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Equus grevyi.

By C. S. Churcher

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Equus grevyi Oustalet, 1882

Grévy's Zebra

Equus grevyi Oustalet, 1882:12. Type locality "region de l'Afrique orientale qu'on appelle le pays des Gallas," Ethiopia; restricted by Roosevelt and Heller (1914:701) to the vicinity of Lake Zwai; however, stated by Rzasnicki (1951:242) as the province of Shoa, Abyssinia.

E[quus] faurei Matschie, 1898:180. Type locality "Schoa und das südliche Abessynien;" restricted by Roosevelt and Heller (1914: 701) to the vicinity of Lake Zwai; erroneously "Lake Rudolf region, Abyssinia" by Allen (1939:558).

CONTEXT AND CONTENT. Order Perissodactyla, Family Equidae, Genus *Equus*, Subgenus *Dolichohippus*. The species is monotypic (Ansell, 1971; Willoughby, 1974).

DIAGNOSIS. *Equus grevyi* is the largest living zebra, standing 135 cm at the shoulder and 125–150 cm at the withers (Groves, 1974; Willoughby, 1974). The stripes are narrow and parallel sided, usually separated by narrower white bands, with a distinct chevron pattern on the hind quarters (Figs. 1, 2A). The head and neck are robust, and the metapodials slender.

The skull of *E. grevyi* has a relatively long rostrum and wide occipital crests that overhang the occipital condyles (Roosevelt and Heller, 1914; Fig. 3). The nasals are slightly concave and the frontoparietals convex in profile, as in *E. quagga* (= *E. burchelli*—Grubb, 1981). Minor cranial features are the transversely broad, usually single posterior palatine foramina, irregularly shaped supraorbital foramina, and mastoids that may enter the temporal areas. Both upper and lower incisors bear marks or infundibula (Churcher and Richardson, 1978).

The upper cheekteeth are larger than in *E. quagga* or *E. zebra*. Plis caballine are absent or weak and plis within fossettes variably developed (Fig. 4A). Parastyles and mesostyles are flat, obliquely truncated, and face mesiobuccally. Protocones are large, seldom elongate on the premolars, and less elongate on the molars than in other equids. Hypocones are distinct and rounded (Churcher and Richardson, 1978).

Ptychostylids are present, vestigial, or absent in the lower cheekteeth (Fig. 4B). Metaconids are rounded, metastylids inflated with a distobuccal point, and entoconids squared. Flexid floors are bent or angled (Churcher and Richardson, 1978).

GENERAL CHARACTERS. The stripe pattern of the type specimen from Shoa (Oustalet, 1882) represents that seen over the range of the Grévy's zebra, although each coat is individually distinct (Kingdon, 1979). Grévy zebras have the narrowest and closest-set stripes of all zebras, averaging 25–38 mm wide and spaced 20 mm apart on the flanks (Fig. 2; Willoughby, 1974). The coat pattern forms as equidistant stripes perpendicular to the dorsal midline during the 5th week of ontogeny (Bard, 1984). The total number of body stripes is ca. 80 on a 5-week-old embryo ca. 32-mm long. The body stripes between the shoulder and hip chevrons number 18–26, including partial or branching stripes. The neck stripes encircle the throat and number 9–16, with the broadest up to 76 mm wide (Roosevelt and Heller, 1914; Willoughby, 1974; Figs. 1, 2A). The body stripes vary in width, with black broader than white or vice versa (Kingdon, 1979).

The clear ash-gray or white belly runs into the white body stripes and reaches the base of the tail (Dorst and Dandelot, 1970; Haltenorth and Diller, 1980). The middorsal black stripe is separated from the flank stripes by two narrow white stripes. Both fore and hind limbs have similar patterns of chevrons above the elbows and knees (Figs. 1, 2). Stripes extend down both legs to the hooves and encircle the lower legs.

The muzzle is ash-gray to almost black, with two dorsal points directed towards the eyes (Fig. 2B). The upper and lower lips have vibrissae and tactile genial hairs (Kingdon, 1979). The stripes on the forehead and cheeks are narrow and none reach the muzzle. The ears are large, rounded, broader towards the tip, thickly furred, with borders of black hairs on the sides and white on the ends from in front and white-tipped and based with a middle black band from behind. The erect mane is higher than the ears, extends from poll to withers, and carries the neck stripes (Figs. 1, 2A). The tail has a black dorsal stripe anteriorly, is cross-banded in the middle, and ends in a whisk of long black hairs. Grévy zebras may have small chestnuts on the forelegs (Groves and Willoughby, 1981). The hoofs are small, oval, and black, with a broad frog. The spoor is small and horse-like (Lydekker, 1926).

Grévy zebras are mule-sized (Ludolfus, 1681) with a robust conformation and a short, deep neck and heavy head, as in "a good-sized pony [*E. caballus*], such as a Connemara [or] Welsh mountain pony" (Willoughby, 1974:337). Shoulder height averages 1.35 m (range, 1.25–1.5 m—Ledger, 1963); males are taller than females (McMahon, 1975). The mean mass of nine male Grévy zebras from Baragoi, Kenya, was 385.8 kg (range, 352.9–430.9 kg—Ledger, 1963); males may attain 451 kg and females 350 kg (King, 1965). The average mass of an adult of either sex is >400 kg (Groves, 1974) or 431–451 kg in zoos (Wallach and Boever, 1983).

The skull is long and narrow, with a long diastema (Fig. 3), the cervical vertebrae are short, reflecting the stout neck (Groves, 1974), and the spine may be proportionately the longest of living equids (Stecher, 1962). The scapulae of *E. grevyi* are proportionately shorter and more robust than those of *E. asinus*. Grévy and common zebras have high narrow ilia in contrast to the low broad ilia of *E. caballus* (Willoughby, 1974). Grévy and common zebras have long bones of similar diameters, but those of Grévy zebras are more slender (McMahon, 1975). The splint metapodials are longer and less reduced than in other living equids (Groves, 1974). The ungual phalanges and hooves are broad posteriorly (Grubb, 1981).

DISTRIBUTION. Grévy zebras occupy arid areas of southern Ethiopia and northern Kenya (Fig. 5). The eastern distribution is north of the Tana River east of Garissa and the Lorian Swamp at

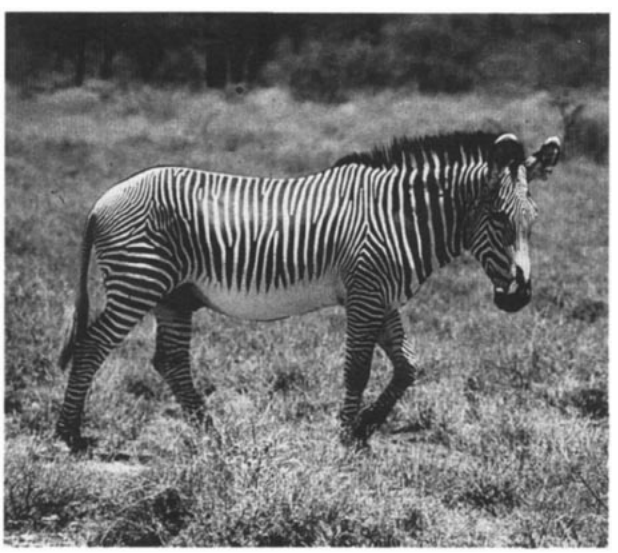

FIG. 1. Adult male Grévy's zebra, *Equus grevyi*, Samburu Game Park, Kenya.

