000 years ago (Churcher and Stalker, 1970) are now considered in error. However, caballine horses survived in Eurasia (Markova et al., 1995) and the circum-Mediterranean region (Uerpmann, 1976). In the Near and Middle East, wild horses survived until a few thousand years ago but were rapidly exterminated as domestic horses became widespread; the same may have happened in North Africa and eastern China, but records thus far are lacking. In western Europe, wild horses persisted well into the historical period. They may have existed in Britain at the time of the Roman invasion (Groves, 1986), and it has been suggested that the Exmoor pony represents this population (Speed and Etherington, 1952-1953); however, Groves (1986), citing Clutton-Brock, believed that wild horses were extinct by the close of the Pleistocene, as in North America. On the continent, Lundholm (1949) found evidence that wild horses survived in Sweden until the early Holocene and were known in the Rhineland until at least the 13th century. They survived in eastern Europe and western and central Asia until the 19th-20th centuries (Bennett, 1992b). Beginning ca. 6,000 years ago, *E. caballus* was taken into domestication and extirpation in the wild began (Anthony and Brown, 1991). The last *E. c. przewalskii* to be captured in the wild was taken into the zoo population in 1947, and all subspecies of *E. caballus* are now thought to be extinct in the wild (Gao and Gu, 1989; Sokolov and Orlov, 1980).

Section VII: Form

Foals are born with a dense pelage consisting of long, soft, curly hairs (“fleece”, Fig. 2, 18), which begins to shed after about seven weeks, a molt which takes 30 – 40 days. The very short, fine, soft mane of the newborn foal grows longer at this time. In the adult, the thick winter coat is shed in summer, beginning when temperatures exceed about 6° C. Shedding begins on the head and neck, progresses to the haunches, flanks and back, then to the front of the legs, and last to shed are the belly and medial and caudal sides of the legs. The whole molt takes 56 days in adults, but up to 75 days in yearlings. Autumn regrowth begins at the end of September and early October. In the Przewalski horse and in northern-derived domestic individuals, a thick growth of guard hairs appears on the jaws first, then on the chest, belly, and shanks. In southern-derived domestic individuals, the beard is present but thinner and long guard hairs do not appear. By early December the winter coat is fully grown (Groves, 1974).

Horses possess callosities near wrist and ankle on fore and hind limbs called “chestnuts,” and others on the fetlock joints called “ergots.” These may represent vestigial toe pads or nonfunctional scent glands (Willoughby, 1974).

The tongue of the horse is spatula-shaped and pink in color, with a relatively smooth dorsal surface. Two or three vallate papillae are present posteriorly on the dorsum; foliate papillae are present near the anterior pillars of the soft palate (Campbell and Lasley, 1975).

The horse has a monogastric, cecal digestive system and the largest and most complex large intestine of any domestic animal. Total intestinal capacity is 211 liters; that of the caecum, 33 liters; of the stomach, 12 liters; of the small intestine, 64 liters; and of the large intestine, 96 liters. The horse’s stomach has a small capacity relative to that of other mammals; it is J-shaped and enlarged in the left extremity. The small intestine is located chiefly in the dorsal part of the left half of the abdominal cavity; the greater omentum is lace-like in form. The large intestine possesses a sacculated construction with longitudinal bands. The large colon is in the ventral abdominal cavity, whereas the small colon lies dorsal to it. The

cecum is large, comma-shaped and sacculated in construction, with four longitudinal bands (Campbell and Lasley, 1975).

The horse's liver weighs 5 kg and comprises 0.8 – 1.5% of body mass. Its structure is trilobate, and it possesses a caudate process. It bears an indenture for the right kidney and a deep esophageal notch. The umbilical fissure is small and shallow, located on the central lobe. No gall bladder is present; the bile duct enters the duodenum beside the pancreatic duct in the diverticulum 12 – 15 cm from the pylorus. The posterior vena cava is embedded for only a short distance along the dorsal border (Frandsen, 1974).

The pancreas weighs about 350 g and comprises 0.06% of the body mass; it is about 50 cm long and 20 – 24 cm wide (Campbell and Lasley, 1975). The horse's right kidney weighs 700 g; its left, 680 g; they measure 15 by 5 cm and 17.5 by 10-12.5 by 5 cm, respectively (Campbell and Lasley, 1975).

The larynx is much longer than wide; its upper opening is oblique. The arytenoid cartilage forms an inverted V-shape; the epiglottic cartilage is shaped as an elongate oval with a sharp apex and rounded, irregular border. The thyroid cartilage articulates with the hyoid bone. The vocal fold is oblique, with its dorsal end more caudal. The average mass of the horse's lungs is 6 kg, large compared with those of other mammals. Total lung capacity averages 42.1 liters, with average reserve and tidal volumes of 9.1 and 7.5 liters, respectively. The horse can draw in as much as 9.0 liters of air per inspiration. The main bronchus divides internally (Frandsen, 1974).

The testis and epididymis of the horse are oval in shape and weigh 200 – 300 g. The head and body of the epididymis is attached to the border of the testis; the tail forms only a slight prominence caudally (White, 1976). The horse's ovaries are bean-shaped and average 51.6 by 28.5 by 32.7 mm. During the breeding season, their average mass is 60 – 70 g, with one larger than the other. The broad ligament attaches in the sublumbar region (Ginther, 1979). The body of the uterus is about 117 mm long; the two horns are each about 38 mm long. The cervix, of uniform diameter and relatively straight, averages 53.1 mm long, and projects into the vagina 2.5 – 5 cm, terminating bluntly. The round ligament is short. Internally the uterus is lined with smooth, folded mucous membrane (Ginther, 1979).

The average mass of the heart in the horse is about 3.4 kg but varies from 0.6 to 0.7% of body mass. The hemizygous vein does not reach the heart; an os cordis is absent. The brachiocephalic trunk is soft and oily (Campbell and Lasley, 1975).

Mean mass of the horse brain is 650 g; frontal and occipital poles are almost equal in size; gyri are extensive. The pons is prominent and the cerebellum is not overlapped much by the cerebrum. The hypophysis is ovoid and large, and the olfactory region is relatively large, with large bulbs and striae. The posterior colliculi are very small in comparison to the anterior colliculi. The endocranial capacity of a horse with a brain mass of 587 g was 626 cc; in *E. caballus* the brain fills about 93.7% of the osseous brain capacity. Average sizes (in mm) for parts of the brain are, cerebral height, 50.0; cerebral breadth, 66.25; anterior lobe, 20.25; medial lobe, 26.25; posterior lobe, 27.70; and total brain length, 176.25 (Edinger, 1948, 1950).

The extent to which the optic nerve fibers cross over to the ipsilateral half of the brain in mammals is dependent on the degree to which the visual fields of the left and right eyes overlap centrally. In the horse, the overlap is restricted to a small nasal area in each field; about 90% of the fibers cross (Phillis,

1976). The main input to the somatosensory cortex in the horse comes from the ipsilateral upper and lower lips, with a major input from the contralateral nostril. The nostril and upper lip are the chief parts of the body employed for tactile exploration. *E. caballus* possesses vibrissae (“whiskers”) supplied with sensitive tactile receptors on the nostrils and muzzle, as well as over the eyes and on the cheeks. Because the objects touched by the nostril come into the visual field and often are recognized by sight rather than by smell, it is probably advantageous to have their cortical representation on the same side as that for visual information. Information from the vibrissae also travels to the brain via this pathway (Phillis, 1976).

Endocranial casts show that the pituitary gland in *Equus* is much larger than in its fossil ancestors. Pituitary hormone mediates not only body growth in general, but also the size of certain body parts (Edinger, 1948).

The skull and teeth of the horse are adapted for grazing (Figs. 8A, 8B, 8C, 9). The maxilla and mandible are long and the point at which the greatest crushing strength can be exerted lies far forward and below the point of articulation. The cranium is small, whereas the orbit is large with a complete postorbital bar. The premolar and molar teeth are hypsodont and the roots of the maxillary teeth extend far into the skull (Fig. 9). The maxilla of the horse is displaced forward of the orbit so that the roots of the teeth do not impinge upon it (Fig. 4). The jaw is likewise deepened in order to accommodate tall teeth (Fig. 7). The three pairs of incisors are single-rooted and blunt (Fig. 8B). Placed at the extreme anterior limit of both upper and lower jaws, they function to grasp forage, which is then torn off against the teeth by head motions. A long diastema is present in both upper and lower jaws (Fig. 4, 7). In males, blunt, conical canines are present in the diastema but are small relative to the skull and mouth (Fig. 8B).

The dental formula is incisors 3/3, canines 0-1/0-1, premolars 3-4/3-4, molars 3/3, total 36-44. The tiny P1 or p1, when present, is called a “wolf tooth.” Other premolars are large, square, and molariform. Morphologically, the cheekteeth are lophodont, showing complex loops and plications of the hypsodont enamel, which change with wear. Dentine and cementum alternate with enamel in the cheekteeth to form durable, self-sharpening surfaces. The cheek teeth also are surrounded and supported externally by cementum (Gobaux and Barrier, 1892)(Fig. 8C).

Sixty to seventy percent of a horse’s weight is carried on the forelimbs when the animal is standing at rest; this accounts for the forelimbs being larger than the hind limbs. The postcranial skeleton as a whole shows proportions typical of ungulates (Fig. 11), in which proximal limb elements are short and distal limb elements are long (Gromova, 1959); McMahon (1975) compared limb elements of *Equus* with other unguligrade quadrupeds. The appendicular skeleton is designed primarily for fore-aft movement; the ribcage is laterally flattened, and all distal joint surfaces are ridged or grooved to inhibit or completely prevent lateral and rotatory movement. The postcranial skeleton shows retention of some primitive characteristics, such as the simple astragalus characteristic of Perissodactyla with a single, deep oblique trochlea, and retention of a large third trochanter on the femoral shaft (Fig. 11). Specialized features include fusion of the distal shafts of the radius and ulna and of tibia and fibula; complete loss of digits I and V and loss of phalanges of digits II and IV from all four limbs, leaving only metapodials III (Carter, 1984); loss of clavicle, as in other cursorial mammals; “cervicalization” of morphology of the first thoracic vertebra; and presence of intertransverse joint surfaces on the last several lumbar vertebrae and on the anterior sacrum (Bennett, 1992c)(Fig. 16). The vertebral formula is 7 cervicals, 18-19 thoracics, 5-6 lumbar, 5-6 fused sacrals, and 18 caudals, total 53-56 (Heptner et al, 1961).

