Equus caballus.  By Deb Bennett and Robert S. Hoffmann

Equus caballus Linnaeus, 1758

Horse

Equus caballus Linnaeus, 1758-72. Type locality “in Europa.” Restricted by Linnaeus (1766:10) to “Scania and Gotlandia” [southern Sweden] (domestic horse).

Equus ferus Boddaert, 1785:159. Type locality “… Woronesk, Russia” [Chichenko, 45 east [48 km] from Bobrovsk, Vorneth district]. From Groves, 1980.

Equus sylvestris Brincken, 1828:49. Type locality “la fore! impe­"ntiale de Bialowize en Lithuanie” [Bialowere Forest, Poland].

Equus przewalskii Poljakov, 1883:1. Type locality “Peski Khanobo [Khanobo] oroko 250 km k yugo-vostoku ot Zaisanskoj posta [prilizhie no ha 46° c. sh. k yugu of oz. Ulyungur]; tsentral’naya Dzhungariya.” [Khanobo (Kanabo) sands, about 250 km SE Zaisan Post (ca. 46°N lat. south of Lake Ulyungur), central Dzungaria = Xinjiang Province, China] (domestic horse).

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


Equus caballus pumpelli Duerst, 1903:297. Type locality “Anau, Turkistan” [ca. 20 km SE Askhabadas, 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.

Equus gnedenkii Antonius, 1912:516. Type locality “… Sagradoffischen Steppen des Gouvernements Chernos …” [Zagradov Steppe, right [W.] bank, Dniepr River, near Kherson, Ukraine].

Equus nipponensis alaskae Hay, 1913:23. Type locality “… near Toly, Alaska, … on Sullivan’s Creek.” Pleistocene.

Equus mexicanus Hibbard, 1955:66. Type locality “… Tajo de Tepuquiquie, Estudio 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 midlendensis 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 (Winnis, 1989), but the holotype dates to recent historic times (R. Graham, in litt.).


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), Kurten and Anderson (1980), and Skorkowski (1938) provide taxonomies and reviews of species.

CONTEXT AND CONTENT. Order Perissodactyla, Suborder Hippomorpha, Family Equidae, Subfamily Equinae, Genus Equus, Subgenus Equus. Following Troudbler (1961), we recognize seven living or recently extinct subspecies, listed below (Bennett, 1992a). 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 ecormorphotypes 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).

Breedes 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; Troudbler, 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 domestics, being now extinct in the wild. All four contributed to the gene pool of 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., 1973). 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 *Prazewalskipferdes*” [The Mongol domestic horse is a direct descendant of the *Przewalski horse*]. The distinctive phenotype (Fig. 1) of these three closely related ecumorphotypes largely devalues horses in response to late Pleistocene steppe-tundra conditions (Bennett, 1992b). A similar scheme was advanced by Groves (1986), although he used different nomenclature.

E. c. alaskan Hay, 1913:2,3, see above. Lamut, or Beringian Horse.
E. c. caballus Linnaeus, 1758:73, see above. Northwestern European Horse.
E. c. ferus Boddaert, 1785:159, see above. Tarpan (*melitensis* Antonius, *sylvestris* Brinken are synonyms).
E. c. mexicanus Hibbard, 1935, see above. American Periglacial Horse (*laurenti* Hay, *midlandensis* Quinn are synonyms).
E. c. mosbachensis von Reichenau, 1903:553, see above. Central European Horse.
E. c. przewalskii Polyakov, 1881:1, see above. Przewalski Horse, Mongolian Wild Horse (*vagenki* Mantschh a synonym).
E. c. pumpeii Duerst, 1908:397, see above. Afro-Turkic Horse.

The assignment of this name to *E. caballus* remains controversial. If it is not, then *algericus* Bautchke, Hadjouis and Eismann 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. Kurten (1996:149) 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).