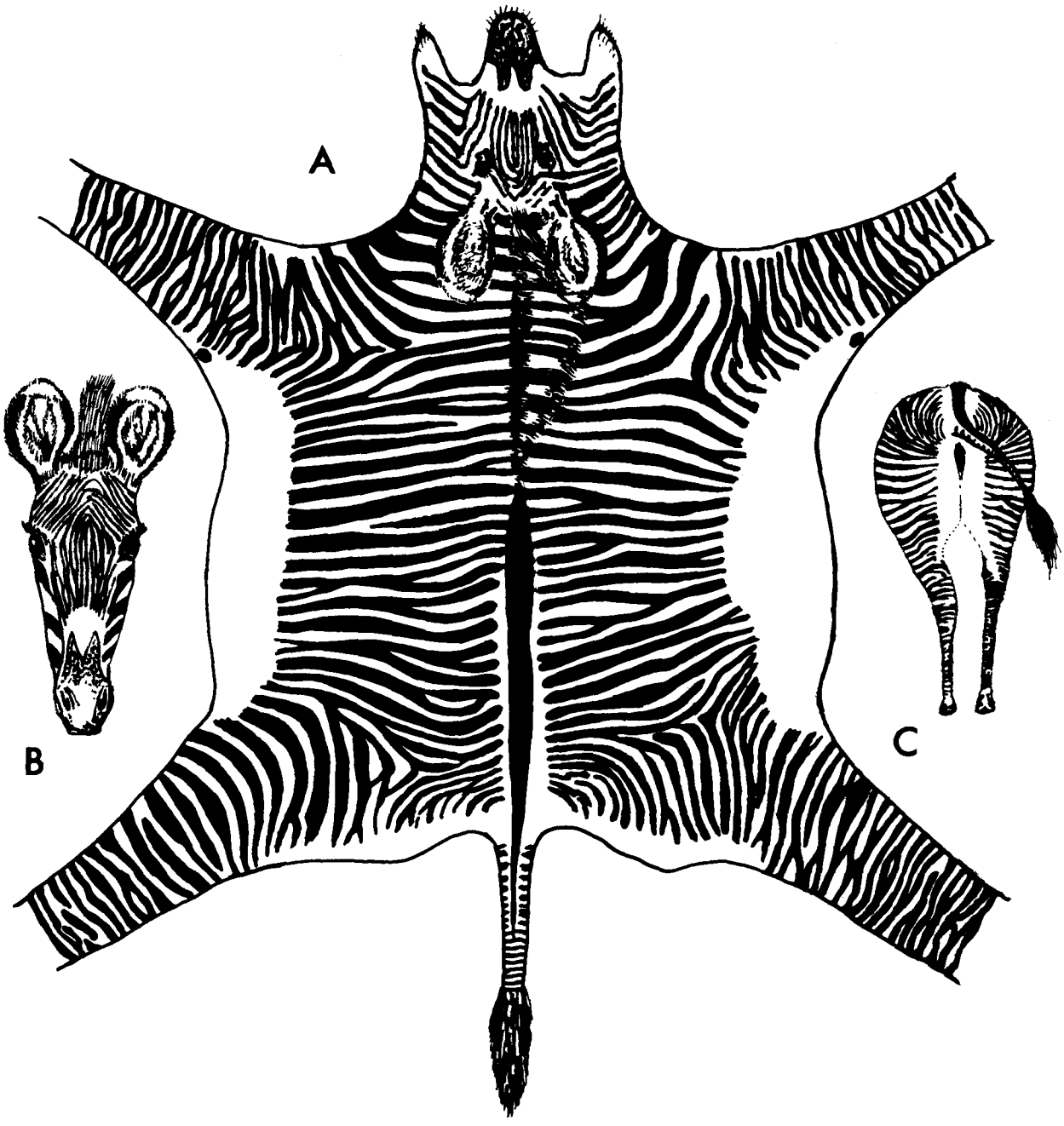

FIG. 2. Stripe patterns of Grévy's zebra, *Equus grevyi*. (A) Skin outline with patterns on left and right sides from different individuals, (B) frontal aspect, and (C) rear aspect, drawn from individuals photographed in Samburu and Meru Game Parks, Kenya.

ca. 1–1°30′S (Sidney, 1965; Stewart and Stewart, 1963). In the west, it lies east and north of a line from Mount Kenya to Ol Donyo Nyiro, and east of Lake Turkana to Ethiopia. In Ethiopia, it ranges east of the Omo River north to Lake Zwai, southeast to Lake Stephanie and to Marsabit in Kenya. It is absent in Boran country (Churcher, 1982; Groves, 1974).

Grévy zebras were recorded from the Galla country (Ludolfus, 1681) and Shoa highlands of Ethiopia, the Ogaden and western Somaliland plains, but not from the upper Webbe Shebeli Valley or the Haud's savannas; Durhi, south of Tug Fafan, was their northern limit (Lydekker, 1912). The Ogaden (Bale) population extended south from the east bank of the Juba River at 2–3°30′N, to the east bank of the Webi Shebeli at Gelib in southern Somalia (Lydekker, 1912). It is now extirpated from the Ogaden (Blower, 1968). Grévy zebras did not occur in British Somaliland in 1905 (Roosevelt and Heller, 1914; Sidney, 1965). It may have occurred on the plains south of Hargeisa (Drake-Brockman, 1910; Sydney, 1965). Somaliland included the Ogaden and Haud populations in 1890–1910 (Moreau et al., 1945).

FOSSIL RECORD. Grévy-type zebras are known from the Early Pleistocene to Recent of northeastern, eastern, and southern Africa (Fig. 5; Churcher and Richardson, 1978). The first African ancestor, *E. numidicus* (Pliocene, 5–2 × 10^6 years ago) comes from the Maghreb and Sudan, and evolved from a North American Pliocene species of *Dolichohippus*. The Late Pliocene to Late Pleistocene Cape (*E. capensis*) and Olduvai (*E. oldowayensis*) zebras descended from *E. numidicus*, are known from South and East Africa, and *E. numidicus* gave rise to the Holocene *E. grevyi*, known fossil from Egypt and East Africa (Churcher, 1970, 1981; Churcher and Watson, in press). *E. grevyi* occurred in Africa during the past 5 × 10^5 years and differs little from *E. oldowayensis* and *E. capensis* in osteology. Cheekteeth of Neolithic (5,000–3,500 before present) *E. grevyi* occur at Dakhleh Oasis, Egypt (Churcher, 1986).