Section VIII: Function

The average resting respiratory rate is 8-15 breaths/min (Gillespie, 1976). When moving rapidly (trot or faster), horses take one breath per stride, timed with flexion and extension of the back (Alexander, 1989). The basal metabolic rate of horses is intermediate among mammals, with oxygen consumption at 110 cubic millimeters per nanogram per hour (Egan, 1976). The normal rectal temperature of the adult horse is 100°F (range, 99-101 [37-38°C]); in a day-old foal, it averages 102°F [39°C] (Willoughby, 1974). The horse lacks a carotid rete, thus it does not pant to keep brain temperatures within an acceptable range. Instead, this species relies on apocrine sweat glands, with activation through circulating adrenalin (Jell, 1976).

The length of time food remains in the stomach varies with the type and consistency of food. Horses require a full day's fast to empty a full stomach, although hunger contractions of the stomach may begin as early as five hours after eating, when the stomach still contains some food. Digestion of food by means of microorganisms is of great importance; therefore most digestive activity occurs in the cecum (Campbell and Lasley, 1975).

Because the horse possesses few (20-40%) long loops of Henle in the kidneys, it is less able to concentrate urine than any congener; under extreme hydropenia it can concentrate urine only to about 2.5 osmol/liter. The horse consequently requires a reliable supply of fresh water; water turnover is 250-350 milliliters per millimole per hour (MacFarlane, 1976). Blood volume averages 9.7% of body mass; normal blood pressure is 80/50 by sphygmomanometer and normal resting heart rate averages 39 beats/minute (range, 32-44; Campbell and Lasley, 1975).

The horse's adaptations for locomotion are many and unique. There is no bony connection between the forelimbs and trunk, but the serratus ventralis and pectoral muscles are arranged to form a sling in which the thorax is suspended. [The clavicle "collarbone" is absent; Fig. 11]. This permits the horse to bound and leap without danger of fracture (Bennett, 1992c). The biceps brachii muscle in the horse is tendinous in its center portion throughout its length from the scapula to the proximal end of the radius. When the elbow joint is extended by the triceps muscle, the radius rotates downward, pulling on the tendinous biceps. This pull acts to automatically extend the shoulder joint whenever the elbow joint is extended (Frandsen, 1974).

An intermediate tubercle occurs between the greater and lesser tubercles on the proximal end of the humerus, across which the biceps runs from the scapula. This derived state confers an increased mechanical advantage at the shoulder joint, by as much as 28% in the horse (Hermanson and McFadden, 1992). Posture is maintained mechanically in both fore and hind limbs by such check and stay systems consisting of tensionally coadjusted pairs of elastic tissues (Fig. 14). These not only maintain posture while standing with little muscular effort, but act automatically to coordinate flexion and extension of joints over which the ligaments and tendons pass (Sack, 1989). The ligaments of the stay system, together with the proximal sesamoid bones, form a sling across the caudal surface of the metacarpophalangeal (fetlock) joint which helps prevent excessive hyperextension (Frandsen, 1974; Thomason, 1992). Structures making up the forelimb stay apparatus include tendons of superficial and deep digital muscles, suspensory ligament ("spring ligament", the modified m. interosseous of digit III); X-shaped intersemoidean ligament connecting the two proximal digital sesamoids, and parallel distal sesamoidean ligaments of the same joint (Stashak, 1987; Thomason, 1992). The check apparatus of the

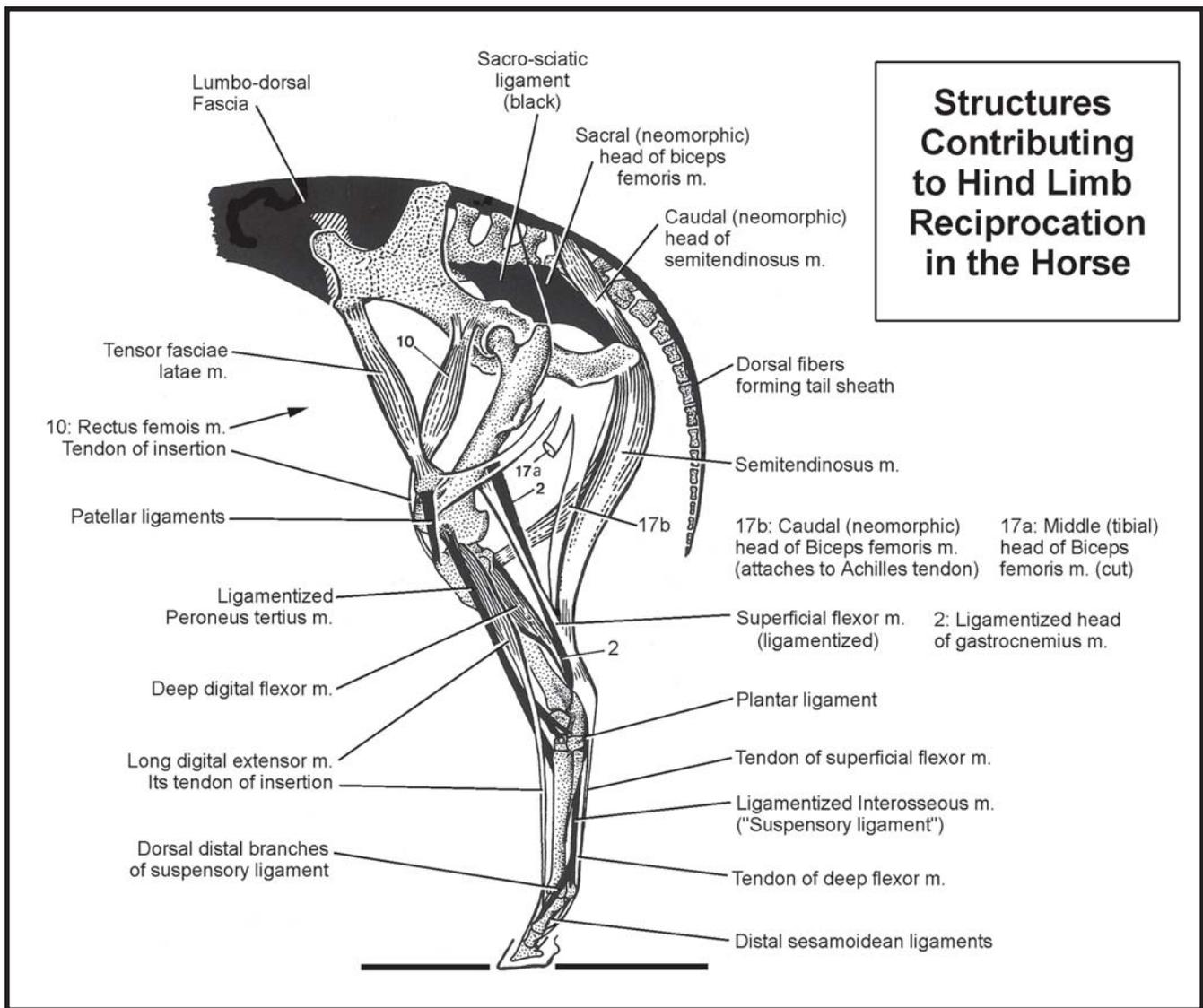


Fig. 14. Structures contributing to hindlimb reciprocation in the horse. Several of the hindlimb muscles have partially or wholly lost their contractile fibers and exist as elastic "ligaments". The existence of reciprocating apparatus in both the fore and hind limbs saves the horse significant caloric expenditure.

forelimb extends from the scapula to the distal phalanx, and with the exception of the long head of the triceps muscle, all structures composing it are tendons of muscles originating on the back of the forelimb, or are more distally situated muscles which have become completely tendinous in the course of evolution of this species (Frandsen, 1974; Stashak, 1987).

The hind limb of the horse possesses a similar stay apparatus (Fig. 14). The peroneus tertius, superficial digital flexor, plantaris and interosseous, all almost entirely tendinous, are important parts of this system (Dimery et al., 1986). These muscles, in combination with the distal end of the femur and the tarsus (Badoux, 1987), form a parallelogram, within which the knee ("stifle") joint and ankle ("hock") joint act as pivots. Their arrangement and balanced tension forces the hock joint to open and close in coordination with the stifle (Sack, 1989; Stashak, 1987).