**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. guanacos*) species in the genus. 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; hypostylar groove deep (Quinn, 1957). Edges of pre- and post-fosses more intensely folded than in congeners (McGrew, 1944). The lower cheekteeth are characterized, as in other caballid horses, by a U-shaped entoflexid between the metaconid and metastylid, in contrast to stenonids, which have a V-shaped entoflexid (Forstén, 1988a).

**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 shellflke squama temporals and is not visible from above (Hipptner et al., 1961). Cranium “unfolded” anteposteriorly as well as laterally broadenened compared with fossil and living congeners (Fig. 2; Groves, 1986). Inferior teeth large and straight with oval metaconid-metastylid columns widely separated; molars usually lacking true isthmuses (Skinner and Hibbard, 1972).

Mid-dorsal stripe always present in wild horses and very common in domestic ones (Salensky, 1990). Shoulder, ankle, and wrist stripes occasionally present in both wild and domestic forms. Shanks, center of mane and tail, tips of ears, and margins of mouth and nostrils black in wild and many domestic horses (Fig. 1). Interruptions of pigmentation on the face and legs, which evidence 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; Zeller, 1963). Nevertheless, both wild and domestic horses are readily distinguishable from congeners on the basis of many skeletal measurements.

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E. *caballus* in the largest species in the genus (Willoughby, 1974). External measurements (in cm) of *E. c. przewalskii* (Klimov and Orlov, 1982; Xiao and Qu, 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, 120-146. Adult mass is 200–300 kg. Cranial measurements of adults (older than four years), in mm; mean ± SE; range) for four wild-caught animals are the following: basal length of skull, 482 ± 3.9 (471–

brown to brick red), brown (a rich sienna in shades nearly to black), liver (flat brown), mouse-gray (was characteristic of *E. 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; Heptner, 1996).

Horses have 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 (Fig. 1), but in extant domestic forms, it grows longer and “falls.” The wild tarpan of eastern Europe, *E. ferus*, showed an intermediate, “partly falling” mane. Extant wild horses are stocky animals with relatively very short ears and large, deep heads (Fig. 1; 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; Zeller, 1963).

Nevertheless, both wild and domestic horses are readily distinguishable from congeners on the basis of many skeletal measurements.

**Fig. 2.** Dorsal, ventral, and lateral views of cranium and lateral view of mandible of adult female *Equus caballus przewalskii*. Museum of Natural History, University of Kansas (KU 138589). Greatest length of skull is 52.7 cm.
than ferus averaged larger ballus the dwarfed insular pony is illustrated C. Afro-Turkic horse (E. c. pumppelia) D. Tarpan (E. c. ferus) For reconstruction of the Beringian horse (E. c. alaskea see Strelkov (1977). The American Periglacial horse (E. c. mexicanus) is not illustrated but probably most closely resembled the Beringian and Mongolian wild horses (Fig. 1).

489) greatest maxillary width, 132.7 ± 0.47 (132-134); mastoid width, 105.5 ± 2.62 (100-110); width of interornital constriction, 87.5 ± 0.95 (86-90); length of nasal, 253.7 ± 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 (104-109); length of molar row, 83.0 ± 1.79 (81-88); length of mandibular rami, 411.7 ± 1.87 (402-422); greatest length of jaw, 432.8 ± 4.15 (420-440); depth of jaw at 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 (69-83).

Geographic variation in wild horses was principally in size, skull shape, limb length (Fig. 3) 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, partly falling mane, slightly smaller molariform teeth, a more pointed muzzle, and a slightly concave facial profile (Hibbard, 1955).

The tarpan (E. c. ferus) and western European subspecies (Fig. 3) c. caballus, averaged larger than ferus or przewalskii, but dwarfed insular populations "island ponies" (Hill, 1957) were relatively small and placed high on the head. The body build was stocky or even bulky, with a heavy neck and steep pelvic angle (Fig. 3). Judging from domestic descendants, the pelage was long and thick, with a tendency for the growth of long hairs "feathers" from the postero-lateral 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, a long flat neck, and long, sturdy legs (Fig. 3). 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 wooly appearance. The southernmost subspecies, E. c. pumppelia (Fig. 4), was small in size but had relatively the longest, slenderest legs and ears. The facial profile was straight or concave ("tile-shaped") 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. 3).

