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Dolichotis patagonum.

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Dolichotis Desmarest, 1820

Cavia Zimmermann, 1780:328.

Dolichotis Desmarest, 1820:205. Type species *Cavia patachonica* Shaw, 1801 (= *Cavia patagonum* Zimmermann, 1780).

Dasyprocta Desmarest, 1822:358. Type species *Cavia patachonica* Shaw, 1801.

Chloromys Desmoulins, 1823:47.

Mara Lesson, 1830:113.

CONTEXT AND CONTENT. Order Rodentia, suborder Hystricognatha (Caviomorpha), superfamily Cavioidea, family Caviidae, subfamily Dolichotinae. The genus *Dolichotis* has 1 extant species.

Dolichotis patagonum (Zimmermann, 1780)

Mara

Cavia patagonum Zimmermann, 1780:328. No type locality given.

Cavia magellanica Kerr, 1792:220. Type locality "Magellan, Argentina."

Cavia patachonica Shaw, 1801:226. Type locality "Patagonia, Argentina."

Mara magellanica Lesson, 1830:113. New name combination.

Dolichotis patagonum Krumbiegel 1941:21. First use of current name.

CONTEXT AND CONTENT. Context as for genus. Two subspecies are recognized based on pelage color and geographical distribution (Cabrera 1953).

D. p. centricola Thomas 1902:242. Type locality "Cruz del Eje, Córdoba Province, Argentina."

D. p. patagonum (Zimmermann, 1780:328). Type locality "Puerto Deseado, Santa Cruz Province, Argentina."

DIAGNOSIS. *Dolichotis patagonum* is distinguished from other cavids by its long ears, short tail, longer limbs, and radius longer than humerus. Anal glands are between the anus and the base of the tail in *Dolichotis,* whereas they are anterior to the anus in other cavids.

GENERAL CHARACTERS. *Dolichotis patagonum* (Fig. 1) is the largest cavid. It resembles the jackrabbit (*Lepus*—Mares and Ojeda 1982; Smythe 1970). Dorsal pelage is agouti gray and the rump exhibits a striking white patch separated from the dorsal fur by a contrasting black area (Genest and Dubost 1974; Redford and Eisenberg 1992). Underparts are white; flanks and chin are orangish. The short tail of the mara is depressed and almost hairless (Cabrera 1953).

General form is modified for cursorial life. Hind limbs are longer and more muscular than forelimbs. Feet are compressed and hooflike. Forefeet have 4 digits, and hind feet have 3 digits (Ellerman 1940).

Mean and range of external measurements (in mm) of adult maras from Argentina are as follows: total length, 707.2, 610–810, $n = 10$; length of hind foot, 140.5, 130–160, $n = 7$; length of ear, 97, 90–103, $n = 7$ (Redford and Eisenberg 1992). Mean weight for 8 males captured in southern Argentina was 7.73 kg ($SD = 0.62$) and for 15 females was 8.33 kg ($SD = 0.74$—Taber 1987). Mean and range of selected skull measurements (in mm; $n = 4$) are as folows: greatest length of skull, 130, 125.8–133.8; length of maxillary toothrow, 27.3, 26.3–28.9; length of mandibular toothrow, 27.5, 26.5–28.8 (Fig. 2).

DISTRIBUTION. *Dolichotis patagonum* only inhabits Argentina and is distributed from 28°S to 50°S (Fig. 3; Honacki et al. 1982). *D. p. centricola* occurs in Catamarca Province, the eastern region of La Rioja Province, the northwest of Córdoba Province, and the southwest of Santiago del Estero Province (Cabrera 1953). *D. p. patagonum* occurs in the central area of Buenos Aires Province, the south of Córdoba Province, San Luis and Mendoza Provinces, and to the south of Argentina to Santa Cruz Province (Cabrera 1953).

FOSSIL RECORD. Fossils of *D. patagonum* are known from Luján in Buenos Aires Province and from near Córdoba (Ameghino 1916). The Caviidae apparently derived from the Eocardiidae and first appeared in the middle Miocene, represented by a specialized subfamily, the Cardiomyinae (Landry 1957; Patterson and Wood 1982; Wood and Patterson 1959). Ancestors of Dolichotinae appeared in the Mesopotamian in the late Miocene, represented by *Paradolichotis* (Landry 1957).