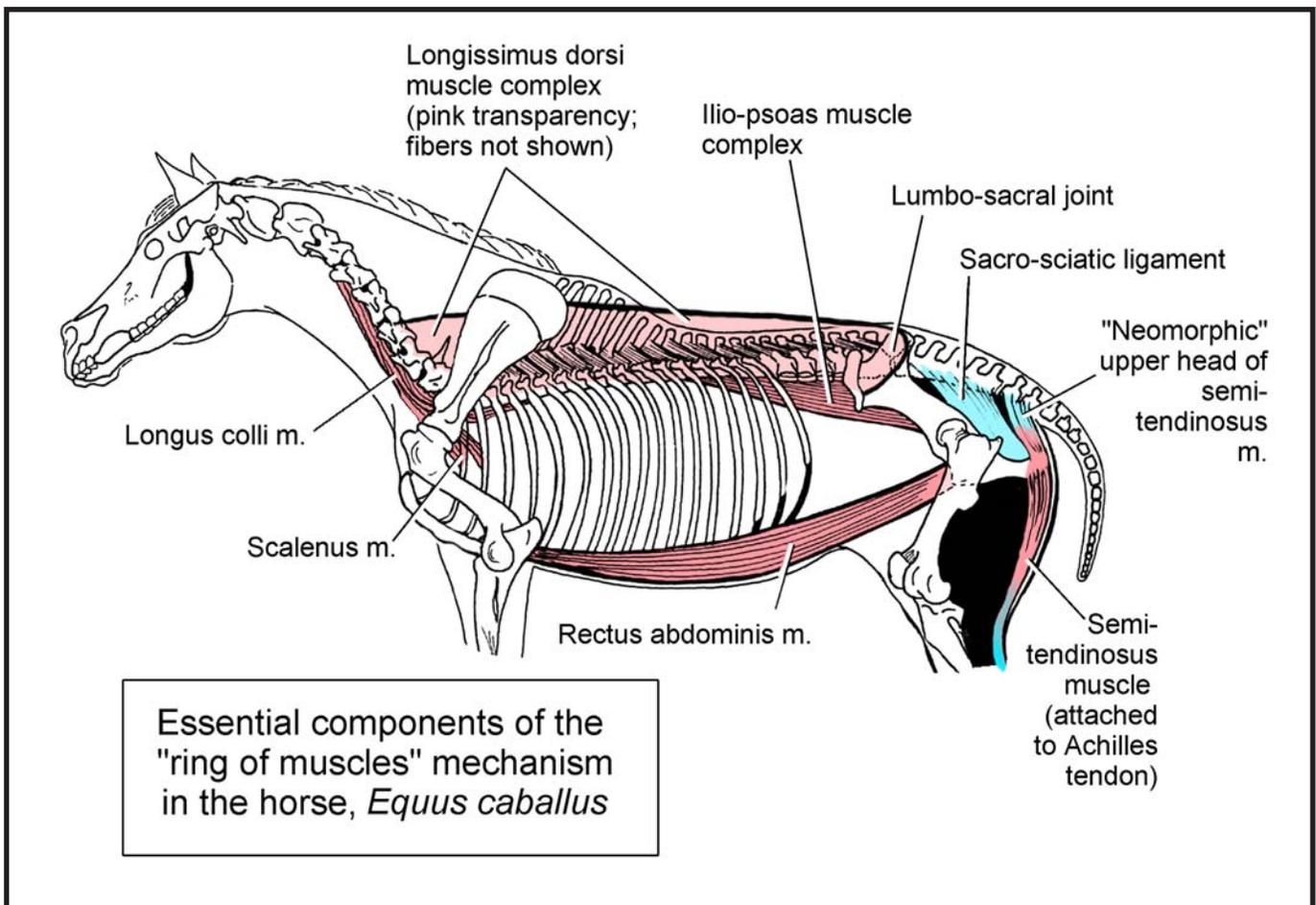
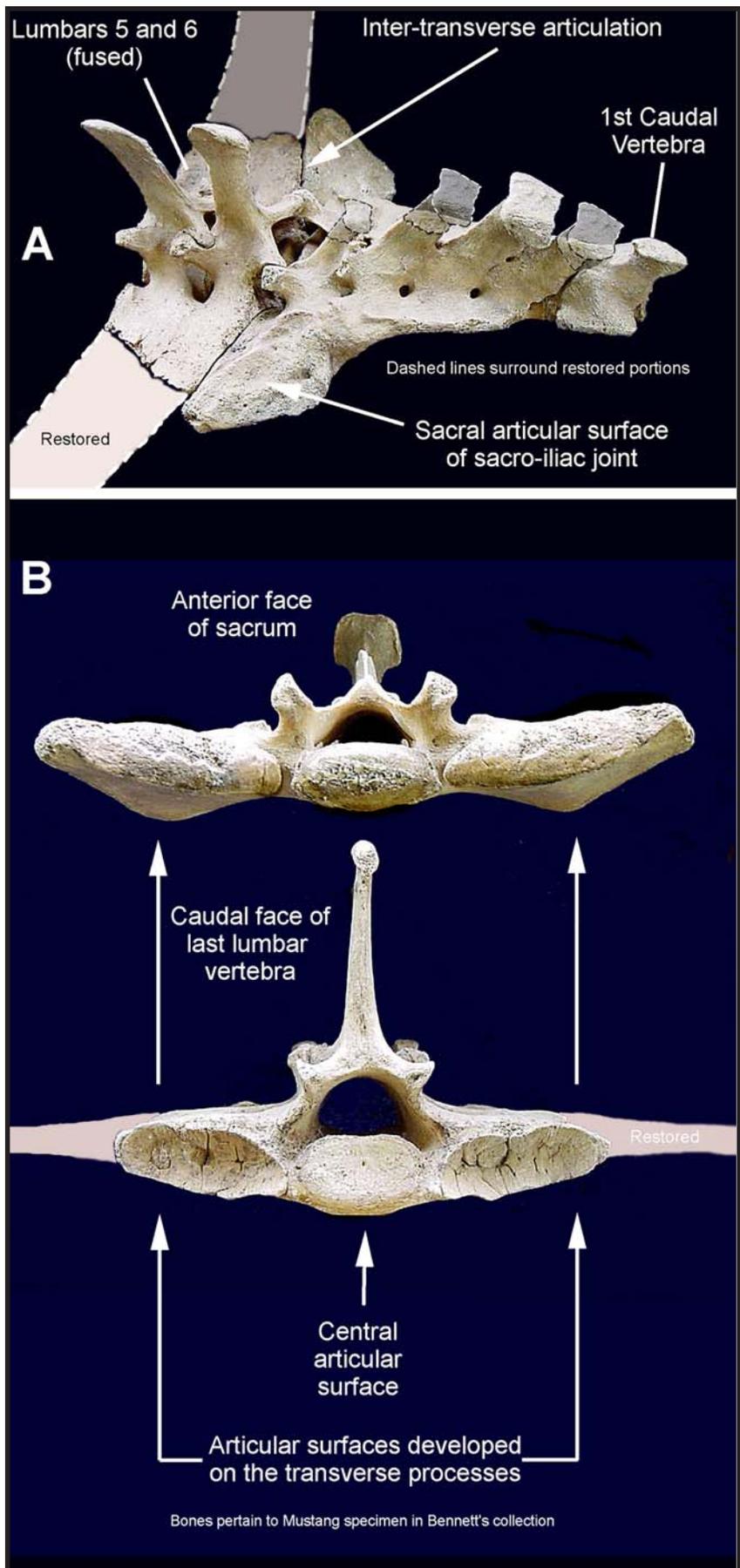


Fig. 15. Essential muscular, ligamentous, and bony components of the “ring of muscles” locomotory mechanism in the horse, *Equus caballus*.

The horse also possesses an elastic mechanism which works in coordination with uniquely adapted joints in the axial skeleton for the regulation of longitudinal flexion and extension of the torso and the concomitant coordination of limb and torso movements. This dorsal ligament system is unique to the horse. The “ring of muscles” (Fig. 15) incorporates the dorsal ligament system with the major appositional muscles of the torso (longissimus dorsi, rectus abdominis, iliopsoas, scalenus, longus colli) to support basculed (correctly balanced) posture of the back, and it is responsible for the undulating movement of the axial skeleton characteristic of the galloping horse (Bennett, 1992c). The horse possesses a relatively long neck; the cervical vertebrae form an “S” shape, with more posterior vertebrae diverging from the dorsal neck surface in the living animal. The posterior part of the “crest” of the neck thus lies far above the caudal cervical vertebrae and is supported subdermally by the nuchal ligament which originates in the dorsal basioccipital region and passes caudad over the ridge formed by prolongation of the neural spines of the first 6-8 thoracic vertebrae (the “withers”). Branches of the ligament insert on each vertebra before its longest fibers finally insert in the center of the horse’s back at or near the thoracolumbar junction. The ligament’s elastic properties permit the head and neck to be supported and balanced in a variety of postures with a minimum of muscular effort (Dimery et al., 1985). Withers, present in equids only since the middle Tertiary, act as a fulcrum for this portion of the dorsal ligament system and function to ensure that when the horse lowers its head or extends it forward, the center of the back is raised (Bennett, 1992c).

Fig. 16. The lumbo-sacral articulation in the horse. A, oblique dorsolateral view of lumbar 5-6, sacrum, and first caudal vertebra. B, anterior view of sacrum (above) and posterior view of lumbar 6 (below).

The lumbo-sacral articulation in *Equus caballus* is unique in both morphology and function. These photographs highlight the inter-transverse articulations which inhibit lateral flexion of the vertebral chain in the anterior lumbar and prevent it in the posterior lumbar and between the posterior lumbar and sacrum. This morphology promotes the species' characteristic "loin coiling" facilitating normal locomotion.