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).

DISTRIBUTION. The known distribution (Fig. 4) 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 Belorus, Ukraine, Russia, and Kazakhstan to western China and Mongolia. Several taxa of Late Glacial E. mosbachensis have been described from China and Japan (Olsen, 1986; 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 (Schweitzer et al., 1982). They survived in the Yukon until at least 13,000 years ago (Moran and Cinq-Mars, 1982), and there is some evidence for a relict population of wild horses in northern Yakutia (Russia) until historic times (Vereshchagin and Barabashkov, 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-Caballero 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 Italic Peninsula to the Tunisian peninsula, but only one specimen is known, from Algeria (Baptache et al., 1984). In the Near East, the horse was probably found in Egypt (Boesneck, 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 (Boesneck and von den Driesch, 1976), through Iraq (Turnbull, 1986) and Iran (Firouz, 1973), as far north as the Caspian Sea and Trans-Caucasus, where the tarpan and "Southwest Asian" (Afro-Turkic) horse occurred, respectively (Vereshchagin, 1953). It then extended southeastward through Turkmenia (Duetsch, 1908) and Uzbekistan to the Syr Darya River (Smith, 1845) and northcentral Afghanistan (Uerpmann, 1978). It was not, however, found in Asia, with the exception of the domestic descendant, the Przewalski horse (Equus ferus).

FOSSIL RECORD. Equus, a monophyletic taxon, is derived from the late Miocene Dinotherium (Quinn, 1957). The genus evolved during Pliocene (Blancan) time, ca. 4 × 10^6 years ago in North America (Forsten, 1989), and is first represented in western North America by E. simplicidens (syn. stiophonensis; Azzaroli, 1992). This medium-sized equid was directly ancestral in North American equids.

America, ca. 3 × 10^6 years ago, to later Blancan species (Azzaroli and Voorhies, 1993). However, ca. 2.5 × 10^6 years ago Equus also migrated to Eurasia via Beringia (Prat, 1980); the oldest species there is E. niobrarensis (Azzaroli, 1990), which was followed by the "dentally primitive" (Forsten, 1989) stenonid horses, so-called after E. stenonis, the most widespread species, which first appeared ca. 2 × 10^6 years ago in both Eurasia and North America. Stenonids, which include zebras, survived in the New World until the late Pleistocene (E. enornis; Azzaroli, 1993), and persisted in Eurasia until at least 1 × 10^6 years ago (middle Pleistocene; Azzaroli, 1990; Kurten, 1968). However, Forsten and Dimitrijevic (1986) argue that E. hydruntinus was a stenonid that survived to the end of the Pleistocene.

The origin of "dentally more advanced" caballoid horses is uncertain. Kurten (1968) suggested that the stenonid E. brevifrons may have given rise to the oldest caballoid ecomorphotype, E. c. mosbachensis, but Azzaroli (1992) believed that another branch from an ancestral simplicidens, the late Pliocene E. idahoensis, was the source of caballoid horses ca. 2 × 10^6 years ago in North America. These then migrated to Eurasia ca. 1 × 10^6 years ago (Azzaroli, 1988), leaving others such as (E. niobrarensis) in North America (Azzaroli, 1996). Initially rare, caballoids were associated with stenonids in Eurasia, but over the next 0.5 × 10^6 years replaced them because of climatic preferences and different niche width (Forsten, 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 lauritzius). These may either have derived from niobrarensis (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 niobrarensis 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 Holocene 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; Kurten, 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 Wurm period, both forest (caballus, mosbachensis) and steppe (ferus) or steppe-tundra (alaskae, przewalskii) forms were found in Europe (Eisenmann et al., 1985; Forsten, 1988b; Zeuner, 1965), 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.