FORM AND FUNCTION. Dental formula is i 1/1, c 0/0, p 1/1, m 3/3, total 20. Nasals are large, very pointed anteriorly, and do not extend as far forward as the premaxillae (Ellerman 1940). Frontals are very broad, and orbits are roofed by an expansion of the frontal bone. Bullae are moderately large. Lachrymals are very large, but the lacrymal canal appears closed in front of the orbit (Ellerman 1940). Cheek teeth are unilaterally hypsodont and evergrowing. Infraorbital foramen has no separate canal for nerve transmission (Ellerman 1940). Females have 4 mammae and a vaginal closure membrane (Weir 1974).

Maras are coprophagous (Kufner and Durañona 1991). In captivity, they are very efficient at converting food to energy and have a lower food consumption per kilogram of metabolic mass than do cattle or sheep (Kufner and Durañona 1991). Food digestibility, turnover time, transit time, and mean retention time of fluid and particle markers from maras and *Cavia porcellus* indicate that both species have similar dilution and retention times of digesta in their cecum and proximal colon (Sakaguchi et al. 1992).

ONTOGENY AND REPRODUCTION. Breeding in southern Argentina is from August to January, and groups of 1–29 pairs gather at single dens (Taber and Macdonald 1992a). In Patagonia, births are highly seasonal, and most occur between September and October, before the summer dry season and after the fall and winter rains (Taber 1987). Pairs reproduce year round. In captivity, maras produce 3 or 4 litters each year (Dubost and Genest 1974), whereas

FIG. 1. Adult *Dolichotis patagonum* from the Mendoza Zoo, Mendoza Province, Argentina, 1997. Photograph by M. F. Tognelli.

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of an adult female mara *Dolichotis patagonum* (Colección IADIZA Mastozoología, CIM 03532). Greatest length of cranium is 128 mm.

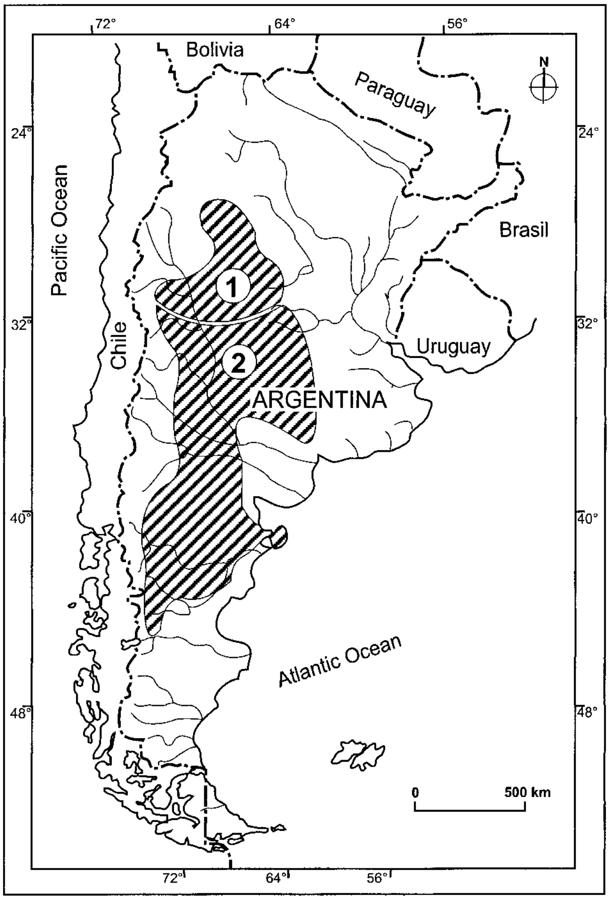

FIG. 3. Distribution of *Dolichotis patagonum* in Argentina: 1, *D. p. centricola*; 2, *D. p. patagonum.*

in the wild, most females produce only 1 litter each year (Taber 1987). Average litter size is 2 (range, 1–3). Young can walk almost immediately postpartum.