FORM AND FUNCTION. Stripes may enhance the size of *E. grevyi* in low light or at close range (Cott, 1940) or may disrupt its outline (Lydekker, 1912; Mottram, 1915). At night or in shade

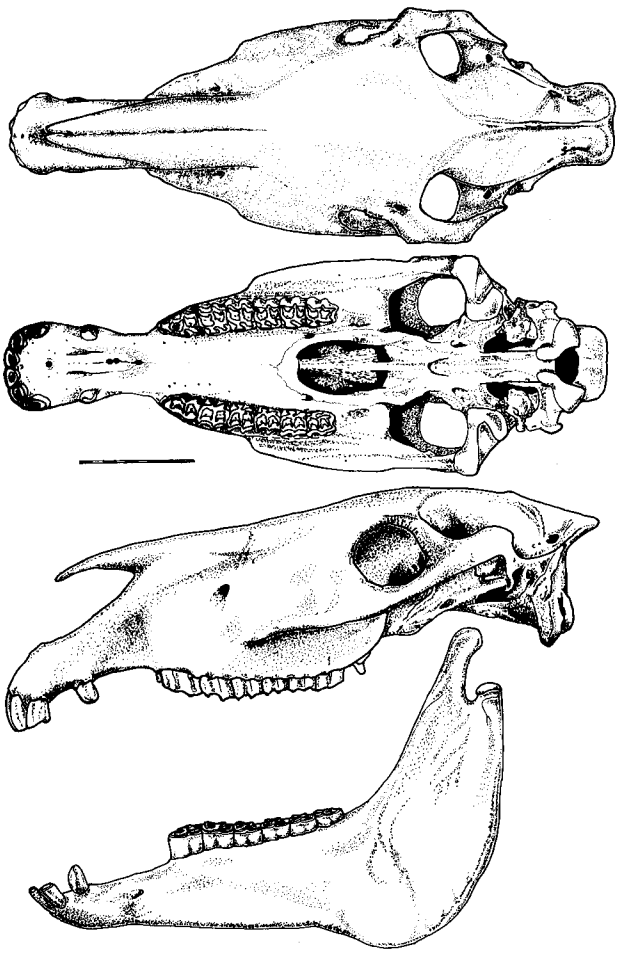

FIG. 3. Dorsal, ventral and lateral views of skull, and lateral view of mandible of a male Grévy's zebra, *Equus grevyi* (author's collection). Length from buccal surface of incisors to posterior surface of occipital condyles = 493 mm. Scale = 50 mm.

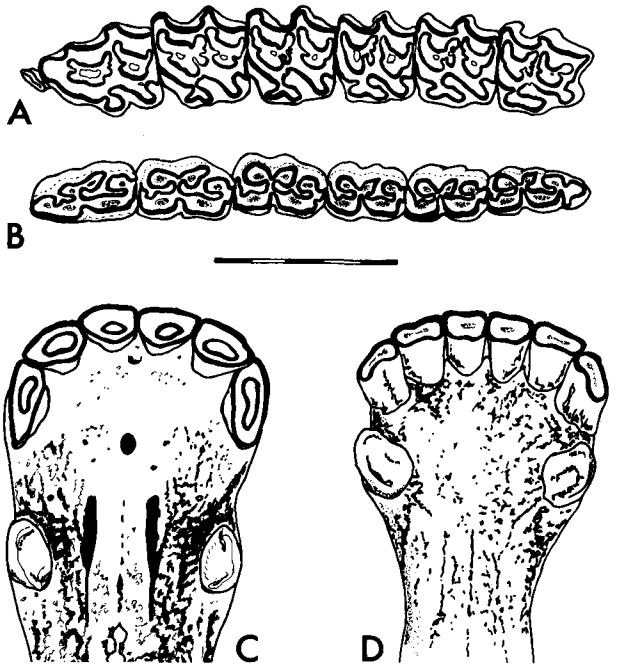

FIG. 4. Occlusal aspects of adult dentitions of male Grevy zebra, *Equus grevyi* (author's collection). (A) Left maxillary cheekteeth, p1–m3, (B) left mandibular cheekteeth, P2–M3, (C) upper incisors and canines, and (D) lower incisors and canines. Enamel patterns shown as heavy black lines, pits in cementum within fossettes lightly outlined, marks or infundibula in crowns of upper incisors open, and secondary dentine in lower incisors and cheekteeth shown stippled. Occlusal lengths of upper and lower cheek-tooth rows = 149 and 151 mm, respectively. Scale = 50 mm.

motionless Grévy zebras are unnoticeable at 15 m in moonlight or 5 m in starlight (Bard, 1984). Behind a screen of small branches its fine stripes blur a standing outline of the Grévy zebra at distances <100 m (Churcher, 1982).

The adult dental formula is i 3/3, c 1/1, p 4/4, m 3/3, total 44, with P1s seldom retained into middle age (Fig. 4A). The deciduous formula is di 3/3, dc 1/1, dp 4/4, total 32 (Churcher and Richardson, 1978). The lower incisors have marks in young adults, and those on i3s may open distolingually and distinguish Grévy zebras from the quaggas (Groves and Willoughby, 1981), but are subgenerically undiagnostic (Skinner, 1972). The strongly molarized premolars, complex enamel patterns forming elaborate platforms for triturating fibrous vegetation, and extreme hyposodonty are advanced equid characters correlated with caecal fermentation (Janis, 1976).

Grévy zebras need less water than quaggas and even less than cattle and thus may occupy an interzone "between the ranges of the arid-adapted wild ass and the water loving *E. quagga*" (Kingdon, 1979:147). It may be that only in this interzone can Grévy zebras successfully compete with the other two wild equids.

Grévy zebras in zoos live 22–30 years (Kingdon, 1979; Read et al., 1990). However, King (1965) reported an 18-year-old wild female.

Grévy zebras in zoos in North American are less cold tolerant than other zebras (Read et al., 1988). Under anaesthetic, their body temperatures are 37.0–37.3°C (G. Crawshaw, pers. comm.) or ≤39°C (Griner, 1983).

ONTOGENY AND REPRODUCTION. Newborn Grévy zebras are large-eared, spindly-legged, and precocious. A newborn at the Dallas Zoo, Texas, stood unsteadily at 6–14 min after birth (Read et al., 1988). By 20 min it tried to walk, and walked short distances at 30 min; by 45 min it ran short distances. It attempted to nurse at 29 min and could do so at 69 min. At 97 min it stood well, at 2 h nursed well, and defecated at 2.5 h.