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**Fig. 4.** Schematic distribution (crosshatching) 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; B, caballus; C, ferus; D, mexicanus; E, mosbachensis; F, przewalskii; G, pumelli. 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.
The final date is now considered to be 11,400 years ago, and dates as late as 8,000 years ago (Chuchrer and Stalker, 1970) are now considered in error. However, caballine horses survived in Eurasia (Markova et al., 1956) 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; they may have been present 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 (Grove, 1986), and it has been suggested that the Exmoor pony represents this population (Speed and Etherington, 1952-1953), however, Grove (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, but in eastern Europe and western and central Asia, until the 19th-20th centuries (Bennett, 1992c). Beginning ca. 6,000 years ago, E. caballus was taken into domestication and extirpation in the wild began (Anthony and Brown, 1991. The 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).

**FORM.** Foals are born with a dense pelage consisting of long, soft, curly hairs ("fleece"); which begins to shed after about seven days, and a new coat takes 30-40 days to develop. 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 72 days in yearlings. The new coat is fully grown 2 months later than the body pelage, and takes 30-50 days to molt completely. 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 (Grove, 1974). Horses possess callous near wrist and ankle on fore and hind limbs called "chestnuts," and others on the flexor 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 thick growth of guard hairs appearing 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 (Grove, 1974). The horse's stomach has a small capacity relative to that of other mammals; it comprises 0.06% of the body mass; both pancreatic and accessory pancreatic ducts are present. The pancreas weighs ca. 350 g and comprises 0.66% of the body mass; both pancreatic and accessory pancreatic ducts are present. The spleen weights 1,000-1,200 g and comprises 0.16% of the body mass; it is ca. 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 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 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 larynx bone. The vocal fold is oblique, with its dorsal end anterior and its ventral end posterior. The average mass of the horse's lungs is 6 kg, large compared with those of other mammals. Total lung capacity averages 42.1 l, with average reserve and tidal volumes of 9.1 and 7.5 l, respectively; the horse can draw in as much as 9.0 l of air per inspiration. The main bronchus divides internally (Frandsen, 1974).

The tests and epididymis of the horse are over 24 cm wide (Campbell and Lasley, 1975). The testes are bean-shaped, and average 51.6 by 28.5 by 32.7 mm. During the breeding season, their average mass is 0.06 l, with one larger than the other. The broad ligament attaches in the sublumbar region (Ginther, 1979). The body of the uterus is ca. 117 mm long; the two horns are each ca. 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 ca. 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 hypoplasia is evident, 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, 50.6; 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 eye overlap centrally. In the horse, the overlap is restricted to a small nasal area in each field; ca. 90% of the fibers cross (Phillips, 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 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 (Phillips, 1976). Endocrine 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 (Fig. 2). 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 orbits are large. The orbit so that the roots of the teeth do not impinge upon it. The jaw is likewise deepened in order to accommodate the tall teeth. The three pairs of incisors are single-rooted and blunt. Placed at the extreme anterior limit of both upper and lower jaws, they are employed for tactile exploration. The premaxillary and molar teeth are hypsodont and the roots of the maxillary teeth extend far into the skull. The maxilla of the horse is displaced forward of the orbit (Fig. 2). 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 orbits are large. The orbit so that the roots of the teeth do not impinge upon it. The jaw is likewise deepened in order to accommodate the tall teeth. The three pairs of incisors are single-rooted and blunt. Placed at the extreme anterior limit of both upper and lower jaws, they are employed for tactile exploration. The premaxillary and molar teeth are hypsodont and the roots of the maxillary teeth extend far into the skull. The maxilla of the horse is displaced forward of the orbit (Fig. 2). 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 orbits are large. The orbit so that the roots of the teeth do not impinge upon it. The jaw is likewise deepened in order to accommodate the tall teeth. The three pairs of incisors are single-rooted and blunt. Placed at the extreme anterior limit of both upper and lower jaws, they are employed for tactile exploration. The premaxillary and molar teeth are hypsodont and the roots of the maxillary teeth extend far into the skull. The maxilla of the horse is displaced forward of the orbit (Fig. 2).

