MAMMALIAN SPECIES No. 794, pp. 1–9, 3 figs.

Equus asinus.

By Martha I. Grinder, Paul R. Krausman, and Robert S. Hoffmann

Published 9 August 2006 by the American Society of Mammalogists

Equus Linnaeus, 1758

Equus Linnaeus, 1758:73. Type species [*Equus*] *caballus* Linnaeus, 1758:73 (domestic), by original designation.

Caballus Rafinesque, 1815:55. Substitute name for [*Equus*] *caballus* Linnaeus, 1758.

Asinus Gray, 1825:244. Type species *Equus vulgaris* (= [*Equus*] *asinus* Linnaeus, 1758:73) by subsequent designation. Not *Asinus* Brisson, 1762:70 which is not Linnaean. Not *Asinus* Frisch, 1775, which is not Linnaean.

Hippotigris Smith, 1841:321. Type species [*Equus*] *zebra* Linnaeus, 1758:74, by original designation.

Zebra Allen, 1909:163. Type species *Equus burchelli granti* de Winton, 1896:319, by original designation. In legend to figures 7, 8d, and 8e (but not figures 3–6 and 9–19, where *Equus* is employed). Evidently a lapsus.

Dolichohippus Heller, 1912:1. Type species *Equus grevyi* Oustalet, 1882:12, by original designation and monotypy.

Microhippus Reichenau, 1915:152. Type species *Equus przewalskii* Polyakov, 1881:1, by monotypy. Not *Microhippus* Matschie, 1922:68, which was used in a subgeneric sense. Not *Microhippus* Pocock, 1948:764, which is preoccupied.

Quagga Shortridge, 1934:397. Type species [*Equus*] *quagga* Gmelin, 1788:213, by monotypy.

Onager Quinn, 1957:10. Type species [*Equus*] *onager* Boddaert, 1784:160, by original designation. Not *Onager* Brisson, 1762:72, which is not Linnaean. Not *Onager* Zimmerman, 1780:80, which was used in a subgeneric sense.

Hemippus Dietrich, 1959:14. Type species *Equus hemippus* I. Geoffroy Saint-Hilaire, 1855a:1214, 1217, by monotypy.

Hemionus Dietrich, 1959:14. Type species *Equus hemionus* Pallas, 1775:394, by original designation. Not *Hemionus* Cuvier, 1821:555, a nomen nudum (Trumler 1961). Not *Hemionus* Stehlin and Graziosi, 1935, which was used as a subgenus.

Hydruntinus Radulesco and Samson, 1962:174. Type species *Equus hydruntinus* Regalia, 1904. Mesolithic to Neolithic subfossil.

CONTEXT AND CONTENT. Order Perissodactyla, suborder Hippomorpha, family Equidae, subfamily Equinae. In general, names used as subgenera or based on fossil specimens are not included in the synonymy above. *Equus* has 1 recently extinct (*E. quagga*) and 7 extant species (Bennet 1980; Groves 1986; Grubb 1993; Schlawe 1986). The following key to the species is modified from Ansell (1971) and Corbet (1978) separates *E. kiang* from *E. heminous* (Bennett 1980; Corbet 1978; Groves and Mazak 1967).

1 Chestnuts (epidermal callosities) on inner surfaces of fore- and hind legs; whole of tail long haired and growing from base; mane long and coarse, but in domestic horses, long and flowing .... *E. caballus*
Chestnuts confined to forelegs; tail tufted, long hair confined to distal half 2
2 Body striping limited to a dorsal line, shoulder stripe, or leg stripes; muzzle pale 3
Body either wholly striped or with striping at least on head and neck; muzzle dark 4
3 Ears very long, >200 mm in adults .... *E. asinus*
Ears shorter, usually <150 mm in adults 5
4 Size up to ca. 150 cm at withers; head and ears large in proportion to body; body markings with numerous vertical stripes behind shoulders, ending on haunches in a triangle pattern .... *E. grevyi*
Smaller size; pattern of striping not as above 6
5 Dorsal pelage dark reddish brown in summer, dark brown in winter; white ventral pelage with a prominent dorsal extension behind shoulder .... *E. kiang*
Body striping limited to transverse markings on legs, little or no dorsal line .... *E. hemionus*
6 Stripes on croup forming gridiron pattern; dewlap present on throat .... *E. zebra*
Stripes on croup not forming gridiron pattern; no dewlap 7
7 Striping whitish on dark ground, usually restricted to head, neck, and foreparts .... *E. quagga*
Striping dark on a light ground, over whole of body, usually at least partly on legs .... *E. burchellii*

Equus asinus Linnaeus, 1758

Wild Ass

Equus asinus Linnaeus, 1758:73. Type locality "in oreinte," restricted by Linnaeus (1746:12) to "Magnatum;" Magnes or Magnesia, eastern Thessaly (Lewis and Short 1907), now in western Turkey, near Manias (Bridgewater and Kurtz 1963), ca. 38.4°N, 27.3°E. Linnaeus based his name on the domesticated ass of Europe, and did not designate a holotype.

Asinus vulgaris Gray, 1825:244–245. Type locality "Inhabits Tartary in the wild state," Tatar, or Turkish region of eastern Europe and western Asia.

Asinus domesticus Smith, 1845:314. Type locality "Syria."

Asinus ferus I. Geoffroy Saint-Hilaire, 1855b:1221. Type locality "d'Abyssinie."

Asinus africanus Fitzinger, 1858:667. Type locality "Nubia," vide Allen 1939:563; a nomen nudum (Groves 1986).

E[*quus*]. *taeniopus* Heuglin, 1861a:15. Type locality "Die Wildesel heissen auf Arabisch: Hamár el Wadi. Mass.: Atgibaraha. Dan.: Debu-Kollo. Som.: Damer-debadeh;" considered "indeterminable" by Harper (1940:201). Type locality "near Berbera, Somalia," vide Groves (1986). Type may be based on hybrids of domestic and wild asses (Groves 1986; Ziccardi 1970). Considered a nomen dubium by Groves (1986).

Asinus taeniopus: Heuglin, 1861b:1 (description of figure 1). Name combination.

FIG. 1. Adult male *Equus asinus*, Ajo, Arizona. Used with permission of the photographer J. R. Morgant.

Asinus africanus Heuglin and Fitzinger, 1867:588. Type locality "im südlichen Nubien und im gazen nordöstlichen Sennaar, swischen Sauakin und der Provinz Berber kis an den Nil," restricted to "Ain Saba (etwa 16,0° N/38,0° O [= W]), Tigre, Eritrea (Schlawe 1980:104).

Equus asinus somaliensis Noack, 1884a:101. Type locality "Somalikuste," restricted to "Berbera (etwa 10,0° N/45,0° O [= W])," northwest Somalia (Schlawe 1980:106).

Asinus taeniopus somaliensis: Noack, 1884b:374. Name combination.

Equus asinus atlanticus Thomas, 1884:45. Type locality "l'oued Sequen," Algeria, Pleistocene; according to Boule (1900), not an ass, but a zebra, *E. burchelli mauritanicus*.

Equus asinus somalicus Sclater, 1885:540, 542. Type locality "Somalica."

Equus nubianus somalicus: Peel, 1900:300. Name combination. Type locality "Guban, the great maritime plain between the [Red] sea and the Gulis range of mountains . . . between Hargaisa and Berbera," Somaliland.

E[*quus*]. (*A*[*sinus*].) *a*[*sinus*]. *taeniopus*: de Beaux, 1928:1. Name combination.

Equus asinus atlanticus Werth, 1930:349, figure 3. Type locality "Enfouss (Annex d'Aflou, El Richa) in Algerien," ca. 300 km SSW Algiers; 34.08°N, 2.03°E. Based on fresco and rock art; renaming of *atlanticus* Thomas, 1884, thus a homonym and unavailable.

Asinus asinus dianae Dollman, 1935:132. Type locality "Hafta Wadi 17° 43′ N., 37° 36′ E., Red Sea Province, south of Tokar, near Eritrean boundary," Anglo-Egyptian Sudan.

Equus asinus africanus: Allen, 1939:563. Name combination.

E[*quus*]. *a*[*sinus*]. *aethiopicus* Denman, 1957:116–117. Type locality "in the Danakil country," Ethiopia; ca. 13°N, 41°W; a nomen nudum.

Asinus africanus arabicus Trumler, 1961:116. Type locality "Inneren Arabiens," Saudi Arabia; a nomen nudum.

Equus asinus hippagrus Schomber, 1963:121. Type locality "Sahara;" perhaps a homonym of *Equus hippagrus* Smith, 1836, used for a feral horse (Groves 1986).