The lumbosacral and last intralumbar joints of horses possess articulating surface on the transverse processes which promote longitudinal flexion but inhibit lateral flexion. Because of this, the joint governing hind limb protraction in horses is the lumbosacral, rather than the coxofemoral joint (Fig. 14). The thick, elastic lumbodorsal fascia have cognate functional importance (Alexander, 1988). The horse's tarsal joint (hock) is connected to the center of its back by a continuous system of elastic structures, the most anterodorsal of which pass over the lumbosacral joint (Fig. 14). This system consists of the ligamentum dorsi and lumbodorsal fascia where they span the thoracic, lumbar, and sacral vertebrae, the anterior fascial part of the gluteus medius muscle, the sacro-sciatic ligament, the semitendinosus and semimembranosus muscles, the biceps femoris muscle, and the Achilles tendon of the gastrocnemius muscle. Each of these muscles is uniquely modified in the horse: the semitendinosus and semimembranosus muscles take their origin high up on the sacrum; the semitendinosus muscle inserts on the tibia and invests the Achilles tendon; and the biceps femoris possesses not only femoral and tibial heads but also invests the Achilles tendon. The net effect of this system is to cause the pelvis and sacrum to passively

rotate downward at the lumbosacral joint as – and to the extent that – the stifles are flexed and the hocks are brought forward beneath the belly. The hind limb can be reciprocally affected also, should the horse strongly contract the rectus abdominis or iliopsoas muscles. This contraction actively pulls the pelvis

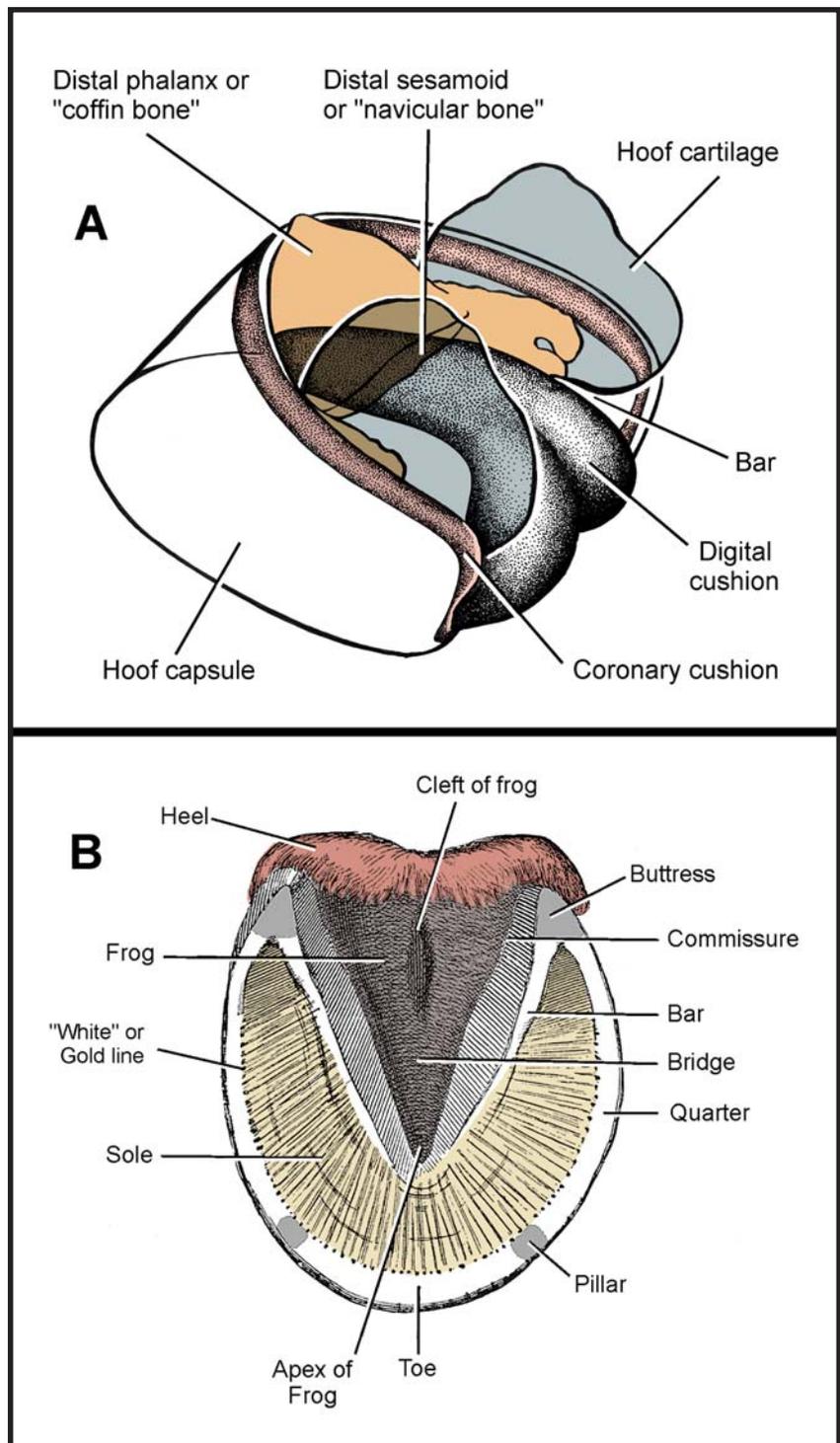


Fig. 17. Hoof structures of the horse. A, oblique dorso-posterior cutaway view. B, volar view. The hooves of *E. caballus* are rounder in shape than those of congeners.

down and forward and flexes the lumbosacral and stifle joints. This in turn affects hind stride length, overall body balance, and the nature of individual bone rotations within each hind limb. Mediation and regulation of back flexions are effected by the positionally placed longissimus dorsi muscle, which in the horse exceeds the size and mass even of the propulsive muscles (Fig. 15; Sack, 1989).

The horse's hoof wall is an insensitive cornified layer of epidermis (keratin) covering the distal end of the digit (Fig. 17). In a galloping horse, the vertical forces acting on each foot may be very great, and magnified on uneven substrates, but "hoof keratin [tolerates] operating strains in any direction [withstanding] ... unpredictable loading ... when the hoof contacts irregular substrata" (Thomason et al., 1992:145). Between the distal phalanx and the cornified hoof lies a highly vascular modified dermis called the corium. Where the outer margin of this subunguis meets the inner margin of the hoof wall, a narrow band called the lamellar junction or gold line (sometimes erroneously called "white line") appears. The elastic horny pad of the mid-sole ("frog") is separated from the distal phalanx, the distal or "navicular" sesamoid, and the insertion of the deep digital flexor tendon by the digital pad, a thick wedge of fibro-fatty subcutaneous tissue. Rhomboid collateral cartilages also are present, attached to the angles of the distal phalanx (Butler, 1974).

Distal circulation in the horse is unique among living ungulates. Because there are no large muscle masses below the carpus and tarsus in the horse, a mechanical blood pumping mechanism is necessary to prevent the feet from freezing in cold weather, as well as for normal circulation. Located on both sides of each lateral cartilage and in the vascular corium are large venous plexi. The compression of these veins by the plantar pad and hoof against the lateral cartilages and distal phalanx acts to pump blood up the leg and back to the heart. Compression of the plexi also acts as a valve to contain blood in the vessels of the foot below the plexi and produce an hydraulic cushion which further serves to dissipate concussion. This action also creates a negative pressure which causes the blood to refill the plexi when the foot is raised and the compressed veins open (Phillis, 1976; Pollitt, 1995; Bowker et al., 1993, 1995, 1997, 1998, 2001).

Horses possess five natural gaits: walk, amble, trot, canter, and gallop, in sequence of increasing speed (Bennett, 1992c; Hildebrand, 1965; Muybridge, 1887). The walk is a slow, flat-footed gait in which individual footfalls (beats) are separated by equally long intervals, and in which there is no period of suspension (when all four feet are off the ground). The step sequence is left hind, left fore, right hind, right fore; the gait proceeds at 6-10 km/h (4-6 mph). The amble is defined exactly as the walk but is [usually] executed with longer steps and greater animation and energy expenditure. When executing this gait, horses are likely to stiffen the torso relative to its condition at the walk. In that circumstance, the gait ceases to be isochronal (Colantuono and DeMoya, 1994) and may either become "trotty" (beats two and three fall closer together than beats one and two) or "pacey" (beats one and two fall closer together than two and three). Executed over speeds of about 8 – 14 km/h (5-9 mph) [although speeds of more than 20 mph can be achieved], the amble is a more energy-efficient gait than the walk. Many but not all horses automatically shift to an amble when fatigued or when circumstances cause them to want to accelerate but prevent them from trotting (Hoyt and Taylor, 1981).

The pace and trot gaits lie at opposite ends of the spectrum of timing coordination. In the pace, unilateral legs work in unison, thereby producing only two beats. When executed with vigor, the two beats of the pace may bracket a brief period of suspension.

The trot is a moderately rapid gait executed over speeds from 6 to 19 km/h (4 to 12 mph). The contralateral pairs of legs work in unison. During the execution of a natural trot, the beats are separated by a period of suspension (Evans et al., 1982). The gait thus has two sounded and two unsounded beats.

The canter is a moderately rapid gait executed over speeds from 10 to 26 km/h (6 to 16 mph). One contralateral pair of legs works in unison, while the other pair is “decoupled.” The footfall order for a right lead canter is left hind, right hind and left fore simultaneously, and right fore. During the execution of a natural canter, a period of suspension follows the impact of the second forefoot, and the gait thus consists of three sounded plus one unsounded beat (Evans et al., 1982).

The gallop is a rapid to very rapid gait, which speeds measured at 26-56 km/h (16-35 mph), or more in an animal running for its life (Willoughby, 1974). Not only the first, but to a greater or lesser degree, the second diagonal pair of legs is “decoupled,” so that the footfall sequence for a right gallop is: left hind, right hind, left fore, right fore. A long period of suspension follows the impact of the second foreleg, but the beats are not evenly spaced; the interval of time separating the strikes of the right hind and left fore (the diagonal pair that would have been coupled had the horse been executing a right canter) is always at least slightly smaller than the other intervals between leg impacts. With increasing speed and stride length, horses change gait to minimize energy consumption (Hoyt and Taylor, 1981; McMahan, 1975), and at high speeds the elastic aponeurosis of the longissimus dorsi muscle, the main extensor of the back, saves energy by storing elastic strain energy (Alexander et al., 1985). MacFadden (1992) discussed evolution of form and function.