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tooth." Other premolars are large, square, and molariform. Morphologically, the cheekteeth are lophodont, showing complex loops and plications of the hypodont enamel, which change with wear. Dentine and cementum alternate with enamel in the cheekteeth to form the pattern of self-sharpening surfaces. The cheek teeth also are surrounded and supported externally by cementum (Goulau and Barrier, 1892).

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, in which proximal limb bones are short and distal limb elements are long (Gregova, 1959); McMahon (1975) compared limb elements of Equus with other unguligrade quadrupeds. The appendicular skeleton is designed primarily for fore-and-aft movement; the ribcage is laterally flattened, and all distal joint surfaces are ridged or grooved to inhibit or completely prevent lateral and rotary movement. The postcranial skeleton shows retention of some primitive characteristics, such as the simple astragalar characteristc of Protoceratocyla with a single, deep oblique trochlea, and retention of a large third trochanter on the femoral shaft. 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 (Carter, 1984); loss of clavicles in other nonruminant mammals; "cervicalization" of the transverse joint surfaces on the last several lumbar vertebrae and on the anterior sacrum (Bennett, 1992c). The vertebral formula is 7 C, 18-19 T, 5-6 L, 5-6 S, and 18 Ca, total 53-56 (Heptner et al., 1961).

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 mmHg g-1 hr-1 (Egan, 1976). The normal rectal temperature of the adult horse is 100°F (range, 99.8-101°F [37.7-38.3°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 adrenaline (Jeff, 1976).

The length of time food remains in the stomach varies with the type and constancy 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 (especially fiber) by means of microorganisms is of great importance; therefore the most digestive activity occurs in the cecum (Campbell and Lasley, 1975).

Because the horse possesses few (20-40%) long loops of Henle's loops, it is less able than other nonruminant ungulates to concentrate urine only to ca. 2.5 osmol/l. The horse consequently requires a reliable supply of fresh water; water turnover is 250-350 ml kg-1 day-1 (MacFarlane, 1976). Blood volume averages 9.7% of body mass; water turnover is 250-350 ml kg-1 day-1 (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/min (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. This permits the horse to bear and leap without danger of fracture (Bennett, 1992c). The biceps femoris muscle in the horse is tendinous in its center portion 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 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 biceps femoris muscles possess 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 and tuck in coordination with uniquely adapted joints in the axial skeleton to ensure that when the horse lowers its head or extends it forward, the center of the back is raised (Bennett, 1992c).

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" incorporates the dorsal ligament system with the major appositional muscles of the torso (longissimus dorsi, rectus abdominus, ilioscapularis, scalenus) to support bascule (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" configuration, with more joints 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 caudal over the ridge formed by prolongation of the neural spines of the first 6-8 thoracic vertebrae (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 the dorsal ligament system; their posterior function is to ensure that when the horse lowers its head or extends it forward, the center of the back is raised (Bennett, 1992c).

The lumboasacral and last interlumbar joints of horses possess articulating surfaces 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 lumbar joint, rather than the coxofemoral joint. 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 lumboasacral joint. This system consists of the lumbosacral fascia and lumbodorsal fascia where they span the thoracic and lumbar; and sacral vertebrae, the x-shaped intersesamoidean 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 biceps femoris muscles possess 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 back at the lumbar 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 abdominus or ilioscapularis muscles.
The footfall order for a right lead canter is left hind, right hind and that the footfall sequence for a right gallop is: left hind, right hind, 

natural canter, a period of suspension follows the impact of the 

sured at 26-56 (16-35 mile/h), or more in an animal running for 

6 to 19 k/h (4 to 12 mile/h). The contralateral pairs of legs work 

fore, right hind, right fore; the gait proceeds at 6-10 kmlh 

(Evans et al., 1982). The canter is a moderately rapid gait executed 

over speeds from 10 to 26 km/h (6 to 16 mile/h). One contralateral 

pair of legs works in unison, while the other pair is “decoupled.” 