Equus asinus africanus saharienis Dupuy, 1966:44. Type locality "Sahara Central . . . sud du massif du Hoggar;" unavailable because epithet is a quadrinomial.

Equus asinus palestinae Ducos, 1968:28, 30. Type locality "Tel-Gat," Jatt. Israel, 32.24°N, 35.02°W (The Times 1967). According to Ducos (1986) a nomen dubium.

Equus melkeinsis Bagtache et al., 1984:610. Type locality "Allobroges, Algerie," Late Pleistocene.

Equus africanus mureybeti Ducos, 1986:241. Type locality "Muraibit . . . in Syria on the right bank of the Euphrates north of Meskene," = Mesken; 36.02°N, 38.04°E (The Times 1967); renaming of *palestinae* Ducos, 1968.

CONTEXT AND CONTENT. Context as above. Four subspecies of *E. asinus* are recognized. *E. a. africanus* may have been recently exterminated; wild populations of *E. a. asinus* disappeared within historic time, and *E. a. melkiensis* disappeared in early Holocene.

E. a. asinus Linnaeus, 1758:73, see above (*domesticus* C. H. Smith, *mureybeiti* Ducos, *palestinae* Ducos, and *vulgaris* Gray are synonyms).

E. a. africanus (Heuglin and Fitzinger, 1867:588), see above (*dianae* Dollman is a synonym).

E. a. melkeinsis Bagtache et al., 1984:610, see above.

E. a. somaliensis Noack, 1884a:101, see above (*nubianus* Peel and *somalicus* Sclater are synonyms).

DIAGNOSIS. Externally, *E. hemionus* (together with *kiang* and *onager*) and *E. asinus* (subgenus *Asinus*; Fig. 1) can be distinguished from *E. caballus* by possession of chestnuts only on forelimbs, rather than on both fore- and hind limbs (Groves and Mazak 1967). In addition, hairs forming mane of *E. asinus* and *E. hemionus* are shorter and softer than in *E. caballus*; tail of *E. caballus* is stiffer, with longer hairs beginning at base, rather than terminally tufted tail as in *E. asinus* or *E. hemionus*. *E. asinus* and *E. hemionus* lack striping found on *E. burchelli*, *E. grevyi*, *E. quagga*, and *E. zebra*. *E. kiang* has a wedge of white behind shoulders that reaches toward rump, and is covered in winter with longer hairs than other *Equus* species (Groves 1974). *E. asinus* can be distinguished from *E. hemionus* by presence of transverse leg stripes, which are much less common in *E. hemionus* (Groves and Mazak 1967).

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of an adult male *Equus asinus* (Chicago Field Museum [FMNH] 20757). Greatest length of skull is 330 mm.

Skulls of *E. asinus* (Fig. 2) and *E. hemionus* are similar to each other, but contrast with those of 6 other species in the genus. External auditory meatus (meatus acousticus) of *E. asinus* projects beyond the squama temporalis, and is therefore easily visible from above, whereas in *E. caballus* and zebras, it is little, if at all visible, being much shorter. Mastoid bone is visible from above in *E. caballus* and zebras but not in asses (Bennett 1980). Other distinguishing cranial features of more primitive *Asinus* are a narrower and squarer lambdoidal crest than in caballines; a greater basicranial–basifacial flexion in *Asinus* than in caballines and zebras; an occipital plane less vertical than in *caballus* so that a horse skull can be balanced on its occiput, whereas *Asinus* skulls are unstable; and when skulls of *Asinus* are viewed from rear, frontal bones cannot be seen, because facial region declines steeply, and top of cranium obscures them (Bennett 1980). In caballines and zebras, frontals are visible beyond line of juncture with line formed by connecting the postorbital bars. In addition, skull of *E. caballus* is elongated with a rounded occiput, a long molar row, and a broad incisor region. *E. kiang*, *E. grevyi*, *E. burchelli*, and *E. quagga* have a high, convex neurocranium, low-placed orbit, and the lateral parts of the frontal bones slope strongly to orbital margins (Groves and Mazak 1967). Finally, postorbital part of skull in *E. asinus* is elongated compared to *E. hemionus* (Groves and Mazak 1967).

Eisenmann (1986) summarizes comparative osteology and odontology of recent *Equus*, emphasizing diagnostic characters of skulls, teeth, and skeletal proportions. She also summarizes use of metapodial bones for identification of Pleistocene and Recent *Equus* (Eisenmann and Beckouche 1986). *E. asinus* can be distinguished from *E. hemionus* by long, slender metapodials of the lat-

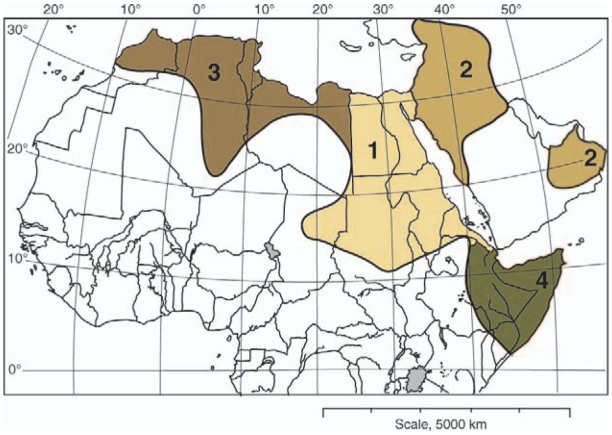

FIG. 3. Approximate historical range of *Equus asinus*. 1, *E. a. africanus*; 2, *E. a. asinus*; 3, *E. a. melkeinsis*; 4, *E. a. somaliensis*.

ter; no specific measurements can be used to designate difference between the 2 species because 18 subspecies of hemiones are distributed among 3 species (*hemionus*, *kiang*, and *onager*—Grubb 1993) in which gradations of metapodial length occur. The longest, most slender metapodials of *E. hemionus* comprise 80% of upper segment length; the breadth is 20% of the length. The metapodials of *E. asinus* comprise only 65% of the length of the upper limb segment; the breadth is 25% of the length (Groves 1974).

Edges of the pre- and postfossettes are more folded in *E. hemionus* than in *E. asinus*, and metaconid–metastylid isthmus on lower cheekteeth of *E. asinus* (Groves 1974) is usually absent in caballines and zebras. Shape of the valley between metaconid and mestastylid of the lower molars is variable and disputed: either V-shaped in horses, U-shaped in asses, and intermediate in hemiones (Groves and Mazak 1967); or V-shaped in zebras and asses, U-shaped in horses, and varying in hemiones from U-shaped in the northeast to V-shaped in the southwest (Groves and Willoughby 1981).

GENERAL CHARACTERISTICS. Height of *E. asinus* at shoulder is 110–140 cm (Clutton-Brock 1992; Lydekker 1905). Ears are long; hooves are small and narrow with no marked difference in size between front and rear hooves (Groves 1974). Long hairs are restricted to distal one-third of tail or less; forelock is absent. A dark, narrow dorsal stripe sometimes reaches from neck to tail and is sometimes discontinuous; it lacks white borders. Usually, either a stripe across the shoulder (in Nubian) or dark transverse barring occurs on legs (in Somalia); individual variation occurs and a geographic cline exists from longer, wider cross-stripes in Nubia through narrower, less well-defined, to no cross-stripe at all in Somalia. North African wild asses have 1 or 2 shoulder stripes and transverse barring on legs (Groves 1986). Near Eastern wild asses were characterized by black ear patches, a single black shoulder stripe, and gray legs, indistinctly barred with black (Pocock 1909). No white occurs on buttocks or rump. General color of upperparts, in all seasons, is gray-fawn. White areas include muzzle, a ring around each eye, undersurface of lower jaw, inside ear, underparts, and inner surface and much of lower portion of legs.

Equus asinus is the smallest species in the genus. Skull and body measurements and other details of morphology are available (Groves and Willoughby 1981). *E. a. africanus* stands 110–122 cm at the shoulder, whereas *E. a. somaliensis* stands 125–130 cm at shoulder. Each subspecies varies in color. Pelage of Nubian wild ass is more reddish, whereas Somali wild ass is more grayish in dorsolateral color, but intergradation occurs in northern Eritrea (Danakil ass [*E. a. taeniopus*]—Groves 1986).