Central milk incisors (di1) erupt before the young is 1-week old, lateral milk incisors (di3) appear at 1 month, adult first incisors (i1) at 2.5 years, and third incisors (i3) are worn at 4.5–5.5 years. Permanent first molars (m1) are in wear at ca. 1 year, second molars (m2) by ca. 2 years, and third molars (m3) by ca. 2.5 years. This eruptive sequence resembles that of horses more than quaggas (King, 1965). Canines normally erupt only in males (Mochi and MacClintock, 1976).

Grévy zebras reach puberty at ca. 4 years. The youngest fertile male was 3 years 7 months old (Dobroruka et al., 1987) although males in zoos may attain sexual potency between 7 months and 4–5 years of age (Read et al., 1988). Males remain potent to 18 years. The testes of a young male measured ca. 115 by 85 by 75 mm and weighed 475 g, with masses of 600 g and 550 g for those from a territorial and an aged male, respectively (King, 1965). Testosterone levels from three males were 41.5, 59.0, and 154.0 μg/100 g of testis (King et al., 1966).

Young female Grévy zebras reach puberty at 3–4 years when ovaries show ovulation fossae (as in *E. g. bohmi*). The diameter of a Graafian follicle is 30 mm and a corpus luteum 45 mm at diestrus. Early pregnancy occurs in both uterine horns. Reduced corpora lutea persist to term, and blood progesterone levels drop steeply during pregnancy. Follicular activity ceases at ca. 34 weeks, and resumes at ca. 42 weeks. Estrus in Grévy zebras in zoos occupies 2–9 days, of which 2–3 are receptive, in a 19–33 day cycle (King, 1965). Postpartum estrus lasts from 9 to 14 days (Nelson, 1986); one female came into estrus about 7 days after parturition (Read et al., 1988).

Female Grévy zebras first produce young at 3–6 years (Read et al., 1988). The youngest to give birth was 4 years 4 months, and impregnated at about 3 years 3 months. The male to female ratio at birth is 1.09:1.00, n = 94 (Dobruruka et al., 1987).

Gestation is ca. 390 days (King, 1965; Riley, in Groves, 1974), longer than any other equid. Recorded zoo females gave birth after 358–438 days ($\bar{X}$ = 409.2—Read et al., 1988).

Nursing lasts for ca. 275 days after gestation, for a total of 665

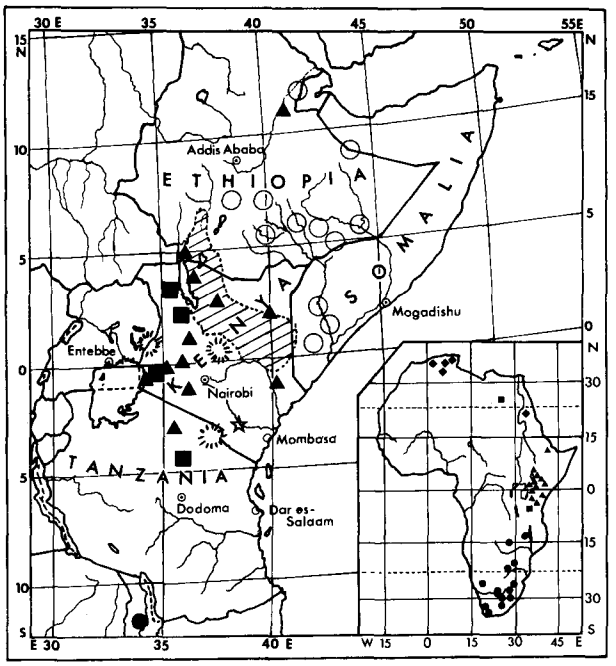

FIG. 5. Distribution of Grévy's zebra, *Equus grevyi*, and fossil records of ancestral forms. Map of East Africa shows area (hatched) occupied by *E. grevyi* in about 1980 (Churcher, 1981; A. G. Robertson, pers. comm. 1983), and where it was observed about 1900–1915 (open circles—Lydekker, 1912; Drake-Brockman, 1910) but is now extirpated. Solid symbols indicate Late Pliocene and Pleistocene fossil records (*E. numidicus*—diamond; *E. oldowayensis*—triangles; *E. capensis*—dots: Churcher and Richardson, 1979; Churcher, 1981); new records of *E. oldowayensis* (squares: Churcher, 1986). Additional records of *E. capensis* from southwest Cape region from specimens in the South African Museum, Cape Town (Churcher, in press). Star indicates introduction in Tsavo National Park. Circular hatchures indicate Mts. Kenya, Elgon, and Kilimanjaro.

days to produce 1 young. A female may breed from 1 to a few months after parturition, with an average frequency of 1 young/2 years (King, 1965; Kingdon, 1979). The mean interval between births at Dvur Kralove Zoo, Czechoslovakia, was ca. 18 months (563.3 days, range 425–1042 days, n = 94; Dobroruka et al., 1987) and in zoos in North America ca. 19.75 months (range 13–27 months, n = 36 births; Read et al., 1988).

Single young usually are born after the long rains in August or September, but births may occur throughout the year; a newborn was recorded in May (Lydekker, 1912). As parturition approaches, the female leaves the nursing herd and enters heavy bush. Birth normally takes place lying down, with the young's hoofs appearing first, and takes 7–8 min. If birth begins with the mother standing, it is completed lying down. The newborn frees itself from the amniotic membranes and crawls towards its mother's head. The mother licks it clean, and ingests the membranes and some amniotic fluid, which may be important in initiating lactation or the maternal bond (King, 1965; King et al., 1966).

When <1 h old, newborn will follow any moving object. The mother keeps other zebra females away (Kingdon, 1979) by threats with lowered head and flattened ears until her young has imprinted on her. During the first 2 days, newborn imprint on the distinctive scent, call, and stripe pattern of the mother (Churcher, 1982). When the maternal bond is firm, the mother joins a group of nursing mothers (Read et al., 1988). Newborn orient on the mothers rump and tail pattern when following. A nursing mother may go to water by herself, leaving the young within the nursery herd (Groves, 1974).

Newborn Grévy zebras stand 90 cm at the shoulders, weigh ca. 40 kg, and have a woolly coat of light chocolate or russet stripes that are darker on the head, neck, and legs (King, 1965). The paler areas are ochreous (Rzasnicki, 1951) or white (Kingdon, 1979). A bushy mane runs from the poll to the tail, and may be slightly erectile (Churcher, 1982; King, 1965). A line of hair also runs down the midline of the belly (Kingdon, 1979). The back mane is shed after a few weeks, leaving the neck mane and a remnant on the rump that may persist into early adulthood (King, 1965). The woolly coat changes to the adult short hair, the stripes darken to black, the paler areas whiten, and the mane shortens and darkens at ca. 5 months (Kingdon, 1979). The young are semi-independent at ca. 7 months, often being left by mother or leaving her for periods of hours. At 8 months, the young stands 1.32 m at the shoulders and eats mainly grass. It is weaned by 9 months (32–42 weeks—King, 1965) but stays with its mother. Young Grévy zebras play together by running, jumping, butting and chasing; they may also try to play with the mother (Kingdon, 1979).