When executing this gait, horses are likely to stiffen the torso rel­

cues to be isochronal (Colantuono and De Moya, 1994) and may 

ceases to be isochronal (Colantuono and De Moya, 1994) and may 

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 k/h (4 to 12 mile/h). The contralateral pairs of legs work in unison, thereby producing only two beats. During the execution of a natural canter, a 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; McMahon, 1975), and at high speeds the elastic aponeurosis of the longissimus dorsi muscle, the main 


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, 1965). 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 (Schafer, 1974). The male sometimes thrusts his nose into the female’s urine stream and may stand for up to 30 s in this posture. It has been theorized that flehmen brings into action Jacobson’s organ (Groves, 1974). Urine of the female in es­

trus contains many estrogenic compounds; as a variety of those that appear to be metabolic products of the gonadotropic hor­

mones that the rutting male is trying to detect (Faulkner and Pi­


Poberty in females begins at 10–24 months of age (mean = 18). Horses are seasonally polyestrus. During the breeding season, the length of time from the beginning of one estrous period to the beginning of the next (diestra) 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. 

In the estrous female, mucous membranes of the labia, vagina, 

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

Gestation averages 335 days (SD = 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; 24% in April, 12% in 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 parturition in May–July (Dobchin, 1970), suggesting that a late summer rut and late spring–early summer birth period may be advan-

anced in wild populations. In the domestic horse, 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 preg-

nancies, although the rate is lower in ponies, but twin foals are rare (1–2%), and one or both may be abnormally small or com-

pletely inviable. Only 14% of twins born to domestic mares survive
to two weeks of age (Ginther, 1979). Males are carried ca. 9.5 days longer than females; twins generally are carried ca. 10 days less than singles (Adssel, 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 the mammary gland and its own nipple cistern. The vein: The udder and nipples of the female are covered with thin, fine hair as well as numerous sebaceous and sweat glands (Campbell and Lasley, 1973). Milk solids comprise 1.3% milk fat, 2.2% protein, 5.9% lactose, and 0.4% minerals. Passive transfer of immunity occurs by 36 h postpartum (Campbell and Lasley, 1975).

The female gives birth in a quiet place, returning ca. 1 day later to the herd; birth occurs at night. As soon as the female returns to the herd (1-2 weeks after the birth; Klimov, 1986d), 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, 1986d). 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 ca. 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, 1985). Birth weight of wild neonates is 25-30 kg; domestic neonates (non-pedigree) 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 4-5 years for females and 6-7 years for males (Willoughby, 1974). Epichyphos 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 (Gott, 1975). The order of eruption of the upper teeth is as follows (lower teeth erupt 0-6 months later): 0-week, di1; 0-2 weeks, dc (if present) and dl1 or 2-4; 4-6 weeks, dl2, 5-6 months, P1 (if present); 6-9 months, dl3; 10-12 months, M1; 2 years, M2; 2.5 years, 1; P1, 3 years, P3; 3.5-4 years, I2, P4, M3; 4.5-5 years, I3 and C (if present; Gott, 1975).

The long facial skull and the large teeth of Equus are correlated with an increase in volume and lengthening of the face and period, of the anterior pituitary lobe. The brain of the horse attains all adult 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 ca. 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 (Edinger, 1948). 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 by ca. age 2 years (Ensminger, 1969), when single testis mass increases (Lydekker, 1912) and in North Africa and the Near and Middle East, savanna, steppe, and semidesert environments (Vereshchajin, 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 returning northward during summer (Heptner et al., 1961). In northeastern 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 (Vereshchajin, 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).