DISTRIBUTION. The late historical distribution of *E. asinus* extended from northwestern Sudan east of the Nile River southeast to the Atbara River in eastern Ethiopia, to Sennar in northern Somalia (Ansell 1971), and northward to about Massawa (Fig. 3; Kingdon 1997; Sidney 1965; Uerpmann 1981; Zarins 1986). Within historic times, *E. asinus* has a continuous range across the northern part of the African continent; it was known from Algeria in the Pleistocene (Bagtache et al. 1984) and reports exist of wild herds surviving in remote areas of the Sahara (Hufnagel 1972). Early historical records place *E. asinus* in northern Egypt (Osborn and Helmy 1980) east of the Nile (Groves 1986) and in southern Egypt (Churcher 1986). It may occur in Near and Middle East and probably also in the Arabian Peninsula, in suitable rocky habitats, but not in flat desert or sand dunes (Groves 1986; Uerpmann 1986).

The wild ass lives in an extremely remote and hostile environment. In 1967, *E. asinus* inhabited the western side of the Red Sea in the hills of northern Eritrea, at 16°30′N, 37°30′E (Ansell 1971; Groves 1974). As of 1983, 1,500 *E. a. africanus* were in southern Sudan, and 2,000 *E. a. somaliensis* were in the Ethiopian Danakil Desert and the Las Anod region of Somalia. As of 1990, the only *E. asinus* living in the wild was *E. a. somaliensis*, in northern Somalia. Feral populations of *E. asinus* exist in many places worldwide and are abundant in the western United States and western Australia (Clutton-Brock 1992). *E. a. asinus* occurred in Arabia (Uerpmann 1981; Zarins 1986).

FOSSIL RECORD. Representatives of Equidae in Africa are known from sites of late middle to late Miocene, up to the present time (Churcher and Richardson 1978). Forms from which *E. asinus* is descendent are 1st known from northern Africa in the early Pleistocene (*E. tabeti*—Churcher 1982) and apparently occupied the Mediterranaean and Red Sea areas by the end of the Pleistocene (Azzaroli 1995). A North American clade in the Blancan may have included putative ancestor of hemiones and asses (Bennett 1980) or hemiones and asses may be autochthonous elements (Forsten 1989). Hemiones appeared in Asia during late middle or upper Pleistocene. African asses appeared in late upper Pleistocene of Levant and North Africa (Forsten 1989). *E. asinus* gradually spread westward across northern Africa during Neolithic times, replacing *E. burchelli*. This replacement may have been due in part to domestication and transport by man (Romer 1928).

FORM AND FUNCTION. *Equus asinus* has narrow, vertical hooves that are suitable for rocky areas (Groves 1974). It has small chestnuts on the forelimbs only, thought to be vestiges of the proximal metatarsal and wrist pad (Bennett 1992). The coat is some shade of fawn or gray, fading to white in the underparts; coat color changes seasonally, but subtly, being more fawn in summer and more gray in winter (Groves 1974; Lydekker 1905).

Dental formula is i 3/3, c 1/1, p 3–4/3, m 3/3, total 40–42. Incisors are bluntly chisel-shaped but their shape changes with age through wear from wider than deep to deeper than wide. They are used to seize plants and break off portions or sometimes uproot the whole plant while foraging. Enamel on the tips folds inward to form a pit that wears off early in life (Groves 1974). Size and volume of hypsodont cheek teeth are greater than that of *Hipparion*, *Dinohippus*, and other early ancestors of *E. asinus*; this is an adaptation to the harder, drier food that is found in the African grassland (Churcher and Richardson 1978). However, asses and hemiones have simpler molar patterns than do caballines (Bennett 1980; Forsten 1989). Complexity and hypsodonty are negatively correlated. Simple enamel pattern on teeth is advantageous for hemiones that eat fast and have food pass through the gut quickly. The simple enamel patterns also result in greater masticating pressure per unit area of enamel, which is advantageous when foraging on tough grass (Forsten 1980).

Equus asinus tolerates hot, dry conditions, often in areas with low-quality forage (Izraely et al. 1989). Feral *E. asinus* respond to cellular and extracellular dehydration by increasing water intake (Jones et al. 1989). They have a higher threshold for thirst than other equids in terms of water intake and latency to drink when fluid deficits develop. Oxygen consumption (VO_2, $\pm SE$) in 2 feral *E. asinus* running at maximal speed on a 9.8% slope was 110 ± 2 ml min^{-1} kg^{-1}, or ca. 22 times pre-exercise VO_2 ($\pm SE$—Mueller et al. 1994). Average heart rate at maximal VO_2 was 223 ± 2 beats/min, or 5 times pre-exercise rate. Blood lactate increased 14-fold and blood glucose did not change. The total energy cost of walking was 2.86 ± 0.06 J m^{-1} kg^{-1} live weight. During 25 min of low- to medium-intensity work, glucose fell below pre-exercise values, whereas plasma hematocrit and cortisol increased.

The heat- and exercise-induced sweating of castrated male domestic donkeys is controlled by adrenergic nerves. Adrenomedullary secretion may contribute to sweating during exercise and cutaneous blood flow is important in the response of the glands to humoral stimulation (Robertshaw and Taylor 1969)

When 5 females considered to be descendants of *E. asinus africanus* were maintained on wheat straw, gross energy intake was 1,134 ± 236 kJ $\text{kg}^{0.75}\text{day}^{-1}$, which was 67% of that recorded when the animals were fed alfalfa hay (±*SE*—Izraely et al. 1989). They also altered resting metabolic rate in response to diet quality. Resting oxygen consumption when fed wheat straw was 13.2 ± 0.71 $\text{kg}^{0.75}\text{day}^{-1}$, half the value recorded when fed alfalfa hay. Neither feed represents a natural diet; nevertheless, *E. asinus* maintained a constant body mass, although their nitrogen budget when fed wheat straw was not balanced. Water turnover rates of 290 ± 60 ml $\text{kg}^{0.75}\text{day}^{-1}$ and 380 ± 30 ml $\text{kg}^{0.75}\text{day}^{-1}$ were obtained in *E. asinus* fed wheat straw and alfalfa hay, respectively. When fed dry roughage, they depended on drinking. By lowering its requirement for metabolic energy, *E. asinus* is able to balance its energy metabolism under adverse nutritional conditions, but only if sufficient forage is available (Izraely et al. 1989).

At ambient temperatures between 10°C and 24°C, rectal temperature of 7 tamed *E. asinus somaliensis* weighing 125–180 kg was 36.4°C ± 0.34 *SD* with a range of 34.7–37.2°C (Maloiy 1971). Piloerection and shivering were observed when the wild asses were exposed to ambient temperatures of 5–15°C. At ambient temperatures between 40°C and 50°C, rectal temperature increased to 39.8°C. The rise between morning and evening body temperatures ranged between 2° and 3°C. At low ambient temperatures (10–24°C) respiratory frequency was 4–30 breaths/min. At ambient temperatures of 40–50°C respiratory frequency increased to 40–136 breaths/min. Heat stress does not appear affect heart rates. At 22°C resting heart rate was 39 beats/min (range 38–45 beats/min) whereas at an ambient temperature of 40°C, heart rate was 42 beats/min (range 41–48 beats/min). Metabolic rate was ca. 586 ml O_2/min. A reduction in metabolic rate occurred when *E. asinus* became dehydrated (Maloiy 1971).

ONTOGENY AND REPRODUCTION. Feral populations in the Chemehuevi Mountains of southern California have no peak breeding season (Woodward and Ohmart 1976). Populations in Death Valley National Monument, California, have a peak breeding season in late spring and summer, but females are polyestrous and mate at all times of the year. The longest observed estrus was 8 days (Moehlman 1974). Populations in Grand Canyon National Park, Arizona, breed during March–July (Ruffner and Carothers 1982). In a western Australian population, >50% of conceptions occurred during August–November, before the onset of the wet season; no conceptions took place during February–July (McCool et al. 1981).

Gestation of *E. asinus* is 365–370 days (Clutton-Brock 1992). Females are sexually mature at 1.5 years of age, but most do not breed until they are 2–3 years old (McCool et al. 1981; Moehlman 1974; Ruffner and Carothers 1982). The most fecund age class of females is 4 year olds, but females up to 14 years old breed (Ruffner and Carothers 1982). Some 9-month-old males produce sperm; all males are sexually mature by 2 years of age (McCool et al. 1981). In a single population of feral wild asses sex ratio at birth was 30% males (sample size not provided—Berger 1983; McCort 1979).

The percentage of females pregnant in a given population varied from 64% for 197 feral wild asses in western Australia (McCool et al. 1981), an average of 69% for 173 wild asses from 3 locations in eastern California (Wolfe et al. 1989), to 77% for 632 wild asses in China Lake, California (Perryman and Muchlinski 1987; Ruffner and Carothers 1982). Females give birth to 1 or 2 foals (McCool et al. 1981; Moehlman 1974). Foals begin nibbling on vegetation at 5 days of age, but weaning does not occur until 12–14 months (Moehlman 1974).