A young Grévy female becomes independent from her mother at 13–18 months (when her mother may be 2–7 months into her next pregnancy—King, 1965). A young Grévy male stays with his mother until at least 3-years old, when he joins a bachelor group or a mixed herd. The loss of the maternal bond allows both adolescent sexes to move from herd to herd, until they become adults. Young wild males cannot gain access to females until at least 5 years old (King, 1965; Klingel, *in* Kingdon, 1979), and thus have a bachelor period of 2–5 years, unlike young females that first breed at 2–4 years.

Adolescent females attract ≤18 males (Klingel, 1974*b*) during the first estrus at ca. 4 years, which may last for 1 week. She presents and displays the typical mating stance, which shows readiness to breed, and attracts males who separate her from her mother (Churcher, 1982). Experienced females in estrus briefly adopt similar postures, but only near the territorial male before being quickly mated. This inconspicuousness in mating by experienced females probably causes less disruption to the nursery and females with young herds (Klingel, 1974*b*).

Sexual activity is highest early in the long rains, in July and August, and less in the short rains of October and November. As females in estrous attract or seek out willing males (Kingdon, 1979), breeding success is probably largely independent of rainfall. Grévy zebras gave birth (n = 94) in every month from 1973 to 1985, with peaks in January and June–August, at the Dvur Kralove Zoo, Czechoslovakia (Dobroruka, et al., 1987). The summer peak coincides with that for wild populations during the long rains.

ECOLOGY. Grévy zebras live in semi-deserts with low vegetation (1 m) or scattered low (3–4 m) *Acacia* bush with herbs and grasses. They prefer stony plains or hills, short grassy flats, or broken country (Churcher, 1982; Willoughby, 1974).

The type specimen of Grévy's zebra and the first specimens known to Europeans came from the cool, seasonally moist, grassy plains near Lake Zwai, at ca. 1,700 m (Churcher, 1982). Grévy's zebras prefer undulating, rocky, bush-country (Drake-Brockman, 1910), and were "found in Somaliland on stony country, covered with scattered bush, and intersected with ravines, at an elevation of about 2500 feet" (= 750 m), or on plains with scattered thorn-bush and durr grass (Swayne, 1900:321). These descriptions describe the country north of the Uaso Nyiro in Kenya.

No Grévy zebras were found in an aerial survey of northeast Kenya in 1957 between Moyale, Garba Tula, and Garissa to the Somali and Ethiopian borders (Stewart, 1963). A census of 151 Grévy zebras in a 40 by 20 mile (±65 by 30 km) area east of Lake Turkana was less than half that of common zebras in the area (Stewart, 1963). Urban and Brown (1968) saw none near the Omo River south of the Maji River during 1965–1967, although herds of 200–300 quaggas were seen during those years and may have contained some Grévy zebras. The highest concentration of Grévy zebras (>0.2/km^2) in 1977 occurred east of Lake Turkana, with 0.1–0.2/km^2 southeast of the Lake towards Mt. Kenya, and in a band ca. 70 km wide along the Uaso Nyiro towards Somalia (Dirschl and Wetmore, 1978).

The population may have fallen from 15,000 in the 1960s (Sidney, 1965) to fewer than 1,500 today outside reserves only in Kenya. A 65% decline was noted on the Samburu-Leroghi Plateau from 1971 to 1978 (Kingdon, 1979). A sample of 287 animals was extrapolated to an estimated 13,718 animals in Kenya in 1977 (Dirschl and Wetmore, 1978). Hunting may have reduced the numbers (Kingdon, 1979). Norris (1976) reported that a license was issued to one hunter to shoot 200 Grévy zebras in Maralal.

Twenty-two Grévy zebras from Isiolo were introduced to Tsavo East National Park in 1964 and dispersed near Aruba and Voi (Fig.

5). After 1967 they formed mixed herds with Bohm zebra. The Aruba–Buchuma herd comprised 18 animals in 1976 and continued into the 1980s. A second group of 30 zebras introduced into Tsavo West National Park in 1977 scattered in northwest Tsavo: four adults and a young were seen in 1980 near the Rombo River (Churcher, 1982). Grévy zebras appear to adjust to the Tsavo Plains and scrub-bush and their historic absence from the area is inexplicable considering the wider Quaternary distribution of *E. grevyi* (Churcher, 1981).

Thirty Grévy zebras reintroduced into Samburu Game Park, within their recent range, became residents between Koitogor Hill and Buffalo Springs north of the Uaso Nyiro (Churcher, 1982).

Male Grévy zebras aggressively defend their territories against allospecifics which suggests that they might fall prey to predators. Kingdon (1979) noted a lion (*Panthera leo*) that died of wounds after killing a male Grévy. Other predators are leopards (*Felis pardus*), spotted hyaenas (*Crocuta crocuta*) and hunting dogs (*Lycaon pictus*—Haltenorth and Diller, 1980).

A diet of Kenya grasses, legumes, and browse provides all the minerals required by Grévy zebras (Dougall, 1963). Legumes provide more protein and phosphorus, but less fiber, than grass or browse. Browse has the most calcium among 50 families of plants in East Africa, but the use of it by Grévy zebras is unknown. Dorst and Dandelot (1970) reported that a variety of foliage was consumed but Klingel (1969) noted only the consumption of grasses by *E. grevyi*.

Grévy zebras subsist on coarse grasses because of efficient trituration by the cheek teeth, followed by cecal fermentation (Janis, 1976), and thus compete indirectly with bovids (Kingdon, 1979). During a series of dry years in the 1970s, the Grévy zebras followed the spread of xeric grasses such as *Pennesetum schimperi* and *Eleusine jaeger* into the northern foothills of Mount Kenya. *P. schimperi* is tough and highly nutritious, and less used by grazing bovids, but almost the only grass found in dung of Grévy zebras on Lema Downs, near Isiolo. This fibrous dung reflects better water conservation than found in cattle (*Bos taurus*). Grévy zebras also exploit the grasses *Chrysopogon ancheri, Cenchrus ciliaris,* and *Enteropogon macrostachys.*

Pathogens observed in 20 Grévy zebras necropsied from 1974 to 1978 at the San Diego Zoo included ascarids (*Parascaris* sp.) in impacted intestines (n = 2 animals), ascaridiasis with trauma (n = 3), and *Strongylus* in the colon (n = 2). *S. vulgaris* caused aneurism (n = 1) or parasitic thrombosis (n = 1) in the mesenteric artery. Ascaridiasis was associated with gastric ulcers (n = 1) and a male with acute enteritis produced *Salmonella taksony* from a gut culture (n = 1). Other pathologies included simple thrombosis of the mesenteric artery (n = 1), primary pneumonia and pleuritis in a female (n = 1), inhalation pneumonia from milk within the bronchi (n = 2 young) or myocardial infarction (n = 1 young), and acute degenerative myocardial lesions attributed to capture myopathy or stress. In a sample of 47 births, young also died from stillbirth (n = 1), failure to nurse (n = 2), or unknown causes (n = 3) (Griner, 1983).