Females first conceive at 8 months of age (Dubost and Genest 1974). In semicaptive conditions, estrus occurs only once every 3–4 months and lasts only 0.5 h (Genest and Dubost 1974). Some females become pregnant soon after giving birth (Taber 1987). Gestation is 91–111 days ($n = 58$) in captivity (Dubost and Genest 1974) and 100 days in the wild (Taber 1987). Pups are nursed for at least 75–78 days, a long lactation period for rodents (Dubost and Genest 1974; Taber 1987).

A progesterone-binding plasma protein is present during pregnancy and is similar to those reported for other hystrycomorphs (Louis et al. 1986). Progesterone rises during pregnancy and declines after parturition. Estradiol-17-β is the predominant estrogen in maras (Louis et al. 1986).

ECOLOGY. *Dolichotis patagonum* occurs in lowland habitats, including forest and creosote bush (*Larrea*) flats in northwestern Argentina. In Península de Valdés, Patagonia, maras prefer sandy and low shrub habitats (Daciuk 1974). Preferred habitats have good cover of shrubs, but overgrazed and bared soils are also used by maras in the Monte Desert biome (Kufner and Chambouleyron 1991). Seasonal home ranges vary from 33.25 to 197.5 ha, with a mean of 97.87 ha (Taber 1987).

Maras are well adapted for cursorial life in open grasslands and shrubland steppe (Olrog and Lucero 1981) and occupy the ecological niche of cursorial mammals in the Patagonian steppe. *D. patagonum* has adaptations favorable for running and communicating in open habitats (e.g., lengthening of limbs, clavicle reduction, well-developed sensory organs—Kirchshofer 1960a). Maras resemble small deer or antelope when walking or running (Kirchshofer 1960a; Mares and Ojeda 1982; Smythe 1970).

Maras are herbivores (Kufner and Durañona 1991). They feed mostly on green vegetation and fruits (Campos 1997). In the Monte Desert, maras have a large dietary overlap with plains vizcachas (*Lagostomus maximus*), livestock (Kufner and Pelliza de Sbriller 1987; Kufner et al. 1992), and European hares (*Lepus europaeus*—Bonino et al. 1997). In the central Monte Desert, maras consume leaves of monocots (70%) and dicots (30%—Campos 1997). Among grasses, they prefer *Chloris, Pappophorum,* and *Trichloris*, and among perennial dicots they prefer *Atriplex lampa, Lycium,* and *Prosopis* (Campos 1997; Kufner and Pelliza de Sbriller 1987). Maras are also opportunists, feeding on herbs that grow after rainy periods (Kufner and Pelliza de Sbriller 1987). *D. patagonum* eats fruit and disperses seeds (especially of *Prosopis flexuosa*) through its feces (Campos and Ojeda 1997). In the southermost part of the Monte Desert, the diet of maras is mostly shrubs. Nevertheless, annual and perennial grasses and forbs are also eaten, especially in spring (Bonino et al. 1997).

Wellcomia dolichotis (Oxyuridae, Nematoda) is a parasite of *D. patagonum.* This nematode differs from congenerics, which parasitize Old World porcupines (Hystricidae), New World porcupines (Erethizontidae), and pacaranas (Dinomyidae—Sutton and Hugot 1987).

Other parasites, *Trichostrongylus retortaeformis* and *Graphi-*

dioides affinis, occur in the stomach and intestines of captive maras (Porteous and Pankhurst 1998; Sutton and Durette-Desset 1995). The intensity and prevalence of infection are related to the social organization of maras. Homogeneity of infection is greater within than between families and adult pairs of these rodents (Porteous and Pankhurst 1998). In zoological parks of London, maras were affected by pseudotuberculosis, with an annual incidence of 14% (Pearsons 1991).

BEHAVIOR. Maras are diurnal (Taber 1987). They spend a large proportion of the day (46%) feeding on grass, herbs, fruits, and seed pods (Taber 1987). Temporal activity rhythms of maras are related to environmental variables (Kufner 1995). Annual activity is positively influenced by light, precipitation, and temperature and negatively influenced by darkness and relative humidity. Daily activity is unimodal in winter and bimodal in other seasons and is related to environmental conditions (Kufner 1995). The preferred temperature is ca. 20°C (Kufner 1995).