ECOLOGY. Within its natural range, *E. asinus* inhabits arid, stony regions dotted with hillocks, which are used as observation posts (Groves 1974, 1986). Temperatures often exceed 50°C in the daytime. *E. asinus* can range 4–6 km from water. The present natural range of *E. asinus* includes drought-stricken areas of Somalia and Ethiopia (Clutton-Brock 1992). In the feral state, *E. asinus* has colonized similarly harsh habitats, such as the Desert Southwest of the United States (Moehlman 1974; Ruffner and Carothers 1982) and western Australia (Wheeler 1987). Wild asses shared an overlapping distribution with the onager (*E. hemiones hemippus*) in the Near and Middle East (Groves 1986; Uerpmann 1981). However, they are likely segregated by habitat, the former on hilly, rocky ground, and the latter on flatter, featureless desert and semidesert (Groves 1986).

Equus asinus will browse or graze on any available forage (Clutton-Brock 1992). Thirty-nine plant species comprised the diet of a population in the Chemehuevi Mountains of California (Woodward and Ohmart 1976). Desert Indian-wheat (*Plantago insularis*) and palo verde (*Ceridium floridum*) were most commonly eaten. The diet consisted of 61% browse, 30% forbs, 4% grass, and 5% other. Riparian vegetation is important forage for *E. asinus* during summer (Hanley and Brady 1977b). Because they are opportunists, feral *E. asinus* have had significant negative impacts on native desert vegetation. The greatest impacts occur near water, but a significant decrease (from 8.7% to 2.8% cover) in total vegetation cover has occurred in areas with *E. asinus* (Hanley and Brady 1977a). In Australia, *E. asinus* feeds in pastures of grasses (*Aristida* and *Triodia* spp.) interspersed with eucalyptus trees (Freeland and Choquenot 1990). *E. asinus* in high-density populations eats lower-quality forage, with a higher crude fiber content, than do animals in low-density populations (Freeland and Choquenot 1990).

In the western United States and in Australia, wild asses do not have predators (Freeland and Choquenot 1990; Woodward and Ohmart 1976). High juvenile mortality, resulting from poor body condition, has occurred more frequently in high-density populations than in low-density populations (Choquenot 1991).

Social organization of *E. asinus* consists of solitary individuals, small groups, large groups, and herds. In Danakil, Ethiopia, 5% of the population was solitary, 28% occurred in groups of 2–6 individuals, 30% in groups of 7–20 individuals, and 36% in herds of 21–60 individuals. Small groups usually consist of a single male with a few females or are all male or all female adults (Klingel 1977). Large groups have 1 or more males and up to 10 females; some large groups consist solely of females. Herds consist of 25% males and the rest females and their young. No permanent groups exist, except small groups of young animals, 2–3 years old, with their mother. Large herds occasionally form during the day to feed, but break up again in the evening (Klingel 1977).

Populations of feral *E. asinus* exist in hot, arid environments throughout the world. Genetic interchange among feral and wild populations has occurred since equids were 1st domesticated 5,000 years ago (Clutton-Brock 1992), but the genetic effect on wild populations is problematic (Groves 1986). Feral populations are extremely hardy generalists, and can survive in many different environments. Once away from human control, they can quickly move long distances to new areas (Clutton-Brock 1992; Groves 1974).

BEHAVIOR. Some male *E. asinus* are territorial, inhabiting and defending specific areas for several weeks (Klingel 1977). The territory is advertised by the presence and behavior of the territorial male, who stands at the territory boundary in a stiff stance, with ears forward. The territorial male waits in this position until an intruding conspecific male approaches to within 10–20 m of his territory boundary, then walks forward to meet the individual. He makes contact naso-nasally and naso-genitally. He then chases the intruder away, following him for up to 1 km. Fights occur rarely, but scars from bites have been observed (McCool et al. 1981). Territories are large (Klingel 1977). Territorial males mark their territory with large dung piles (Klingel 1977). These piles are not necessarily at the territory boundaries. In desert areas, where the landscape is homogenous and territories are large, dung piles may allow a male to recognize his territory. Groups of nonterritorial individuals also defecate in large dung piles (McCool et al. 1981).

Males leave their territories for short periods to walk to drinking places (Klingel 1974). They may keep their territories throughout the year, even during the dry season when mares, foals, and nonterritorial stallions leave the area because of a shortage of food and water. Fidelity to permanently maintained territories and behavioral isolation of adjacent groups results in significant intergroup heterogeneity in genotype and allele frequencies (Blake and Douglas 1981).

Territorial males are dominant over conspecifics (Klingel 1977). Adults of both sexes are dominant over juveniles. No regular leadership is observable in large groups; any adult can lead the group for a short time. No antagonistic behavior occurs when leadership changes. Herds being culled from the air were likely to scatter if the male of the group was killed first, but when the male survived, he attempted to lead the group (McCool et al. 1981).

In Ethiopia, only territorial males mate (Klingel 1977), although feral territorial and nonterritorial males also can mate (Moehlman 1974). Territorial males copulated longer, were less likely to be interrupted, and were more successful at keeping other males away from the mated female than were nonterritorial males.

Mating activity gradually increases up to 2 days before females ovulate (Henry et al. 1991). Females in estrus frequently adopt a copulatory stance, with their hind legs apart, and their tail held at a 45° angle (Klingel 1977; Moehlman 1974). The male approaches from behind and sniffs the female's genitalia. Often, he vocalizes to initiate precopulatory interaction (Henry et al. 1991). The female kicks at the male in a ritualized manner and moves away from him in a slow canter (Klingel 1977; Moehlman 1974). The male follows the female for 20 m. Both individuals stop or the female pushes back against the male. He mounts her and they move a few steps in a circle. Penetration occurs immediately and ejaculation occurs after several pelvic thrusts. If copulation is completed, the male dismounts and the female sheds a secretion from her genitalia. The male sniffs at the secretion, displays flehmen, and urinates on it. They both then browse. If the female wishes to interrupt copulation before its completion, she walks or bounds out from under the male (Moehlman 1974). Interruptions are also caused by offspring of the female (approaching the copulating pair and kicking at the male), other females (crowding between the copulating pair), or subordinate males (threatening, pushing, or fighting with the copulating male).

Pregnant females have been observed in the evening and again the next morning with foals (Moehlman 1974); therefore, at least some parturition takes place at night. The female spends most of the 1st day postpartum within 1 m of the foal. She does not let any other conspecifics approach it, and she maintains almost continual tactile contact by nuzzling and grooming the foal. For a month, the foal spends 71% of its time within 1 m of its mother. From 1 to 2 months of age, the foal spends 35% of its time within 1 m of its mother; most of its time is spent 1–4 m from her. At 1 year, the foal still spends most of its time within 10 m of its mother (Klingel 1974; Moehlman 1974).

Equus asinus travels along well-used paths that often radiate from water sources (McCool et al. 1981). The most common modes of movement are a symmetrical walk or trot and an asymmetrical gallop. While resting, the head is held at a comfortable angle with the ears back. Rest periods last from 1 min to 2.5 h, and are sometimes coordinated in large groups. *E. asinus* feeds by browsing for ca. 0.75 min, then walking 1–7 steps to a new foraging site. It drinks steadily for up to 4.5 min, moving its ears back and forth. If interrupted by a sudden noise or social interaction it will lift its head to investigate the stimulus. Water holes are approached with caution; most drinking takes place from 1600 h to midnight. *E. asinus* is active day and night, the number and duration of bouts varying with the individual and climate. The Death Valley, California, population on average spent 51% of time feeding, with a peak at 1700 h; 36% of time was resting and standing, and 9% was walking (Moehlman 1974).

Equus asinus uses auditory, visual, tactile, and olfactory communication. Five vocalizations occur. The bray is the most complex and is used when meeting conspecifics, during copulation, in antagonistic encounters, and by foals separated from their mothers. Grunts and growls are antagonistic vocalizations. Whuffles are used to communicate position relative to other animals. The snort is an alarm vocalization. Visual communication can be divided into frontal threats and rear threats. Frontal threats include, in order of increasing intensity, turning toward a conspecific, putting the ears back, a fast-walk chase, and a trot–run chase. Rear threats, usually given by a female to an approaching male, include, in increasing intensity, pivoting the hindquarters toward the approaching male, lifting a rear hoof, lifting a rear hoof higher, kicking backward with 1 hoof, and kicking backward with 2 hooves. Tactile communication takes the form of naso-nasal or naso-genital contact or mutual grooming of the withers (Moehlman 1974). Olfactory communication consists mainly of flehmen behavior, in which the head is raised with the muzzle toward the sky, the upper lip is compressed and drawn forward, the upper teeth and gums are exposed, and nostrils are wrinkled. Such behavior exposes a vomeronasal organ (Moehlman 1974).