Grévy zebras are susceptible to anthrox and tetanus (Griner, 1983) and to the rinderpest myxovirus from which survivors are subsequently immune (Nelson, 1986). External parasites, mainly on animals in zoos, include lice (*Trichodectes equi*), mange mites (*Chorioptes bovis* and *Sarcoptes* sp.), and ticks (*Amblyomma* sp.). Internal parasites include stomach bots (*Gasterophilus pecorum*), ascarids (*Parascaris equorum* larvae in the lungs or adults in the large intestine, *Oxyuris equi* and *Dictyocaulus* sp. in the lungs, and *Strongylus vulgaris* in the large intestine), and tapeworms (*Anoplocephala* sp.) in the intestine or as cysts in the muscles (Griner, 1983; Nelson, 1986).

Glossina (tsetse fly) does not feed on Grévy zebras or quagga (Weitz and Glasgow, 1956). Harrison (1940:27) observed Grévy zebras "at a range of forty to fifty yards and, on three occasions when tsetses were swarming around the observer, none was seen on the zebra." This aversion to zebras by *G. morsitans* and *G. swynnertoni* may explain why Grévy zebras carry no trypanosomiasis (Weitz and Glasgow, 1956).

The hemoprotozoan *Babesia* infects zebras (Denning, 1966; Wallach and Boever, 1983) and is spread by blood-sucking ectoparasites, such as ticks (Acarina). Denning (1966) provisionally identified *Babesia* (*Nuttallia*) *equi* from Grévy zebras and postulated that all East African zebras are infected.

BEHAVIOR. Grévy zebras have no permanent adult bonds or a herd system as in *E. quagga* and *E. zebra* (Groves, 1974; Klingel, 1974*a*, 1974*b*). Groups of Grévy zebras have no leaders, although males usually dominate females. Adults may live alone on territories, in bachelor or nursery groups, or mixed herds, none of which is permanent, as do the asses, *E. asinus* and *E. hemionus* (Klingel, 1977). Male Grévy zebras defend individual territories of 2.5–10 km^2 ($\bar{X}$ = 5.8 km^2), whose boundaries follow natural features, such as watercourses, and are occupied year-round. These are established in dry rocky terrain (Keast, 1965; Klingel, 1974*b*) and are as large as those of male asses (Klingel, 1972).

Resident males patrol their territorial boundaries, marking them with urine and peripheral dung piles, and advertise their presence by braying (Klingel, 1972, 1974*b*). This male territoriality may derive from the Eocene *Hyracotherium* (Churcher, 1982). Territorial males tolerate other males in their territory but, if an estrous female enters, the resident male usually drives the visitor away (Groves, 1974; Kingdon, 1979; Klingel 1974*a*, 1974*b*).

A territorial male meets a challenger with head, neck, and ears extended forward (Klingel, 1969, 1974*b*). He then flattens his ears, raises his head, and bares his teeth in threat. In an earnest challenge, he may fight with teeth, biting at the neck, back, flanks, legs or rear while seeking an advantage, or rearing and flailing with the forehooves (Klingel, 1974*b*), and may vocalize (Kingdon, 1979). A crucial leg hold can bring both to their knees, where they may continue to wrestle. In a severe hold, the bitten male ceases struggling and, after a pause, the biter will release his hold. If the bitten male retires, the fight is over. When repulsed, a loser may pitch and throw his rear hooves in the air while fleeing, but without making contact (Churcher, 1982).

Females repel aggressive or defeated males by kicking with the hind legs. When threatened, the female stands back toward the attacker with one hindleg raised, ready to kick if assaulted; if in earnest, both hindlegs kick together (Kingdon, 1979).

Most fights among males occur at the 20–50 m wide territorial boundaries (Klingel, 1974*b*), or on vacant land. Males crossing another's territory are submissive to the owner. Fights occur only where both assume equal status (Klingel, 1974*b*). Boundaries and meeting places are marked with urine and dung piles 30–40 cm high created by many males during several years. Single males or females do not mark. The marks possibly inform visiting non-territorial males and females which individuals are the local territorial males (Kingdon, 1979).

Territorial males seek out visiting males for company or to expel them. They show their status by holding their heads high, arching their necks, and exhibiting stiff high-stepping gaits. These males are often large, battle-scarred, and older. Submissive males lower their heads, extend their tails, and greet the dominant male by nuzzling its chest or groin.

A moving, relaxed Grévy zebra may twitch its ears back and forth or windmill them. When slightly disturbed, it may raise its head and flick its ears. When alerted, the raised head points towards the disturbance, or the black backs of the ears show the direction of a sound. An arched or swishing tail may precede threatening (Kingdon, 1979) and ears back and teeth bared convey serious intent (Read et al., 1988).

Estrous females urinate frequently which intrigues or arouses males, who approach with measured steps, or prance with arched neck, chin down, and ears pricked horizontally forward (Read et al., 1988). The male sniffs her urine, inhales the scent, and raises his head in the flehmen grimace (Klingel, 1969). He follows her closely, sniffing, flehming, nipping, nuzzling, jostling, or wrestling her until she responds (Read et al., 1988). She may sniff submissively, nuzzle, nip, butt his groin, or laterally and posteriorly sexually present (Kingdon, 1979; Zeeb and Kleinschmidt, 1963) and may be moved deep into his territory (Kingdon, 1979). All other animals may be seen as rivals and be driven away.

A reluctant female resists by kicking the male's chest with both hind legs as he approaches her rear and by running away. Captive confinement establishes the male's territory and may make him more persistent. When ready to copulate, the female elevates her hind quarters, with tail raised to one side, ears back, and the open-mouth Rossigheit smile (Klingel, 1974*b*). Other females do not interfere with mating.

An estrous female on neutral ground may be competed for by up to 9 males (Klingel, 1969). Males may bark or bray loudly with a

drawn-out squeak during courting and copulating, or copulate with ears back and teeth bared (Read et al., 1988). This behavior may intimidate other males and subdue the female (Kingdon, 1979). Copulation by a territorial male is undisturbed by other males.

Male zebras copulate from the rear, supporting themselves by forearms and wrists on the females' shoulders. The male's head is down, his neck arched, and he continues to bark, or may bite, nip, or nuzzle the female's neck or mane, and may show flehmen before each copulation. Copulation is usually quickest the first time, but may take 3–10 min. Intervals between copulations vary from 30 min to 3 h. The female stands or moves slowly forwards (King, 1965). After 20–35 min of foreplay, a captive male readily copulated. However, by the end of the mating sequence, the female had to seduce the male by overt facial expressions and presenting behavior (Zeeb and Kleinschmidt, 1963).