Section IX: Ontogeny and Reproduction

Male domestic horses are capable of breeding at any time during the year, but in the Northern Hemisphere there is a strong peak in sex drive and fertility from April to June (Ginther, 1979). During this season, the alpha male becomes very restless and energetic as he constantly rounds up and disciplines the herd, and prepares to defend it against other males (Waring, 1983). At this time the behavior known as flehmen becomes most evident. In this activity, the male sniffs the urine of mares, drawing his lips back and upwards while wrinkling his nostrils (Schäfer, 1974). The male sometimes thrusts his nose into the female’s urine stream and may stand up for up to 30 seconds in this posture. It has been theorized that flehmen brings into action Jacobson’s organ (Groves, 1974). Urine of the female in estrus contains much estrogen (as well as a variety of other sterols that appear to be metabolic products of the gonadotrophic hormones) that the rutting male is trying to detect (Faulkner and Pineda, 1975). Mountfort et al. (1994) provide details of reproductive endocrinology.

Puberty in females begins at 10-24 months of age (mean = 18). Horses are seasonally polyestrous. During the breeding season, the length of time from the beginning of one estrous period to the beginning of the next (diestrus) has been reported to vary between 7 and 124 days (Frandsen, 1974); however, the mean is 21 days (Ginther, 1979). The average length of the estrous period in the mare is 6.5 days (range, 4.5 – 8.9; Ginther, 1979), but there is wide variation. Ovulation is spontaneous, and usually occurs from 1 to 2 days before the end of estrus; thus fertility rises during estrus to a peak two days before the end of estrus, then falls off abruptly (Campbell and Lasley, 1975). The timing of copulation within the estrous period has a great influence on the chance of impregnation. Insemination just prior to ovulation in domestic horses has been found to be 86% successful; at the time of ovulation, 74% successful, and 2-10 hours after ovulation, 30% (Frandsen, 1974). The wild or feral male does not usually mount his own

daughters or other females that have grown up with his herd (Berger and Cunningham, 1987; Waring, 1983).

In the estrous female, mucous membranes of the labia, vagina, and cervix become more intensely pink, moist, and glistening; these signs pass off rapidly after ovulation (Ginther, 1979). A mare in estrus displays a characteristic pre-mating behavior, holding her tail stiffly to one side or out behind her, everting the vulvar labia (“winking”), squatting, urinating in short bursts (“squirting”), and displaying a “mating face” (Ginther, 1979; Schäfer, 1974). If not entirely ready to mate, she may refuse the male with ears laid back, shrill squeals, kicking, or striking (Ginther, 1979; Groves, 1974).

Gestation averages 335 days (standard deviation = 9.5). The recorded range for wild, feral, and domestic horses is 287 – 419 days

(Frandsen, 1974; Willoughby, 1974). Impregnation and birth may occur at any time between early spring and late autumn, but females impregnated during April-May in the Northern Hemisphere give birth during the following spring (March-April), just prior to the new rut (Asdell, 1964). At Askania Nova, Ukraine, 48% of the captive Przewalski horse herd gave birth in May, and 16% each in April and June; similarly, at Prague the captive herd gave birth to 17.5% of foals in April, 37.5% in May, and 20% in June. Limited observations on wild *E. c. przewalskii* indicate mating in August-September, and

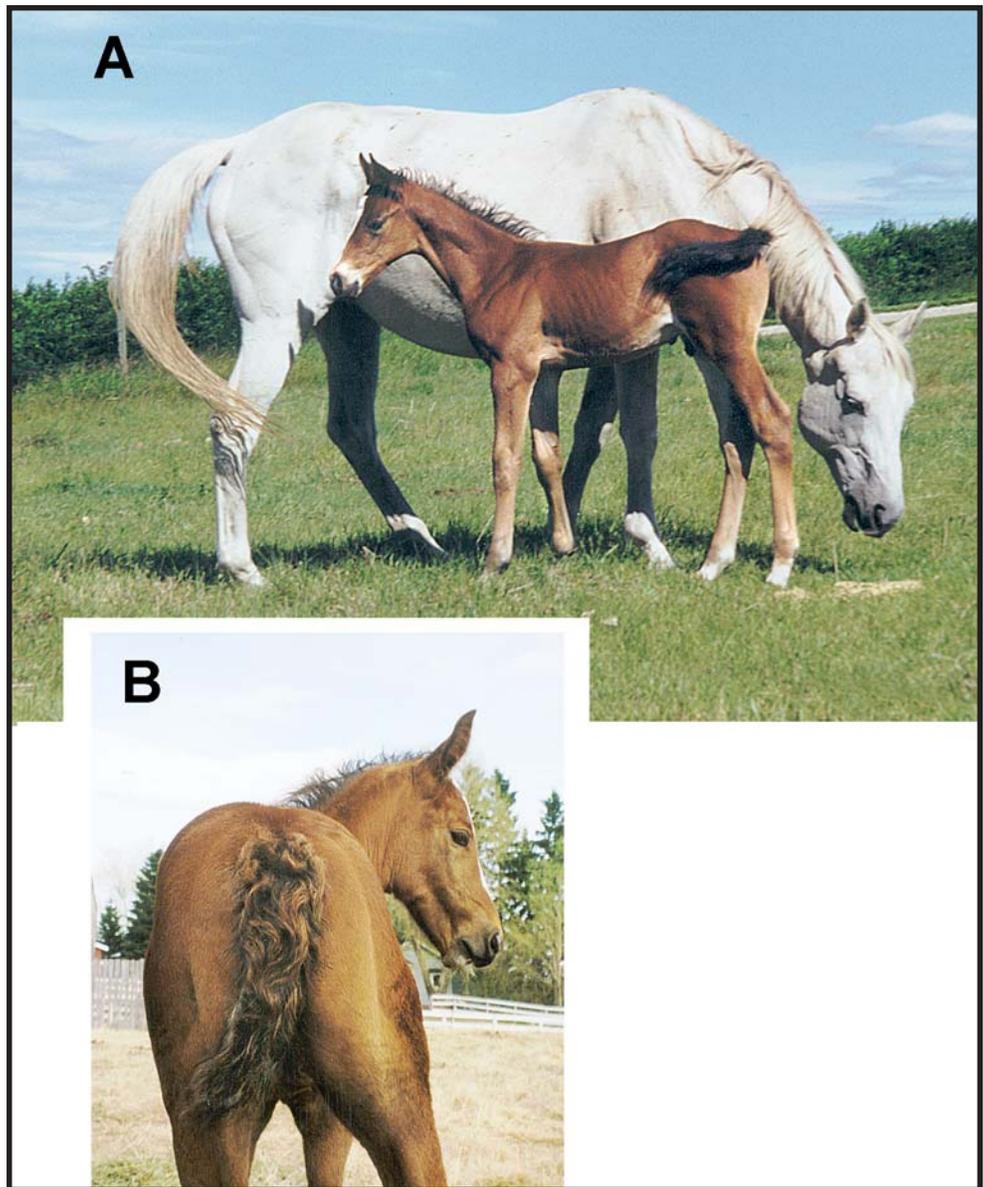


Fig. 18. Morphology of domestic mare and foals. Young juvenile horses have very fine, sparse manes; short, often curly tail hairs; ears relatively long in comparison to head length; and a bulging forehead. These characteristics are present in both domestic horses and *E. c. przewalskii*, but compare the height and relatively slight build of these month-old domestic foals to the Mongolian Wild Horses in Fig. 2. (Lesley Kerfoot photos).

parturition in May-July (Dobchin, 1970), suggesting that a late summer rut and late spring-early summer birth period may be advantageous in the harsher climate of Mongolia. However, in Ukrainia, breeding ends by late summer (Klimov, 1986b).

Normally, only one foal is produced per gestation. Rupture of more than one follicle per estrous period is observed in many domestic horse pregnancies, although the rate is lower in ponies, but twin foals are rare (1-2%), and one or both may be abnormally small or completely inviable. Only 14% of twins born to domestic mares survive to two weeks of age (Ginther, 1979). Males are carried about 9.5 days longer than females; twins generally are carried about 10 days less than singles (Asdell, 1964).

The mammary glands of the horse consist of one nipple on each side attached to one-half of the udder. Each nipple has two streak canals and two nipple cisterns, each of which is continuous with a separate gland cistern and its system of 2-4 ducts and alveoli. The udder and nipples of the female are covered with thin, fine hair as well as numerous sebaceous and sweat glands (Campbell and Lasley, 1975). Milk solids comprise 1.3% milk fat, 2.2% protein, 5.9% lactose, and 0.4% minerals. Passive transfer of immunity occurs by 36 hours postpartum (Campbell and Lasley, 1975).

The female gives birth in a quiet place, returning about 9 days later to the herd; birth occurs at night. As soon as the female returns to the herd (1-2 weeks after the birth; Klimov, 1986b), postpartum estrus is experienced, which averages 7-9 days in length in domestic females. It begins in more than 90% of domestic females 5-12 days after parturition. In autumn and winter, females usually are anestrus (Klimov, 1986b). When the neonate is born, the female removes the birth membranes with her teeth but does not eat them. Neonates are precocious and are born with a complete, fine pelage, and with ears and eyes open. Most neonates stand within an hour of birth, and can walk beside the female 4-5 hours after birth (Ensminger, 1969). At birth, the neonate has a relatively shorter neck, back and tail, smaller hooves and larger eyes and head than its adult counterpart (Willoughby, 1974).

Young nurse for brief periods (45-60 seconds; Waring, 1983). They grow rapidly and may begin to take solid food as early as 1 week of age. They remain very close to their mothers for the first month, following her, but in the second month they begin to forage, and are gradually weaned to solid food over a 2-year period (Boyd, 1988). Birth weight of wild neonates is 25-30 kg; domestic neonates (non-ponies) average 40 kg. This doubles in 4 weeks and then the animal grows with continually decreasing velocity until it reaches full maturity, at about age 5 years for females and 6-7 years for males (Willoughby, 1974). Epiphyses of the long bones fuse over the entire period from just prenatal (distal elements) to 4 years of age (proximal elements). Vertebral epiphyses do not fuse until the 5th year or later (Getty, 1975).