Play is practiced primarily by foals and yearlings (Moehlman 1974). It consists of short runs, quick stops, pivots, runs in the opposite direction, leaps, bucks, and kicks. Stones and twigs are sometimes used in play. Juveniles play in the vicinity of their mother or other adults, who ignore them (Moehlman 1974). Adults play with conspecifics, other animals, and people with whom they are familiar (D. Bennett, pers. comm.).

GENETICS. *Equus asinus* is the progenitor of the domestic donkey or feral burro. All domesticated feral burros that have been mated with wild *E. asinus* produce fertile offspring. The domestic male *E. asinus* is commonly bred with the female *E. caballus* to produce the usually sterile mule. The large head and long ears of a mule resemble *E. asinus*, whereas its body is like that of *E. caballus*. The female *E. asinus* is less commonly bred with the male *E. caballus* to produce the usually sterile hinny. The small head and short ears of the hinny resemble *E. caballus*, whereas its body resembles *E. asinus* (Clutton-Brock 1992).

Equus asinus has $2N = 62$ (Clutton-Brock 1992). A G-banded karyotype of *E. asinus* shows 19 pairs of metacentric chromosomes and 11 pairs of acrocentric chromosomes (Ryder et al. 1978). A wide range of fundamental numbers in autosomes (98–118) indicates different numbers of metacentric and submetacentric autosomes (Orlov and Bulatova 1983). X is a submetacentric chromosome. Y is an acrocentric chromosome. A C-banded karyotype shows 12 pairs of metacentric chromosomes: 4 pairs are deficient in the material that stains as constitutive heterochromatin under conditions in which the centromeres of all the acrocentric chromosomes and the remaining 8 pairs of metacentric chromosomes stain darkly. The Y chromosome is largely heterochromatic. The X chromosome lacks constitutive heterochromatin at the centromere, but a prominent interstitial C-band is present in the medial area of each long arm (Cribiu and de Giovanni 1978).

The submetacentric nature of the X chromosome is evidence for a divergence of *E. asinus* from the main line of equid evolution (Cribiu and de Giovanni 1978). Comparison of amino acid sequences of *E. asinus* with those of *E. caballus* reveals a 61% homology (Leigh and Stewart 1990). Most differences are in the C-terminal extension, due to 2 nucleotide insertions in the *E. asinus* sequence, leading to a reading-frame shift. Amino acid homology in the disulfide core region is 81%. Four transferrin polymorphisms, 2 albumin polymorphisms, and 1 6-phosphogluconate dehydrogenase are unique to *E. asinus* (Bell 1994). The species can be separated into 3 groups based on erythrocyte K^+ and Na^+ polymorphisms. One group has a lower number of polymorphisms than the mammalian normal, 1 is equal to the normal, and another is above normal (Miseta et al. 1993). Hemoglobin studies reveal that *E. asinus* has only 1 hemoglobin detectable with electrophoresis in contrast to polymorphisms in the horse involving alpha chain duplication. When alpha and beta chain sequences are compared, wild asses, onagers, and zebras are related more to each other than they are to horses (Clegg 1974). Among 6 alternative trees based on mitochondrial DNA, the 3 zebra species (*burchelli*, *grevyi*, and *zebra*) usually form a single branch, whereas *asinus* and *hemionus* form another, and *caballus* (including *E. c. przewalski*) represents a 3rd branch most divergent from the other 2 (George and Ryder 1986).

CONSERVATION STATUS. The International Union for the Conservation of Nature and Natural Resources has listed *E. a. somaliensis* as an endangered species since 1968 (Clutton-Brock 1992; Moehlman 1974) and may be the most endangered equine species on earth (Clark 1983). *E. asinus* was not, as of 1983, listed by the Convention on International Trade in Endangered Species of Flora and Fauna as an Appendix I species. The main population center of surviving *E. a. somaliensis* is in Ethiopia, along the northern stretches of the Awash River. The habitat is harsh, and it is a traditional no-man's-land between the constantly warring Issa and Affar tribes. The Eritrean revolutions and the Sahel drought also were detrimental to populations of *E. asinus*. Livestock grazing is on the increase, which affects the wild ass by leaving them with no food and by concentrating animals at water holes, which the wild ass will then not use.

REMARKS. Based on morphology, domestication of the wild ass probably occurred 1st in either the Near East (Dennler de la Tour 1975; Hehn 1885) or based on historical evidence, in northeastern Egypt (Pocock 1909) or northwestern Africa (Antonius 1938). It may have occurred in Arabia (Groves et al. 1966), but this conclusion was based on the view that the Nubian and Somali wild asses should be ruled out as ancestors on morphological grounds (Groves 1986). However, Clutton-Brock (1992) claimed that depictions of domestic asses of ancient Egypt were of the Nubian type, which were depicted as a hunted animal in ancient Egyptian art.

Archeological remains are rare in the early Holocene, and discriminating wild from early domestic asses is virtually impossible (Clutton-Brock 1987). However, the oldest specimen of wild ass is claimed to be from Syria (Ducos 1986), dated to ca. 9,000 BC (Burleigh 1986), whereas the oldest domestic ass appears in Egypt ca. 4,000 BC and in Mesopotamia (Dennler de la Tour 1975), or in late 4th millennium Sumer (Postgate 1986), and southern Iran by ca. 2,800 BC (Zeder 1986). This is later by ca. 6,000 years than the domestication of the horse (Anthony and Brown 1991) and contacts with neighboring horse nomads to the north and northeast may have stimulated ass domestication. The chronology suggests that the 1st domestication of wild asses occurred in northern Africa or the adjacent Near East, and domestic ass breeding spread eastward into Mesopotamia and Iran. Its spread north and west into Europe can only be conjectured. Hehn (1885) described movement northward through Anatolia to Greece, and thence around the Adriatic Sea to Italy and southern Europe. Clutton-Brock (1987) thinks it likely that the North African ass was imported into southern Europe from Algeria by the Romans before the wild population was exterminated.

The practice of crossbreeding the ass with other equids may be nearly as old as its domestication. The 1st equid to be mated to the domestic donkey was the onager (*Equus hemionus*), the earliest hybrid being ca. 3,000 BC in Palestine (Burleigh 1986). At about the same time in southern Iran, the domestic ass was the most common equid, but wild onagers were hunted for their meat, and evidence is lacking for ass–onager interbreeding (Zeder 1986). Later, when domestic horses were brought into Asia Minor from the north, domestic asses were crossed with them to produce mules. Greek texts place the 1st mule breeding in what is now northwestern Anatolia (Hehn 1885), and by the end of the 3rd millennium, onagers ceased to be used in Mesopotama, being replaced by horses. Farther east and south, the 1st mule remains to be identified in Iran are dated to ca. 1,800 BC (Zeder 1986).

Large populations of feral *E. asinus* exist in the western United States (Perryman and Muchlinski 1987; Ruffner and Carothers 1982). The 1st written record of asses introduced into the Americas by Spanish explorers was that of Ganzalo Jimenez de Quesada in 1536 (Cabrera 1945). However, they may have accompanied horses and other livestock that were brought by Columbus's 2nd voyage to Hispaniola in 1494 (Bennett 1998). A little more than a century later, in 1598, Juan De Onate brought horses to the southern Great Plains at Santa Fe (Bennett 1998), and a year later, in 1599, donkeys were present near present-day El Paso (Zarn et al. 1977); probably soon after, some individuals escaped to form feral populations (Clutton-Brock 1992). Before the advent of the railroad in the 19th century, no large feral populations existed because they were too valuable to be allowed to escape (Ruffner and Carothers 1982). In the last several centuries, feral populations of *E. asinus* have grown and compete with native ungulates and livestock for scarce rangeland resources (Hanley and Brady 1977b; Perryman and Muchlinski 1987; Ruffner and Carothers 1982; Seegmiller and Ohmart 1981; Woodward and Ohmart 1976). The Wild, Free-Roaming Horse and Burro Act of 1971 requires the protection, management, and control of wild free-roaming horses and burros on public lands. The National Park Service is specifically exempt from this law and has removed feral *E. asinus* causing environmental damage in parks. Some animals have been shot, whereas others have been removed alive and put up for adoption (National Park Service 1980).