Grévy zebras openly tolerate Bohm zebras (*E. quagga bohmi*) over a common range where groups of 5–14 Grévy zebras mix within larger herds of Bohm zebras. No solitary Bohm males were seen compared with 17 lone Grévy males (Keast, 1965). Grévy zebras may be solitary, or associate in herds of 6–20 animals (Kingdon, 1979; Swayne, 1900). However, herds of 322 and 311 Grévy zebras were reported from Samburu and the El Barta Plains in 1955, one herd composed of 800–900 animals east of the Shaba Hills in 1953, and another herd of 230 animals (Klingel, 1974*b*; Sidney, 1965).

Bohm zebras are more numerous south of the Uaso Nyiro River and Grévy zebras more numerous in the broken thornbush north of the River. Mixed herds of 160 and 250 animals in the Isiolo-Samburu area were larger than either species form alone and were about 75% Grévy zebras. The usual mixed herd is 15–20 animals, with 3–5 of them Grévy zebras (20–25%). At Samburu, on the Uaso Nyiro River, the ratio of Bohm to Grévy zebras was 2:1. North of the Tana River, similar sized groups contained only 1–3 Grévy zebras (Keast, 1965). Mixed herds travel with the scarcer species clustered near the center and show no tendency to separate during flight (Keast, 1965; Klingel, 1974*b*). The creation of mixed herds appears mutually beneficial against predators (Keast, 1965).

Bickering between zebras is directed towards conspecifics in mixed herds (Keast, 1965). Mixed herds graze away from water in early morning, rest in the shade during mid-day, and return to water in mid-afternoon. They graze away from water overnight, returning to drink in the early morning. Grévy zebras prefer to drink daily, but can go without water for up to 3 days, and may dig as deep as 60 cm for water (Haltenorth and Diller, 1980). Grévy males bite to defend their water holes (Klingel, 1974*b*). In exceptionally dry seasons Grévy zebras gather in large herds within daily reach of water (Kingdon, 1979).

Grévy zebras graze in-line-abreast on a broad front and walk in-line-astern when unalarmed (Kingdon, 1979). Orientation on the tail of the lead animal probably is the basis of the walking order and much herd behavior may derive from the following behavior of the newborn on its mother. The stripes around the tail and the white inguinal area may provide a flight signal, as in the waterbuck (*Kobus ellipsyprymnus*) or gemsbok (*Oryx g. gazella*). When a walking line halts, those behind either come up to the level with the leaders on a broad front, form small groups along the line-of-advance, or turn 90° from the line-of-advance to graze on a broad front. In the last formation, if the lead animal grazes slightly toward the old line-of-advance, those behind move up on the outside flank of the animal next in line, and thus swing the broad front through 90° to advance in the original direction. When content, Grévy zebras often graze in open arc formations which enable them to watch for predators, and to be more selective and less competitive in feeding (Kingdon, 1979).

When grazing Grévy zebras maintain the extended organization by sight (Kingdon, 1979). They bunch when alarmed, and the closer they bunch the greater the apprehension. Watering involves potential danger from predators or interactions with larger mammals, such as elephants (*Loxodonta africana*) or Cape buffalos (*Syncerus caffer*), and is a herd activity, unless the drinker is a territorial male who may then associate with other species.

At midday Grévy zebras rest in small groups either facing outwards in the open, beneath a large solitary tree, or are paired head to tail, to detect threats (Kingdon, 1979). In northern Kenya, zebras associate for mutual protection from predators with ungulates, such as the wildebeest (*Connochaetes taurinus*), beisa oryx (*Oryx gazella beisa*), waterbuck (*Kobus ellipsiprymnus*), kudu (*Tragelaphus strepsiceros*), and eland (*Taurotragus oryx*), or giraffe (*Giraffa camelopardalis*—Haltenorth and Diller, 1980; Lydekker, 1926; Roosevelt and Heller, 1914).

Territorial males and mother-and-young pairs are the stable units of Grévy zebra society. Non-breeding males, because of immaturity, old age, condition, or disease, freely graze together. Young males form bachelor groups and females-with-young nursery groups, of 20–50 animals, but are free to leave or join at will (Kingdon, 1979). Females are freer to move than all other groups but young males, move through territories of males in search of better grazing or water, and are seldom far from such resources. Klingel (1972) noted that all-male, all-female, or all-nursing mothers' groups often maintain their identities, even in herds of 200 animals.

Territorial males can go 2–3 days without watering and, as it may be some distance to water, water irregularly. Breeding males occupy territories year-round and only join the mixed-grazing herds on common land in extreme conditions (Klingel 1969, 1974*a*, 1974*b*). Non-breeding males accompany females throughout the year, while the solitary breeding males remain on station.

Grévy zebras usually do not mutually groom, as do quaggas (Mochi and MacClintock, 1976). All zebras can twitch their skins to dislodge flies, using a subcutaneous musculature that is absent where the hind-quarters are flicked by the tail. Toilet is conducted by tail swishing, rubbing the head against the legs or against parts of a conspecific, scratching with a hindhoof, and nipping with incisors. Rolling in dust, water, or mud helps protect against insects; when dried mud falls away it dislodges ticks or other ectoparasites. Zebras roll or scratch against trees, rocks, or termite mounds to relieve itchy skin, hair, or parasites (Haltenorth and Diller, 1980; Lydekker, 1926).

Grévy zebras move differently than quaggas, using a heads-up slashing trot or gallop (Roosevelt and Heller, 1914); quaggas canter or gallop with heads held lower (Shortridge, 1934). Alarmed Grévy zebras give deep, hoarse grunts which carry well and resemble those of lions (Groves and Willoughby, 1981). They may whistle or squeal when alarmed, fighting, or in pain or fear. Fright or warnings elicit a loud snort, sometimes with stamping forelegs. Males bray when defending their territories, driving a female, or repelling another male. Barks may accompany driving a female or copulation (Read et al., 1988). There are two alarm calls, a snort when frightened, and a hoarse call made by breathing with the mouth open, as in braying (Haltenorth and Diller, 1980). A horse-like, long, low volume snort or loose-lipped blowing expresses contentment. Young Grévy zebras in distress squeal, which brings their mothers and alerts nearby. Male Grévy zebras penned in the San Diego Wild Animal Park deliberately trampled conspecific young and they had to be separated (Griner, 1983).

GENETICS. Grévy zebras have 2n = 46 chromosomes, 32 metacentric and 12 acrocentric, with both X and Y metacentric or submetacentric (Benirschke and Malouf, 1977; Mutton et al., 1964). Zoo hybrids with ass, horse, Hartmann's mountain zebra and quaggas only are known (Gray, 1972; Ryder et al., 1978).