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Predators of 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, 1985a), and lynx are known 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). Potential food items: Haloxylon ammodendron, Artemisia xerophytica, Nauphothyton erinaceum, Carex stenophyllades, Lasiagrass splendens, Tamarix ramosissima, Kalidium gracile, Sipia gobia, Cynanum sorgense, Anabasis brendofila, Caragana spinosa, Altium polyrhizum, Oxytrops aciphylla, Zygophyllum percarpium, 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 up to four days; in summer, they dug holes with their hooves, drinking the water collected in the central pituitary lobe. The brain of the horse attains all adult 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).

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groups of bachelor or solitary males (Klinov, 1986a; Waring, 1983). Differences in herd structure (Berger, 1986; Ebhardt, 1962; Schafer, 1974) may stem from the multiple origins of the domestic horse (Elハード, 1955; Trumler, 1961; Zieh, 1959) and are influenced by habitat structure and food availability (Rubenstein, 1986). The herd is cohesive and moves in single file, 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 10–12 km. If the herd is threatened by a predator, the alpha male may attack it, threatening 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 stand around their herd with ears laid back and heads lowered into a threatening position, and chase, bite, and kick females, while fe­male mates generally kick back at males (Ensminger, 1969; Schafer, 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 depends 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; Schafer, 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 forehead is almost 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; Schafer, 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 tongue and jaws, without showing its teeth, while the lower incisors contact the upper lip. 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 <10% of their time in activity. Only 2–5% 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 the remaining males least. After one week, they actually spent 60% of the day feeding on solid food for a longer period (7–15%) than they spent in suckling (Dobroruka, 1961). Summaries of ethological data for E. caballus can be found in Berger (1986) and Waring (1982).

**GENETICS.** The chromosome number of domestic horses is 2n = 64; the karyotype consists of 15 pairs of metacentric to sub­metacentric 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 submetacentric autosomes and 18 pairs of acrocentric 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 biarmed and two pairs of unarmored autosomes (Short, 1975), but comparative DNA between the cytotypes indicated that they diverged well before humans domesticated the 2n = 64 type (Ryder, 1986). 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 Falila 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 Kaulishv 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 feras 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 numbers, the mitochondrial DNA between the extant domestic and Mongolia wild horses (Ryder, 1986), has led several authors to place the tarpan (which they assume to have had the same chromosome complement as domestic horses) and Przewalski horse in separate species (Gromov and Baranova, 1981). However, no serious 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 (Spoenberg, 1996). According to some authors, hair color in the horse is due mainly to one pigment, melanin, and differences in color are caused by genetic variations in the amount and location of the pigment (Greene, 1939; Spoenberg 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 melanin present 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 coat colors. 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).

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; Zeamer, 1960). The Przewalski horses (Przewalski, 1889) are now entirely extinct in the wild. Captive stocks exhibited signs of inbreeding and undesirable artificial selection (Sokolov and Orlov, 1986), although inbreeding now has 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 areas, as well as risks to the reduced "wild" gene pool due to high probability of interbreeding with domestic horses, militate against successful reintroduction outside of the Dzungarian 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.

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 (Dnepe) about 200 km SE Kiev ca. 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 (I'Hote, 1953), but the earliest strong evidence for domestication already finds the horse hobbled and, after death, placed in a ritual context. It has been hypothesized that the steps intermediate between human interaction with horses as prey and domesticated beasts of burden include a phase of captive-domestication (Ryder, 1964), 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 maternal females (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 ethological 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 acculturization necessary to train horses for riding, as well as the realization that riding as 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, 1973). In mountainous areas, the very few other large terrestrial animals available for food, clothing, and shelter (Bennett, 1998; Legrain, 1946; I'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 (Chenexv-Trench, 1970). Peoples of mountainous countries, especially in northern Europe and northern Europe and later Native Americans, have idealized or idolized the horse as a bringer of luck, power, and sexual potency. Virtually every war, revolution, invasion, or political change by the time of the Hittites to World War I involved E. caballus to a significant extent (Bennett, 1998; Chenex-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, in 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 coun-
tries, the present-day horse population has attained greater num-
bers than at any time in history (Willoughby, 1974). Genetic di-
versity among horses has, however, declined seriously in those sec-
tions 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.

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