A similar situation has occurred in Western Australia. Domesticated *E. asinus* was brought to that continent for labor and transportation. After the railroads became established, escaped animals formed large feral populations. Feral *E. asinus* causes soil erosion and pasture degradation. Management of feral *E. asinus* includes culling from helicopters and from the ground; however, *E. asinus* has a high reproductive rate in these areas, and constant culling is needed to maintain low population numbers (McCool et al. 1981; Wheeler 1987).

The scientific name of the wild ass is derived from 2 Latin words, *Equus* meaning horse, and *asinus* meaning ass, which is derived from an archaic word, *asnos*, from asia Minor (Hehn 1885; Nielson 1958).

We are grateful to D. Bennett, who made many useful suggestions on this manuscript. V. Eisenmann and A. Forsten reviewed earlier drafts. Y. Petryszn photographed the skulls. P. M. Velazco obtained skull measurements. The Cullman Library of the Smithsonian Institution provided valuable reference information.

LITERATURE CITED

ALLEN, G. M. 1939. A checklist of African mammals. Bulletin of the Museum of Comparative Zoology at Harvard College 83: 1–763.

ALLEN, J. A. 1909. Mammals from British East Africa, collected by the Tjäder Expedition of 1906. Bulletin of the American Museum of Natural History 26:147–175.

ANSELL, W. F. H. 1971. Order Perissodactyla. Part 14 in The mammals of Africa: an identification manual (J. Meester and H. W. Setzer, eds.). Smithsonian Institution Press, Washington, D.C.

ANTHONY, D. W., AND D. R. BROWN. 1991. The origins of horseback riding. Antiquity 65:22–38.

ANTONIUS, O. 1938. On the geographical distribution, in former times and today, of the Recent Equidae. Proceedings of the Zoological Society of London, B. Biological Sciences 107(for 1937):557–564.

AZZAROLI, A. 1995. A synopsis of the Quaternary species of *Equus* in North America. Bollettino della Società Paleontologica Italiana 34:205–221.

BAGTACHE, B., D. HADJOUIS, AND V. EISENMANN. 1984. Presence d'un *Equus* caballing (*E. algericus* n. sp.) et d'un autre espece nouvelle d'*Equus* (*E. melkiensis* n. sp.) dans l'Alterian des Allobroges, Algerie. Comptes Rendus de l'Academie des Sciences, Paris, Serie II:609–612.

BELL, K. 1994. Blood protein polymorphisms in the donkey (*Equus asinus*). Animal Genetics 25:109–113.

BENNETT, D. K. 1980. Stripes do not a zebra make, part I: a cladistic analysis of *Equus*. Systematic Zoology 29:272–287.

BENNETT, D. K. 1992. The evolution of the horse. Pp. 1–40 in Horse breeding and management (J. W. Evans, ed.). Elsevier, Amsterdam, Netherlands.

BENNETT, D. [K.] 1998. Conquerors: the roots of New World horsemanship. Amigo Publications, Inc., Solvang, California.

BERGER, J. 1983. Predation, sex ratios, and male competition in equids (Mammalia: Perissodactyla). Journal of Zoology (London) 201:205–216.

BLAKE, J. G., AND C. L. DOUGLAS. 1981. Spatial variation in transferring allele frequencies among herds of feral donkeys in Death Valley National Monument, California. Journal of Mammalogy 62:58–63.

BODDAERT, P. 1784. Elenchus animalium. C. R. Hake, Rotterdam, Netherlands.

BOULE, M. 1900 (for 1899). Observations sur quelques équidés fossiles. Bulletin de la Société Géologique de France, Series 3, 27:531–542.

BRIDGEWATER, W., AND K. KURTZ (eds.). 1963. The Columbia encyclopedia. Third edition. Columbia University Press, New York.

BRISSON, A. D. [=M. J.] 1762. Regnum animale in classes IX. Distributum, sive synopsis methodica. Theodorum Haak, Lugduni Batavorum [= Leiden], Netherlands.

BURLEIGH, R. 1986. Chronology of some early domestic equids in Egypt and western Asia. Pp. 230–236 in Equids in the ancient world (R. H. Meadow and H. P. Uerpmann, eds.). Ludwig Reichert Verlag, Wiesbaden, Germany.

CABRERA, A. 1945. Caballos de America. Editorial Sudamerica, Buenos Aires, Argentina.

CHOQUENOT, D. 1991. Density-dependent growth, body condition, and demography in feral donkeys: testing the food hypothesis. Ecology 72:805–813.

CHURCHER, C. S. 1982. Oldest ass recovered from Olduvai Gorge, Tanzania, and the origin of asses. Journal of Paleontology 56: 1124–1132.

CHURCHER, C. S. 1986. Equid remains from Neolithic horizons at Dakhleh Oasis, western desert of Egypt. Pp. 413–421 in Equids in the ancient world (R. H. Meadow and H. P. Uerpmann, eds.). Ludwig Reichert Verlag, Wiesbaden, Germany.

CHURCHER, C. S., AND M. L. RICHARDSON. 1978. Equidae. Pp.

379–422 in Evolution of African mammals (V. J. Maglio and H. B. S. Cooke, eds.). Harvard University Press, Cambridge, Massachusetts.

Clark, B. 1983. African wild ass. Oryx 17:28–31.

Clegg, J. B. 1974. Horse hemoglobin polymorphism. Annals of the New York Academy of Sciences 241:61–69

Clutton-Brock, J. 1987. A natural history of domesticated mammals. Cambridge University Press and British Museum (Natural History), Cambridge, United Kingdom.

Clutton-Brock, J. 1992. Horse power: a history of the horse and donkey in human societies. Harvard University Press, Cambridge, Massachusetts.

Corbet, G. B. 1978. The mammals of the Palaearctic region: a taxonomic review. British Museum of Natural History, London, United Kingdom.

Cribiu, E. P., and A. de Giovanni. 1978. Le caryotype du cheval domestique (*Equus caballus*) de l'ane (*Equus asinus*) et du mulet par la methode des bandes C. Annales de Genetique et de Selection Animale 10:161–170.

Cuvier, G. 1821. Dictionnaire des sciences naturelles, dans lequel on traite méthodiquement des différens êtres de la nature, considérés soit en eux-mêmes, d'après l'état actuel de nos connoissances, soit relativement à l'utilité qu'en peuvent retirer la médecine, l'agriculture, le commerce et les arts. Volume 20. F. G. Levrault, Strasbourg, Austria, and Le Normant, Paris, France.

de Beaux, O. 1928. Riabilitazione del termine "*taeniopus* Heuglin" per l'asino sevatico samalo. Bollettino dei Musei di Zoologia e Anatomia Comparata della R. Università di Genova 8(27):1–13.

Denman, E. 1957. Animal Africa. Robert Hale Limited, London, England.

Dennler de la Tour, G. 1975. Frühgeschichtliche haltung und Zucht von Halbesein. Säugetierkunde Mitteilungen 23:101–107.

de Winton, E. W. 1896. Two new subspecies of zebra from central and east Africa. Annals and Magazine of Natural History, Series 6, 17:319.

Dietrich, W. O. 1959. *Hemionus* Pallas im Pleistozän von Berlin. Vertebrata Palasiatica 3:13–22.

Dollman, J. G. 1935. A new race of wild ass from the Sudan, *Asinus asinus dianae*, subsp. nov. Proceedings of the Linnaean Society of London 147:132–134.

Ducos, P. 1968. l'Origin des animaux domestiques en Palestine. Publications de l'Institut de Prehistoire de l'Universite de Bordeaux, Memorie 6:26–30.

Ducos, P. 1986. The equid of Tell Muraibit, Syria. Pp. 237–245 in Equids in the ancient world (R. H. Meadow and H. P. Uerpmann, eds.). Ludwig Reichert Verlag, Wiesbaden, Germany.

Dupuy, A. 1966. Especes menaces du territore Algerien. Travaux de l'Institut de Recherches Sahariennes 25:29–56.

Eisenmann, V. 1986. Comparative osteology of modern and fossil horses, half-asses, and asses. Pp. 67–116 in Equids in the ancient world (R. H. Meadow and H. P. Uerpmann, eds.). Ludwig Reichert Verlag, Wiesbaden, Germany.

Eisenmann, V., and S. Beckouche. 1986. Identification and discrimination of metapodials from Pleistocene and modern *Equus*, wild and domestic. Pp. 117–163 in Equids in the ancient world (R. H. Meadow and H. P. Uerpmann, eds.). Ludwig Reichert Verlag, Wiesbaden, Germany.

Fitzinger, L. J. 1857–1860. Wissenschaftlische-populare Naturgeschichte der Saugethiere in ihren sammtlichen Hauptformen. Hebst einer Einleitung in die Naturgeschichte uberhaupt and in die Lehre von Thieren insbesondere. Ein Hilfsbuch fur Lehrer auch beim Unterrichte der Blinden. (Atlas 1860) 6 Bande complet. 3 (not seen, cited in Schlawe 1980).