The order or eruption of the upper teeth is as follows (lower teeth erupt 0-6 months later): 0-1 weeks, deciduous incisor 1 ("central"); 0-2 weeks, deciduous canine (if present) and deciduous premolars 2-4; 4-6 weeks, deciduous second incisor ("intermediate"); 5-6 months, first premolar ("wolf tooth", if present); 6-9 months, deciduous third incisor ("laterals"); 10-12 months, molar 1; 2 years, molar 2; 2.5 years, first permanent incisor ("central"); 3 years, premolar 3; 3.5-4 years, incisor 2 ("intermediate"), premolar 4, and molar 3; 4-5 years, incisor 3 ("lateral") and C (if present; Getty, 1975).

The long facial skull and the large teeth of *Equus* are correlated with a great increase in volume, during the later Tertiary period, of the anterior pituitary lobe. The brain of the horse attains all adult



Fig. 19A. Domestic horses derive from formerly wild subspecies of *Equus caballus*. This Belgian mare derives almost exclusively from *E. c. caballus*. Note the bulky body, short back, deep wide chest, deep rather heavy head, small ear relative to head length, distally placed nostrils, large round feet, general tendency to hairiness with “feathers” on the distal limbs and the woolly quality of the pelage, both body coat and mane and tail. (Deb Bennett photo). See Figs. 19B and 19C for comparison

characteristics, except size, well before birth. Adult brain size is attained before the horse is 2 years old, whereas total body size will still increase by one-fifth to one-fourth, and body mass by at least one-third (Edinger, 1948).

Young female horses may come into estrus for the first time at about 11 months of age, but few domestic females are fertile until the summer of their second year, and neither wild nor domestic females are usually capable of carrying a fetus to term without debilitation until the age of 4 years, when they attain full size (Ginther, 1979; Groves, 1974). Male horses are not fully fertile until their 6th year (Pickett, et al., 1970), although young males from about the 16th month of life onward are capable of attaining and maintaining an erection and of achieving intromission. Significant semen production begins at about age 2 years (Ensminger, 1969), when single testis weight in most individuals reaches 90g (Pickett et al., 1970). Most males breed for the first time in their 5th year (Groves, 1974). Half of all male domestic horses which have single testis mass of greater than or equal to 30 g are fertile; 100% of domestic males are fertile with single testis mass of 90g (Asdell, 1964). Spermatozoa can live only 6 hours in the vagina but up to 12 hours in the uterus (Frandsen, 1974); a single observation in a recently castrated male shows that sperm may remain alive in the male tract for up to 3 weeks (Pickett, et al., 1970). The



Fig. 19B. Domestic horses derive from formerly wild subspecies of *Equus caballus*. This Warmblood gelding is a cross between Thoroughbred and Warmblood ancestors, but markedly demonstrates many Warmblood characteristics present in *E. c. mosbachensis*. Note the long torso, narrow body, flat neck, long stout limbs, long ears, long head with arched facial profile, eye small and placed high in the head. This animal is paradigmatic of all that which is morphologically primitive in the species (Deb Bennett photo).

spermatozoon has a characteristically curved tip and lacks a head cap. The oldest recorded breeding age in a Przewalski mare is 24 years, the same as for domestic females; males may breed up to the age of 36 years (Groves, 1974; Mountfort et al., 1994).

Section X: Ecology

The large, round hoofs, hairy fetlocks, small ears, compact body shape, and thick pelage of the wild Przewalski horse, as well as the fossil distribution of its ecomorphotype, bespeak adaptations for cold climate in tundra and steppe and for marshy ground, as does the entire Pleistocene distribution of the form (Bennett, 1992b). For these reasons, the last known habitat of the wild horse, the high semidesert steppes of Mongolia and Dzhungaria (Fig. 4), is an example of survival in a refugium to which it was not well adapted (Dierendonck and DeVries, 1996; Sokolov and Orlov, 1986). This steppe lies between 900 and 1,600 m above sea level. It is stony and sandy country on the borders of the Gobi Desert, dotted with tamarisk (*Tamarix*), sagebrush (*Artemisia*), and saxaul (*Haloxylon ammodendron*; Groves, 1974).



Fig. 19C. Domestic horses derive from formerly wild subspecies of *Equus caballus*. This Arabian mare derives almost wholly from the Afro-Turkic subspecies, *E. c. pumpelli*. The overall size is less than in 19A or 19B, and the build more gracile. The animal is markedly less hirsute than 19A and shows negative, rather than positive cranial flexion. The eye is larger and the ear is longer relative to head length than in either 19A or 19B, and the frontal sinuses are inflated — characteristics seen in other mammalian subspecies adapted to xeric climates (Deb Bennett photo).

Saxaul is the most characteristic plant, and may grow in bushes 250 cm high. Although it is shrubby and dry looking, it has a juicy bark. There are also tussock grasses, some up to 1.8m high (Groves, 1974). Detailed studies of the food habits of wild *E. c. przewalskii* have not been made, but Dobchin (1970) lists the following species as potential food items: *Haloxylon ammodendron*, *Artemisia xerophytica*, *Nannophyton erinbaceum*, *Carex stenophylloides*, *Lasiagrostis splendens*, *Tamarix ramosissima*, *Kalidium gracile*, *Stipa gobia*, *Cynomorium songaricum*, *Anabasis brevifolia*, *Caragana spinosa*, *Allium polyrhizum*, *Oxytropia aciphylla*, *Zygophyllum pterocarpum*, and *Iris bungei*.

In summer the steppe is dry and hot; in winter, cold and bleak, with frequent snowstorms. Throughout the year horses had to go without water for periods of up to four days; in summer, they dug holes with

their hooves, drinking the brackish groundwater. They usually visited waterholes at night (Dobchin, 1970) and grazed most often in late evening and early morning to escape the heat of the summer sun (Klimov, 1986a). Early-morning feeding also provided dewfall moisture (Willoughby, 1974). During midday, they stood in places sheltered from the wind, or on hills where they avoided biting flies (Dobchin, 1970). While feeding, or in flight after disturbance, wild horses usually moved against the wind. In the late spring – early summer period, when vegetation is relatively lush, Mongolian horses often went far from water sources and apparently could survive for longer times without access to free water (Dobchin, 1970). Seasonal movements were dictated by precipitation patterns (Klimov, 1986a).

The tarpan (*E. c. ferus*) seems to have inhabited both steppe and open forest environments (Groves, 1974). In Ukraine and eastern Russia, wild horses preferred steppes in proximity to lakes, and drainage projects associated with agriculture contributed to the decline of wild horses there (Heptner et al., 1961). In northwestern Europe, wild horses inhabited forest, swamp, meadow, and tundra; in central and southern Europe, forest edge, woodland, montane valleys, and marsh (Lydekker, 1912); and in North Africa and the Near and Middle East, savanna, steppe, and semidesert environments (Vereschagin, 1959); this subspecies (*algericus*) was the most xeric-adapted, with relatively longer, slenderer limbs; shorter, finer pelage; larger frontal sinuses; narrower, harder hoofs; and longer ears. Several ancient island populations of *caballus* also are known, which are characterized by small size (Shetland and Exmoor ponies, Bennett, 1992b).

In domestic horses, sex ratio at birth is essentially 1:1 (Berger, 1983; Waring, 1983).

At least some wild horse subspecies were at one time migratory, as demanded by the vicissitudes of climate in their original range, moving to lower latitudes during winter and retreating northward during summer (Heptner et al., 1961). In Mongolia, regular migrations between summer range in the Gobi, and winter range on south slopes of adjacent mountain ranges, have been observed (Dobchin, 1970). Predators on the last known Przewalski horse population are not described, but wolves inhabited their former range and are presumed to have preyed at least upon the young and sick. Wolves, coyotes (Berger, 1985b), and mountain lions (Turner et al., 1992) are major predators for North American feral horses. In interspecific interactions with other ungulates, these horses were dominant in 95% of encounters (Berger, 1985a).

Infectious diseases of horses are known to be caused by so many kinds of microorganisms and parasites that they cannot be enumerated here by species (Anonymous, 1981; Naviaux, 1985). Maximum recorded age at death for Przewalski horses is 36 years; in domestic horses it is 61 years (Willoughby, 1974).

Section XI: Behavior.

The basic wild horse herd usually consists of an alpha male, who remains close by in the breeding season, and five or six unrelated females with young of different ages, and groups of bachelor or solitary males (Klimov, 1986a; Waring, 1983). Differences in herd structure (Berger, 1986; Ebhardt, 1962; Schaffer, 1974) may stem from the multiple origins of the domestic horse (Ebhardt, 1958; Trumler, 1961; Zeeb, 1959) and are influenced by habitat structure and food availability (Rubenstein, 1986). The herd is cohesive and moves in single file, normally with the alpha male in the rear, but in the lead when there is threat of danger ahead. When the alpha male snorts an alarm, the herd flees in single file with

young toward the center; the alpha male keeps to the side of the apparent danger. A frightened herd may flee up to 19-12 km. If the herd is threatened by a predator, the alpha male may attack it, springing forward and using teeth and hooves (Dobroruka, 1961).

Normally males remain somewhat apart from the rest of the herd, 8-20 m or more away. Signals are transmitted by body movements and vocalizations. When rounding up females, males slink around their herd with ears laid back and head lowered into a threatening position, and chase, bite, and kick females, while females generally kick back at males (Ensminger, 1969; Schäfer, 1974). In captive populations kept in small enclosures, males may sometimes kill females by biting (Dobroruka, 1961).