A male Grévy zebra x female ass (*E. asinus*) cross is easily obtained, and grows rapidly. It has the color and conformation of the ass, with a black middorsal stripe, and narrower and closer set leg and body stripes than the zebra (Gray, 1972). The crosses are sexually active but appear infertile to each other or in either backcross (Rzasnicki, 1936). The reciprocal cross is also possible (Gray, 1972), and both are superior to either parent in action, conformation, and disposition (Riley, 1910).

The male Grévy zebra (2n = 46) x female horse (*E. caballus*) (2n = 64) cross is difficult to obtain as male Grévy zebras do not mate readily with female horses (Gray, 1972). Hybrids (2n = 55) of both sexes, obtained by artificial insemination, are sterile (Roberts, 1929) due to the blocking of spermatogenesis at the late pachytene stage (King et al., 1966). The hybrids are horse-like, intermediate in mass between the parental species and larger than either parent, chocolate brown regardless of mother's colors, with narrow black stripes in the distinct Grévy pattern, and the zebra's tufted tail (Gray, 1972; Kingdon, 1979; Roberts, 1929). These hybrids (zebroids) were used by Raymond Hook of Nanyuki, Kenya, as pack animals and had calm dispositions, worked well (Roberts, 1929), and withstood the altitude, heat, and cold of Mt. Kenya (Churcher, 1982). Zeeb (1961) reported that zebroids were trainable but kicked.

A male Grévy zebra × female Hartmann's mountain zebra (*E. zebra hartmannae*) cross was born at Schönbrunn after 406 days gestation (Gray, 1972). It resembled Grévy's zebra in conformation, coat pattern and colors, grew rapidly, and was lively. The male Grévy zebra x female mountain zebra (*E. z. zebra*) cross is difficult because of a high rate of spontaneous abortion (R. Hook, reported by Groves, 1974), which disagrees with the Schönbrunn report.

Grévy zebra × common zebra (*E. quagga*) crosses occur only in captivity. The offspring are striped as are quaggas, but down to the hooves, as in Grévy's zebra (Grubb, 1981). Gray (1972) reported a skin in Zimmermann Ltd. Taxidermy, Nairobi (fig. 10 in King, 1965), as a possible wild cross, but it shows a variant pattern of *E. g. bohmi* (Kingdon, 1979, plate opposite p. 139, top left).

Extensive homologies between the G-banded chromosomes of *E. quagga* and *E. grevyi* are reported in hybrids with 2n = 45 and three chromosomes unpaired (Ryder et al., 1978). Compared to *E. grevyi* (2n = 46), *E. quagga* (2n = 44) has an extra pair of metacentric chromosomes, but lacks two acrocentric pairs. Grubb (1981) suggested Robertsonian fusion caused the divergence and supported the conclusion of Groves (1974) that *E. grevyi* has a more primitive chromosomal morphology.

REMARKS. The name zebra may come from the Galla *zecora* or Congolese *zebra* (Hamilton Smith, 1841; Ludolfus, 1681). Common names are Grévy's or Imperial zebra (English), zèbre de Grévy (French), and Grevy-zebra (German). The Swahili *punda milia* (= striped donkey) is any zebra, but *kangani* applies only to Grévy's zebra, as do *kanka* (N'dorobo), *kanga* or *loiborokurum* (Samburru), *haree* (Kilianguli), and *damer feru* or *faro* (Somali).

Grévy zebras (*hippotigris*) were first shown to Europeans in the colosseum in Rome by the Emperor Caracalla (Marcus Aurelius Antoninus, 211–217 AD; Mochi and MacClintock, 1976). They were rediscovered in the 17th century when King Assaghedus of Shoa, in Ethiopia, sent three animals "ex sylvis ultra Habessiniam" to the Ottoman Sultan (Ludolfus, 1681:57; Lydekker, 1912).

Menelik II, King of Shoa and Emperor of Abyssinia, sent a live animal to Jules Grévy, President of France, in 1882. It died upon arrival, was stuffed, and exhibited in the Museum National d'Histoire Naturelle, Paris. Oustalet (1882) described the skin as the type specimen of *Equus grevyi*, honoring the President.

Pocock (1902:308) described *E. grevyi berberensis* from the high plains at "Duhri, Ogardain [= Ogaden], 3,000 feet alt., in Somaliland [= Ethiopia]" (*not* Berbera; Lydekker, 1908), which is based on a chocolate-brown and ochre-striped coat (Pocock, 1910). The type specimen of Pocock's subspecies is now considered to represent a juvenile individual (Rzasnicki, 1951). *E. faurei* (Matschie, 1898) is also from Shoa and resembles the type specimen in pelage.

A number of generic and subgeneric names have been proposed for this unique zebra: *Dolichohippus grevyi* (Heller, 1912:1); *Equus* [*Megacephalon*] *grevyi* (Hilzheimer, 1912*a*:95), not *Megacephalon* (Gray, 1846); *Grevya* (Hilzheimer, 1912*b*:476), to replace *Megacephalon* (Hilzheimer, 1912*a*); *Ludolphozecora* (Griffini, 1912: 382), to replace *Megacephalon* (Hilzheimer, 1912*a*); and *Megacephalonella* (Strand, 1943:216), to replace *Megacephalon* (Hilzheimer, 1912*a*). In addition, the genera *Sterrohippus*, *Kraterohippus*, and *Kolpohippus* (van Hoepen, 1930) and at least 15 specific names are available for African fossil species related to *E. grevyi* (Churcher and Richardson, 1978).

The present range of Grévy zebras (Fig. 5) is reduced by the loss of the Ethiopian populations from Shoa highlands and the Ogaden plains, where extinction occurred about 1912 (Churcher, 1982). Grévy zebras in the Ogaden and Somalia have been hunted since 1920, and warfare during the 1970s–1990s has extirpated it from its eastern range. Today, Grévy zebras are poached for flesh and decorative hides, further reducing their numbers and range (Kingdon, 1979).

Mr. Rattray of Archer's Post, Kenya, captured and broke both sexes of Grévy zebras in 1925, and noted that it is "a much larger and more powerful animal, and is not so vicious as the Burchell zebra. Within a few weeks of capture, I have inspanned [harnessed] them to pull well and steadily" (Churcher, 1982:17). Dr. W. E. Hastings worked a 2-year-old male with harrow and drag for 12 days (Roberts, 1929). Despite their suitability and resistance to African diseases, their use gave way to motorized transport.

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Editors of this account were TROY L. BEST, GUY N. CAMERON, ALFRED L. GARDENER, and KARL F. KOOPMAN. Managing editor was JOSEPH F. MERRITT.

CHARLES S. CHURCHER, DEPARTMENT OF ZOOLOGY, UNIVERSITY OF TORONTO, TORONTO, ONTARIO, CANADA, M5S 1A1 AND DEPARTMENT OF VERTEBRATE PALAEONTOLOGY, ROYAL ONTARIO MUSEUM, TORONTO, ONTARIO, CANADA M5S 2C6.