Forsten, A. 1989. Horse diversity through the ages. Biological Review 64:279–304.

Frechkop, S. 1967. La distribution geographique et les nombres specifiques de chromosomes des Equides. Mammalia 31:295–299.

Freeland, W. J., and D. Choquenot. 1990. Determinants of herbivore carrying capacity: plants, nutrients, and *Equus asinus* in northern Australia. Ecology 71:589–597.

Frisch, J. L. 1775. Das natur-system der veirfussigen theire. Publisher unknown, Glogau, Germany.

Geoffroy-Saint-Hilaire, I. 1855a. Sur deux chevaux sauvages, d'une espèce nouvelle (*Equus hemippus*), donnés par S. M. l'Impératrice à la Ménagerie du Muséum d'Histoire Naturelle. Compte Rendus de Academie des Sciences Paris 41:1214–1219.

Geoffroy-Saint-Hilaire, I. 1855b. Sur le genre cheval, et en particulier sur 'hémione et l'onagre. Compte Rendus de Academie des Sciences Paris 41:1220–1224.

George, M., Jr., and O. A. Ryder. 1986. Mitochondrial DNA evolution in the genus *Equus*. Molecular Biology and Evolution 3:535–546.

Gmelin, J. F. 1788. Revision of 'Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis synonymis, locis' by C. Linneaus. G. E. Beir, Lipsiae, Germany 1:1–232.

Gray, J. E. 1825. A revision of the family Equidae. Zoological Journal 31:241–556.

Groves, C. P. 1974. Horses, asses and zebras in the wild. David and Charles, London, United Kingdom.

Groves, C. P. 1986. The taxonomy, distribution, and adaptations of recent equids. Pp. 11–65 in Equids in the ancient world (R. H. Meadow and H. P. Uerpmann, eds.). Ludwig Reichert Verlag, Wiesbaden, Germany.

Groves, C. P., and V. Mazak. 1967. On some taxonomic problems of Asiatic wild asses; with the description of a new subspecies (Perissodactyla; Equidae). Zeitschrift für Säugetierkunde 32:321–384.

Groves, C. P., and D. P. Willoughby. 1981. Studies on the taxonomy and phylogeny of the genus *Equus*. Subgeneric classification of the recent species. Mammalia 45:321–354.

Groves, C. P., F. Ziccardi, and A. Toschi. 1966. Taxonomy. Pp. 2–11 in Sull' Asino Selvatico Africano. Supplemento ala Ricerche de Zoologia Aplicata alla Caccia 5:1–11.

Grubb, P. 1993. Order Perissodactyla. Pp. 369–372 in Mammal species of the world (D. E. Wilson and D. M. Reider, eds.). Second edition. Smithsonian Institution Press, Washington, D.C.

Hanley, T. A. 1977a. Feral burro impact on a Sonoran Desert range. Journal of Range Management 30:374–377.

Hanley, T. A., and W. W. Brady. 1977b. Seasonal fluctuation in nutrient content of feral burro forages, Lower Colorado River Valley, Arizona. Journal of Range Management 30:370–373.

Harper, F. 1940. The nomenclature and type localities of certain Old World mammals. Journal of Mammalogy 21:191–203.

Hehn [Heyn], V. 1885. The wanderings of plants and animals from their first home (J. S. Stallybrass, ed.). Swan Sonnenschein and Company, London, England.

Heller, E. 1912. New genera and races of African ungulates. Smithsonian Miscellaneous Collections 60(8):1–16.

Henry, M., S. M. McDonnell, L. D. Lodi, and E. L. Gastal. 1991. Pasture mating behaviour of donkeys (*Equus asinus*) at natural and induced oestrus. Journal of Reproduction and Fertility 44(supplement):77–86.

Heuglin, T., von. 1861a. Forschungen über die Fauna des Rothen Meeres und der Somali-Küste. Ein systematisches Verzeichniss der Säugerthiere und Vögel, welche in diesen Regionen bisher beobachtet worden sind, mit Rüchsicht auf geogr. Petermann's Mittheilungen aus Justus Perthes' Geographischer Anstalt über Wichtige Neue Erforschungen auf dem Gesammtgebiete der Geographie. Justus Perthes, Gotha, Germany.

Heuglin, T., von. 1861b. Diagnosen neuer Säugethiere aus Afrika am Rothern Meere. Nova Acta Academis Caesar Leopoldino-carolinian (Jena) 28(10):1–5, 2 plates.

Heuglin, T., von, and L. J. Fitzinger. 1867. Systematische Übersicht der Saügethiere Nordost-Afrika's mit einschluss der arabischen Küste, des rothen Meeres, der Somali- und der Nilquellen-Länder, südwärts bis zum vierten Grade nördlicher Breite. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-naturwissenschaftliche Classe 54: 537–611.

Hufnagl, E. 1972. Libyan mammals. Oleander Press, Cambridge University Press, United Kingdom.

Izraely, H., I. Choshniak, C. E. Steven, and A. Shkolnik. 1989. Energy digestion and nitrogen economy of the domesticated donkey (*Equus asinus asinus*) in relation to food quality. Journal of Arid Environments 17:97–101.

Jones, N. L., K. A. Houpt, and T. R. Houpt. 1989. Stimuli of thirst in donkeys (*Equus asinus*). Physiology and Behavior 46: 661–665.

Kingdon, J. 1997. The Kingdon field guide to African mammals. Academic Press, London, United Kingdom.

Klingel, H. 1974. A comparison of the social behaviour of the Equidae. Pp. 124–132 in The behaviour of ungulates and its relation to management (V. Geist and F. R. Walther, eds.). International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.

Klingel, H. 1977. Observations on social organization and behaviour of African and Asiatic wild asses. Zeitschrift für Tierpsychologie 44:323–331.

Leigh, S. E. A., and F. Stewart. 1990. Partial cDNA sequence for the donkey chorionic gonadotropin-B subunit suggests evolution from an ancestral LH-B gene. Journal of Molecular Endocrinology 4:143–150.

Lewis, C. T., and C. Short. 1907. Harper's Latin dictionary. American Book Company, New York.

Linnaeus, C. 1746. Fauna Svecica, sistens Animalia Svecica regni: Quadrupedia, Aves, Amphibia, Pisces, Insecta, Vermes, distributa per classes and ordines, genera & species, cum differentiis specierum sysnonymis autorum, nominibus incolarum, locis habitationum, descriptionibus insectorum. Laurentii Salvii, Stockholm, Sweden.

Linnaeus, C. 1758. System naturae per gena tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentis, synonymis, locis. Tenth edition. Laurentii Salvii, Stockholm, Sweden.

Lydekker, R. 1905. Notes on the specimens of wild asses in English collections. Novitates Zoologie, London 11:583–596.

Maloiy, G. M. O. 1971. Temperature regulation in the Somali donkey (*Equus asinus*). Comparative Biochemistry and Physiology, A. Comparative Physiology 39:403–412.

Matschie, P. 1922. Bemerkungen über einige tibetanische Säugetiere. Sitzungsberichte der Gesellschaft Naturforschender Fruende zu Berlin 1922(3–5):65–77.

McCool, C. J., C. C. Pollitt, G. R. Fallon, and A. F. Turner. 1981. Studies of feral donkeys in the Victoria River–Kimberlys area. Australian Veterinary Journal 57:444–449.

McCort, W. D. 1979. Behavior of feral horses and ponies. Journal of Animal Science 58:493–499.

Miseta, A., P. Bogner, M. Kellermayer, D. N. Wheatley, I. Takacs, G. Nagy, and I. L. Cameron. 1993. Erythrocyte potassium and sodium polymorphisms in donkey (*Equus asinus*). Comparative Biochemistry and Physiology, A. Comparative Physiology 106:479–482.

Moehlman, P. 1974. Behavior and ecology of feral asses (*Equus asinus*). Ph.D. dissertation, University of Wisconsin, Madison, 251 pp.

Mueller, P. J., M. T. Jones, R. E. Rawson, P. J. Van Soest, and H. F. Hintz. 1994. Effect of increasing work rate on metabolic responses of the donkey (*Equus asinus*). Journal of Applied Physiology 77:1431–1438.

National Park Service. 1980. Proposed feral burro management and ecosystem restoration plan. National Park Service, Grand Canyon National Park, Arizona.

Neilson, W. A. (ed.). 1958. Webster's new international dictionary of the English language. Second edition. G. and C. Merriam Company, Springfield, Massachusetts.