When approaching a food source, females with young go first, followed by older juveniles, then single females. Alpha males may eat or drink at any time, the rest of the herd temporarily yielding. Herd feeding order reflects positions in the herd hierarchy, which depend on sex, age, and individual variations such as size and pugnacity. In general, males dominate females and adult animals dominate juveniles of both sexes; females with young dominate infertile females (Dobroruka, 1961; Ensminger, 1969). The dominant female also seems to have an important role in determining the time and direction of daily movement. Many of the behaviors of other herd members are directed to her, not to the alpha male, who is not a herd member in the fullest sense (Berger, 1986; Dobroruka, 1961; Schäfer, 1974; Waring, 1983).

Females defend young by kicking at potential aggressors with hind feet. Kicking with the hind feet may be used for defense or offense, or sometimes by a female to discipline a rambunctious offspring. It has been asserted that striking with the forefeet is almost exclusively confined to fighting among males or between males and sexually unreceptive females (Dobroruka, 1961), but this is untrue (Berger, in litt). Herd hierarchy is usually reinforced by biting, kicking, and threat and submission gestures and expressions (Ensminger, 1969; Schäfer, 1974).

Horses have many facial expressions which convey social meaning. A horse may express a positive reaction by opening its mouth to expose the incisors and gums, while keeping the ears directed upward and forward. Aggression is expressed in the same way, but with the ears laid flat and the nostrils compressed. Submissive facial expressions may be shown by young horses in response to threat gestures of an older animal. The submissive animal opens its mouth slightly and makes nibbling and smacking movements with its tongue and jaws, without actually bringing the upper and lower incisors into contact. The corners of the mouth are drawn down and back, and the ears turned laterally from the sides of the head, with the openings directed downward. When the young horse assumes this expression, the adult ceases hostilities.

The facial expression of the sexually receptive female is a modified form of this expression. Another kind of submissive behavior, which occurs at the end of a fight between males or females, consists of the winning animal laying its head on the loser's rump. If the latter permits this, it is a sign of surrender, and hostilities cease. This behavior may be related to a mating behavior wherein the male, prior to mounting, lays his head on the female's rump. This behavior, also observed in other species of *Equus*, may be analogous to presentation of the hindquarters, a gesture of appeasement seen in primates.

Fear is expressed through profuse sweating, foaming, shivering, and rolling of the eyes. Horses twitch their tails rapidly when worried or irritated; they may also stamp their front feet. Expectation of either



Fig. 20. An adult female Przewalski mare photographed during the autumn season at the Monarto Game Preserve outside Adelaide, Australia (Deb Bennett photo). Note the characteristic dun coloration, erect mane, slightly convex facial profile, and broad muzzle.



Fig. 21. Przewalski stallion (second from left) has a stouter build, heavier head, and crestier neck than any mare in his harem. Photographed at Monarto Game Preserve, April, 2008 (Deb Bennett photo).

pleasurable (grooming, eating, release from constraint) or painful sensations (being whipped or kicked, or having a painful bit in its mouth) is expressed by prolonging the semi-prehensile upper lip into a “point” (Schäfer, 1974).

Both wild and domestic horses neigh, vocalizations which can be interpreted as a wish for, or expectation of, food, water, or the company of other horses (Willoughby, 1974). A rutting male utters a laugh-like or “giggling” neigh ending in a grunt towards a female in estrus, or may trumpet, scream, or grunt toward a rival male separated from him by a fence; he may paw or stamp the ground or engage in “passage” (highly cadenced trot gait produced by excited horses of either sex). A female squeals if she refuses the male or when she defends her offspring from an enemy, and as she does this her ears are laid back and her tail tucked in. Different characteristic body movements and facial expressions, especially as regards display of the canines, are known to accompany vocalizations interpreted as being for different purposes (Dobroruka, 1961; Schäfer, 1974).

The most basic form of autogrooming is a simple flicking of the skin by specialized subcutaneous musculature. To remove irritating insects or water, the horse stands with legs apart and neck stretched forward, shaking the body. Horses also make use of a sudden flick of the head, tail, or hind foot (Keiper and Berger, 1982). They may rub the face and eyes against the legs or use the hind foot to scratch the head and ears. The head and neck also may be rubbed against trees and the rump may be scratched on a fencepost or tree stump. Juveniles scratch their backs against their mother’s belly. Both wild and domestic horses roll in dust, manure, or mud. Adults rise with the forelegs first, although young may rise with the hind legs first as do deer and cattle (Schäfer, 1974; Waring, 1983).

Herd cohesiveness is reinforced by mutual or allogrooming. Biting is the most highly developed form of mutual grooming, although a horse may sometimes bite its own body and legs. [To initiate grooming], one horse approaches another with the “invitation face,” mouth closed and upper lip pulled slightly forward. When engaged in mutual grooming, the two horses stand counterparallel, and each nips at the other’s back and flanks, pulling out loose hairs. This activity is most often seen in spring and summer, as the thick winter coat is being shed (Dobroruka, 1961).

Horses do not sleep steadily throughout the night, but waken and feed at intervals (Belling, 1990). Domestic horses rarely sleep more than two hours at a time, nor do they lie down more than one hour at a time (Willoughby, 1974). Some horses sleep standing up, but all horses lie down at times, whether sleeping or merely resting. When lying down, a horse sometimes lies flat, on one side and cheek, but more often lies on the bent legs of one side, with its head and neck upright or inclined to the same side (e.g., sternal recumbency). To lie down, a horse kneels on the front legs, then sinks down behind (Dobroruka, 1961).

Alpha males are more continually restless and alert than other herd members. Among feral horses, two dominant males spent 25-45% of their time in motion, whereas other herd members spent less than 10% of their time in this activity. Only 5-6% of the alpha male’s time was spent asleep; the other herd members slept 20-27% of the time, with the exception of two females with week-old young, who also slept less. The young themselves slept for 50% of the time (Belling, 1990). Two females spent 70-85% of their time feeding; their young were next in length of time; subadult females still less, and dominant males least. After one week, young were already feeding on solid food for a longer time (7-15%) than



Fig. 22. A Przewalski mare lays her ears back, signalling other herd members to back off and leave her portion of the food alone. Przewalski and domestic horses share a large suite of characteristic behaviors. (Deb Bennett photo).

Fig. 23. A Przewalski mare wheels to her left. Note the fluid crossing of the forelegs. Przewalski and domestic horses share basic athletic capabilities. Several thousand years of selective breeding have changed the body-conformation of domestic horses; note the lack of “withers” in the Przewalskis, their thick and strong neck, and their overall substantial and chunky build. (Deb Bennett photo).



they spent in suckling (Dobroruka, 1961). Summaries of ethological data for *E. caballus* can be found in Berger (1986) and Waring (1982).

Section XII: Genetics

The chromosome number of domestic horses is $2n = 64$; the karyotype consists of 15 pairs of metacentric to sub-metacentric autosomes and 16 pairs of acrocentric autosomes. The fundamental number of autosomes is $Fna = 92$. The X chromosome is a large metacentric, and the Y chromosome a small acrocentric. The wild ancestors of the domestic horse must have had this karyotype (Benirschke et al., 1965). Ryder and Hansen (1979) demonstrated that in the Przewalski horse, $2n = 66$. Its karyotype also consists of $Fna = 92$, but with 14 pairs of metacentric or sub-metacentric autosomes and 18 pairs of

autocentric autosomes (Benirschke et al., 1965; Short, 1975, originally reported as 13 and 19 pairs, respectively). The difference between these two karyotypes is a matter of Robertsonian fusion or fission between one pair of banded and two pairs of unbanded autosomes (Short, 1975), but comparisons of mitochondrial DNA between the cytotypes indicated that they diverged well before humans domesticated the $2n = 64$ type (Ryder, 1986a).

The complete interfertility of Przewalski and domestic and feral horses is well documented (Groves, 1974; Zeuner, 1963). Furthermore, the extinction of wild horses was due partly to persecution brought on by the frequency with which wild males abducted domestic mares (Zeuner, 1963). On the basis of early observations by Pallas and others, tarpans and Przewalski horses are inferred to have formed a broad zone of hybridization, indicating that they were also interfertile (Groves, 1974; Heptner, 1961). The zone of intergradation lay between the Volga and Ural Rivers, on the steppes north of the Caspian Sea, extending north to the southern end of the Ural Mountains, south of the latitude of Kuibyshev and Magnitogorsk (Fig. 4). The testimony of 18th and 19th century observers suggests that wild horses in this zone did not show gradual introgression of pelage color, but instead consisted of herds of yellowish-dun *przewalskii* or darker, grayish *ferus* horses, with some individuals of intermediate color (Heptner et al., 1961). This could be interpreted as evidence of restricted gene flow, and, together with the documented differences in chromosome number and mitochondrial DNA between extant domestic and Mongolian wild horses (Ryder, 1986), has led several authors to place the tapan (which they assume to have had the same chromosome complement as domestic horses) and Przewalski horses in separate species (Gromova and Baranova, 1981). However, no serious pre- or post-mating mechanisms for reproductive isolation seem to have existed.

Biochemical evolution in *Equus* was reviewed by George and Ryder (1986) and genetics of the Przewalski horse by Ryder (1994). Coat colors and patterns in domestic horses have been studied as genetic manifestations, and the literature on this subject is large and conflicting (Sponenberg, 1996). According to some authors, hair color in the horse is due mainly to one pigment, melanin, and differences in color are caused by systematic variations in the amount and location of the pigment (Gremmel, 1939; Sponenberg et al., 1988). The pigment is never found scattered diffusely throughout the hair shaft, but always as clusters of granules. Scattered small, smooth clusters of granules permit light to pass through the hair and produce the lighter, reddish and yellowish coat colors; densely packed, large, irregular clusters of pigment permit no light transmission, giving a black color to the hair. Variations in pigment clusters between these extremes are found in intermediate coats. The diluted appearance of dun horses is caused by a reduction in the total amount of melanin present and a greater concentration of pigment on one side of the hair shaft than the other. A lack of pigment clusters in the superficial part of the cortex was seen in hairs from brown or white muzzles of dark horses (Gremmel, 1939).