Noack, T. 1884a. Neues aus der Tierhandlung von Karl Hagenbeck, sowie aus dem Zoologischen Garten Hamburg. Zoologische Garten 25:100–115.

Noack, T. 1884b. Zur Fauna des Somalilandes. Zoologische Garten 25:374–375.

Orlov, V. N., and N. S. Bulatova. 1983. Sravnitel'naya Tsitogenetika I Kariosistematika Mlekopitayushikh. [Comparative cytogenetics and caryosystematics of mammals.]. Nauka, Moscow, Russia.

Osborn, D. J., and I. Helmy. 1980. The contemporary land mammals of Egypt (including Sinai). Fieldiana: Zoology (New Series) 5:1–579.

Oustalet, E. 1882. Une novelle espèce de zebre: le zèbre de Grévy (*Equus grevyi*). La Nature (Paris) 10:12–14.

Pallas, P. S. 1775. *Equus hemionus*, mongolis dshikketaei dictus. Academie Sciences Petropoli [St. Petersburg] 19:394–417.

Peel, C. V. A. 1900. Somaliland: being an account of two expeditions into the far interior together with a complete list of every animal and bird known to inhabit that country, and a list of reptiles collected by the author. F. E. Robinson & Co., London, England (reprinted 1986, Darf Publishers Ltd., London, United Kingdom).

Perryman, P., and A. Muchlinski. 1987. Population dynamics of feral burros at the Naval Weapons Center, China Lake, California. Journal of Mammalogy 68:435–438.

Pocock, R. I. 1909. On the agriotype of domestic asses. Annals and Magazine of Natural History 4:523–528.

Pocock, R. I. 1948. Comments on some races of the Asiatic wild asses (*Microhippus*), with a description of the skull of the Chigetai. Proceedings of the Zoological Society of London 117: 764–767.

Polyakov, I. S. 1881. Loshad' Przheval'skovo (*Equus przewalskii* n. sp.). Izdanie Imperatorskavo Russkavo Geograficheskavo Obshchestva 17:1–20.

Postgate, J. N. 1986. The equids of Sumer, again. Pp. 194–206 in Equids in the ancient world (R. H. Meadow and H. P. Uerpmann, eds.). Ludwig Reichert Verlag, Wiesbaden, Germany.

Quinn, J. H. 1957. Pleistocene Equidae of Texas. University of Texas, Bureau of Economic Geology, Report of Investigations 33:1–51.

Radulesco, C., and P. Samson. 1962. Remarques sur quelques equides quarternaires de Roumanie. Zoologischer Anzeiger 169:170–179.

Rafinesque, C. S. 1815. Analyse de la nature; ou, tableau de l'universe et des corps organises. Jean Barravecchia, Palermo, Italy.

Reichenau, W., von. 1915. Beiträge zur näheren kenntnis fossiler pferde aus deutschem Pleistozän, insbesondere über die entwicklung und die abkaustadien des gebisses vom Hochterrassenpferd (Equus mosbachensis v. R.). Abhandlungen der Grossherzoglich Hessischen Geologischen Landesanstalt zu Darmstadt 7(1):1–155, 14 plates.

Robertshaw, D., and C. R. Taylor. 1969. Sweat gland function of the donkey. American Journal of Physiology 219:1522–1527.

Romer, A. S. 1928. Pleistocene mammals of Africa. Fauna of the Paleolithic station of Mechta-el-Arbi. Bulletin of Logan Museum 1:80–163.

Ruffner, G. A., and S. W. Carothers. 1982. Age structure, condition and reproduction of two *Equus asinus* (Equidae) populations from Grand Canyon National Park, Arizona. Southwestern Naturalist 27:403–411.

Ryder, O. A., N. C. Epel, and K. Benirschke. 1978. Chromosome banding studies of the Equidae. Cytogenetics and Cell Genetics 20:323–350.

Schlawe, L. 1980. Kritisches zur Nomenklatur und taxonomischen Beurteilung von *Equus africanus* (Fitzinger, 1858). Equus (Prague) 2:101–127.

Schlawe, L. 1986. Seltene Pfleglinge aus Dschungarei und Mongolei: Kulane, *Equus hemionus hemionus* Pallas, 1775. Zoologische Garten, Neue Folge 56:299–323.

Schomber, H. W. 1963. Wildlife in the Sudan. Part IV. Desert and semi-desert game animals. African Wildlife 17:117–124.

Sclater, P. L. 1885. On some mammals from Somali-land. Proceedings of the Zoological Society (for 1884):538–542.

Seegmiller, R. F., and R. D. Ohmart. 1981. Ecological relationships of feral burros and desert bighorn sheep. Wildlife Monographs 78:1–58.

Shortridge, G. C. 1934. The mammals of south west Africa. W. Heinemann, London, England.

Sidney, J. 1965. The past and present distribution of some African ungulates. Transactions of the Zoological Society of London 30:1–397.

Smith, C. H. 1841. The naturalist's library (W. Jardine, ed.). Volume 20. Mammalia. Horses. W. H. Lizars, Edinburgh, Scotland (not seen, cited in Allen 1939).

Smith, C. H. 1845. The naturalist's library (W. Jardine, ed.). Second edition. Volume 20. Mammalia. Horses. W. H. Lizars, Edinburgh, Scotland.

Stehlin, H. V., and Graziosi, P. 1935. Richerche sugli Asinidi fossili d'Europa. Memoires de la Societe Paleontologique Suisse 56:1–73, plates 1–10.

The Times. 1967. Atlas of the world. Comprehensive edition. The

Times of London, J. Bartholomew & Sons, Houghton Mifflin Company, Boston, Massachusetts.

Thomas, P. 1884. Recherches stratigraphiques et paléontologiques sur quelques formations d'eau douce de l'Algérie. Memoires de Société Geologique de France 3(2):1–51.

Trumler, E. 1961. Entwurf einer systematik der rezenten equiden und ihrer fossilen verwandten. Säugetierkundiche Mitteilungen, Stuttgart 9:109–125.

Uerpmann, H. P. 1981. The major faunal areas of the Middle East during the late Pleistocene and early Holocene. Pp. 99–106 in Colloques Internationaux du C. N. R. S. No. 598–Prehistoire du Levant, Paris, France.

Uerpmann, H. P. 1986. Halafian equid remains from Shams ed-Din Tannira in northern Syria. Pp. 246–265 in Equids in the ancient world (R. H. Meadow and H. P. Uerpmann, eds.). Ludwig Reichert Verlag, Wiesbaden, Germany.

Werth, E. 1930. Zur Abstammung des Hausesels. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin (for 1929):342–355.

Wheeler, S. H. 1987. An assessment of donkey control in Kimberly. Western Australia Journal of Agriculture 25:24–26.

Wolfe, M. L., L. C. Ellis, and R. MacMullen. 1989. Reproductive rates of feral horses and burros. Journal of Wildlife Management 53:916–924.

Woodward, S. L., and R. D. Ohmart. 1976. Habitat use and fecal analysis of feral burros (*Equus asinus*), Chemehuevi Mountains, California, 1974. Journal of Range Management 29:482–485.

Zarins, J. 1986. Equids associated with human burials in third millennium B.C. Mesopotamia: two complementary facets. Pp. 164–193 in Equids in the ancient world (R. H. Meadow and H. P. Uerpmann, eds.). Ludwig Reichert Verlag, Wiesbaden, Germany.

Zarn, M., T. Heller, and K. Collins. 1977. Wild, free-roaming burros. State of present knowledge. Technical Note 294. Department of the Interior and Department of Agriculture, Washington, D.C.

Zeder, M. A. 1986. The equid remains from Tal-e Malyan, southern Iran. Pp. 366–412 in Equids in the ancient world (R. H. Meadow and H. P. Uerpmann, eds.). Ludwig Reichert Verlag, Wiesbaden, Germany.

Ziccardi, F. 1970. The African wild ass: part I. African Wild Life 24:202–208.

Zimmerman, E. A. W. 1780. Geographische Beschichte des Menschen und der vierfusigen Theire. Weygandschen Buchhandlung, Leipzig, Germany 2:1–432.

Associate editors of this account were Elaine Anderson, Leslie Carraway, and Lui Marinelli. Editor was Virginia Hayssen.

Martha I. Grinder (deceased) and Paul R. Krausman, Wildlife and Fisheries Program, 325 Biological Sciences East Building, School of Renewable Natural Resources, The University of Arizona, Tucson, Arizona 85721. Robert S. Hoffmann, Senior Scientist, Division of Mammals, NHB 390, MRC 108, Smithsonian Institution, P.O. Box 30712, Washington, D.C. 20013-7012.