Section XIII: Conservation Status

Eurasian wild horse populations, widespread in the early Holocene, dwindled progressively. Extinction was effected by a two-step process: absorption into a growing domestic population and hunting of remaining wild forms (Groves, 1974; Lundholm, 1949; Zeuner, 1963). The Przewalski horse survived in the wild longer than other subspecies primarily because it inhabited remote regions of Mongolia not much frequented by man (Sokolov and Orlov, 1986), and secondarily because it was less well adapted to man's tasks than other forms of the species (Ebhardt, 1958). In areas of denser human settlement, such

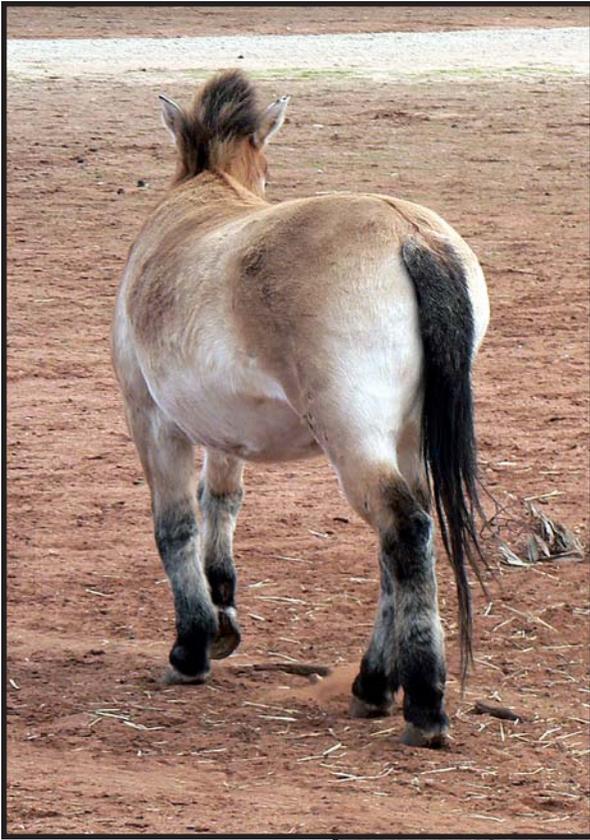


Fig. 24 (left): A Przewalski mare in rear view. Note the characteristic "tail cap", composed of short, stiff hairs that stand out horizontally to cover the perineal area. This view shows the almost incredibly stout limbs found in Przewalski horses: whereas domestic horses average 7 to 8 inches of bone per 1,000 lbs. of weight, Przewalskis average twice that. Loss of "bone substance" (cannon-tendon circumference) is a common sequel to domestication. (Deb Bennett photo).

Fig. 25 (below): A group of Przewalski mares in front and rear view. Note the convex facial profiles in skulls broad across both the orbits and the nostrils. Erect manes and tail cap show up well here.



as the Near East, North Africa, and western Europe, wild horses were exterminated in early historical times (Brentjes, 1972; Lehmann, 1973). In eastern Europe and western Asia, wild horses survived until late historical times in many areas. Forest populations were extirpated in Latvia in 1814 and in Poland in the late 18th and early 19th centuries (Pucek, 1981). Steppe populations persisted a bit longer; the last wild tarpan of record was killed in December, 1879, in the Tavrichesk steppe 35 km from Askaniya Nova, Ukraine, and an animal caught near Kherson lived in the Moscow Zoological Park until the 1880s. However, captive-bred animals were maintained on stud farms until 1918, when the last *E. c. ferus* of wild stock died (Heptner et al., 1961).

The Mongolian wild horse was made known to science when a skin and skull were presented to the Russian explorer Przewalski at the end of his second (1878) or the start of his third (1879) Tibetan expedition by the master of the Zaisan post, A.K. Tikhonov (Weeks, 1977) – ironically, just about the time the last free-living tarpans were killed. Then, after several failures, Falz-Fein succeeded in 1900 in bringing *E. c. przewalskii* into captivity, followed by Hagenbeck in 1901. Subsequently, the Przewalski horse has been bred in captivity at a number of places, and the present world population is in excess of 1200 (Dierendonck and DeVries, 1996). A history of its discovery and subsequent husbandry are presented in Garrott et al. (1966) and Weeks (1977).

The apparent disappearance of the wild horse in Mongolia (Sokolov and Orlov, 1986) may mean that the species is now entirely extinct in the wild. Captive stocks exhibited signs of inbreeding and undesirable artificial selection (Sokolov and Orlov, 1986), although inbreeding has now been reduced (Ryder, 1993). It would be of utmost value if one or more populations were reintroduced into the wild. Ideally, this would be in the context of a livestock-free preserve in an area of optimal habitat, such as the Eurasian steppe zone or the foothill grasslands of the Khangai (Dierendonck and DeVries, 1996). However, competition with domestic livestock and other agriculture in these ecological zones, as well as the risks to the reduced “wild” gene pool due to high probability of interbreeding with domestic horses, militate against successful introduction outside of the Dzhungarian Gobi, in the semidesert-to-desert zone of Mongolia and China (Ryder, 1993). Although less densely settled by humans, these areas are on the margins of the wild horse’s historical range and habitat.

Section XIV: Remarks

“Bit wear” – the beveling of the anterior premolars by the metal bit seen in subfossil remains – indicates that *E. caballus* was ridden by semi-sedentary tribes of the Sredny Stog culture inhabiting the upper terraces of the Dnieper (Dnepr) about 200 km SE of Kiev about 4,000 B.C. (Anthony and Brown, 1991). The first taming of the horse probably was a secondary result of human interest in the species as food; both cave paintings and subfossil archaeological remains attest to a taste for horseflesh (l’Hôte, 1953). The earliest strong evidence for domestication already finds the horse bitted and, after death, placed in a ritual context.

It has been hypothesized that the steps intermediate between human interaction with horses as prey and horses as domesticated beasts of burden include a phase of cripple-capture of females either already gravid or impregnated while in captivity, and a phase of juvenile capture (Groves, 1974; Willoughby, 1974). It is easy to envision raising juveniles which as adults would be tame; adult Przewalski horses are wary of man, although juveniles are not afraid until warned by their [mothers] (Groves, 1974). Juveniles may originally have been captured in late spring, to be fattened through summer and autumn and then

slaughtered and eaten during the lean winter months. It seems certain, based on historical and ehtological evidence, that captive females continued to be impregnated by wild males for a very long time. Domestic male juveniles probably were also eaten (Groves, 1974).

The social context and level of acculturation necessary to train horses for riding, as well as the realization that riding is an activity useful to humans, must have come later than their original capture and taming. Horse nomads, subsisting primarily on herds of sheep and cattle, probably forced “the collapse of the high civilizations of southeast Europe” (Diamond, 1991), and also may have carried the Proto-Indo-European language throughout Eurasia (Bennett, 1998). Only after contact with culturally less urbanized horse people from the north did the southern river valley civilizations realize the potential advantages in terms of convenience, food-gathering, and political power inherent in riding (Legrain, 1946).

Political and cultural systems from earliest historical times onwards in Eurasia, North Africa, and later in the Americas depended until recently almost exclusively upon the horse as the main agent of transport and of political influence as well as sometimes of food, clothing, and shelter (Bennett, 1998; Legrain, 1946; l’Hote, 1953; Willoughby, 1974). While oxen continued to be used in Africa, southeast Asia, and southern Europe for centuries, in northern and western Europe the horse was early employed as a draft animal (Chenevix-Trench, 1970). Peoples of mountainous countries, especially in northwestern Europe and northern and central Asia, have made extensive use of the horse as a pack animal (Chenevix-Trench, 1970; Willoughby, 1974). Civilizations from Egypt, Assyria, Babylon, Greece, and Rome, to the Celts of northwestern Europe, and later Native Americans, have idolized or deified the horse as a bringer of luck, power, and sexual potency. Virtually every war, revolution, invasion, or political change in the Old World from the time of the Hittites to World War I involved *E. caballus* to a significant extent (Bennett, 1998; Chenevix-Trench, 1970). Paupers have been elevated to the status of kings on the backs of horses, and often have been painted and their visages preserved for posterity on just that throne (Mackay-Smith et al., 1983).

During Roman times, and more recently since about 1750, many horses have been bred for speed, and horse racing became the third largest sport in the United States in terms of money earnings (Mackay-Smith, 1983). By judicious crossing of bloodlines originating in the different wild populations of *E. caballus*, and by careful and consistent selection of superior stock, breeds of horses adapted to a wide variety of tasks have been produced in nearly every country in the world. Despite a large drop in population numbers of domestic horses after World War II, especially in industrialized countries, the present-day horse population has attained greater numbers than at any time in history (Willoughby, 1974). Genetic diversity among horses has, however, declined seriously in those sections of the industry which operate from closed registries (Bowling, 1990). The scientific name of the horse is derived from two Latin words, “*equus*” meaning horse, and “*caballus*” meaning nag.

The authors gratefully thank Robert Patterson, Thor Holmes, Jim McAllister, W. C. Wozencraft, S. Reid, Matthew Mackay-Smith, Todd Williams, and J. and C. Warner for their help. R. McNeil Alexander, Joel Berger, Anne Forstén, Colin Groves, V. E. Sokolov, and B.J. Stafford read the manuscript and provided helpful criticism and literature references. Ellen B. Wells, late chief of Special Library Collections, and D.T. Steere, Jr., Smithsonian Institution Libraries, were of particular help in obtaining many references. Orlov et al. (1986) provided a bibliography of Russian references.

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