Social organization of maras involves a unique combination of monogamy and communal breeding (Taber and Macdonald 1992a). Maras are strongly monogamous. Pairs remain constant across years, and replacement of a partner occurs only upon its death (Genest and Dubost 1974). The pair bond is maintained almost exclusively by the male, who follows the female wherever she goes (Taber 1987). Critical factors leading to monogamy in maras are the dispersion of food and the brevity of the female's period of sexual receptivity (Taber 1987).

Males mark females with urine, mark the ground near her with anal gland secretions and feces, and defend the zone around her. Thus, the area around a female represents a mobile territory (Genest and Dubost 1974).

Pairs breed either alone at solitary burrows or communally at settlements where up to 29 pairs share warrens (Taber and Macdonald 1992a). During the breeding season, maras can dig dens to raise their pups (Taber 1987). Maras exhibit no active co-operation among mothers (Dubost and Genest 1974; Genest and Dubost 1974; Taber and Macdonald 1992a, 1992b). From 1 to 33 pups, representing litters from 1 to 22 adult pairs, are grouped together in dens. Pup mortality is high, caused by predators such as felids (*Oncifelis, Puma concolor*), grisons (*Galictis*), foxes (*Pseudalopex*), birds of prey (*Bubo, Geranoetus*), and humans and by disease and hypothermia (Taber 1987). Thus, communal denning is associated with increased protection from predators for pups and adults (Taber 1987). Survival of pups from dens with larger memberships was higher than that from dens used by few pairs (Taber 1987).

Usually 1 pair at a time visits the den for ca. 1 h to nurse young during the day, while other parents circle around the den (Ganslosser and Wehnelt 1997). Females usually nurse only 1 or 2 pups at a time (Taber 1987). In captivity, nursing bouts lasted 5–40 minutes (MacNamara 1980). Within a given nursing session, a female may at least occasionally nurse pups belonging to other females (Taber 1987). Despite the efforts of females to prevent these other pups from suckling, some pups are able to steal milk (Dubost and Genest 1974; Taber and Macdonald 1992a). Females seem to use both smell and sound to identify their own offspring among the pups at a den.

Juvenile development can be divided into 3 phases: hider stage, follower stage, and postweaning stage (Ganslosser and Wehnelt 1997). During the hider stage (1–3 weeks), pups remain in or near the den. The relationship among pups is characterized by low interindividual distance, frequent body contact, huddling, allogrooming, and extended play. In the follower stage (4–13 weeks), young leave the den during the day to graze with their parents until weaning (Ganslosser and Wehnelt 1997).

Individuals of a mara settlement were observed to forage intensively ca. 1 ha/day within 2.5 km of the communal warrens within drifting daily ranges of 11 ha, seasonal ranges of 98 ha, and annual ranges of 193 ha. Home ranges were continuously drifting, so long-term movements of neighboring pairs overlapped substantially. Different ecological and social factors (e.g., seasonal resource availability, interference competition, and predation) favor either territoriality or communal herds. The resulting compromise is a social system unique among mammals (Taber and MacDonald 1992a).

Activity patterns differ between the sexes, especially during the breeding season. Female maras, because of the energetic demands of gestation and lactation, spend more time feeding than males. However, males spend most of the day sitting, a behavior associated with vigilance for potential predators (Taber 1987).

During grazing or slow locomotion, partners emit vocalizations consisting of alternating calls (Genest and Dubost 1974). An inflected 'wheet' is emitted when seeking contact, and a low repetitive grunt may be made when following a conspecific (Eisenberg 1974). In a threatening situation, maras show piloerection and may tooth chatter while emitting low grunts. Also, when grooming, *Dolichotis* produces a series of short grunts (Eisenberg 1974).

Scent marking (anal dragging and urination) is very common in maras and is associated with complex and intense social interactions (Genest and Dubost 1974). Anal dragging involves scratching and sniffing the soil before sitting upright with arched back and the anogenital region flattened to the ground (Taber and Macdonald 1984). Urination may include projection of a jet of urine onto another individual (Kirchshofer 1960b). Usually, a male stands up on his hind legs and urinates onto a female's rump. She often immediately responds by spraying a jet of urine backwards onto the face of the male (Genest and Dubost 1974). A male's urination over his partner is associated with repelling other males (Genest and Dubost 1974; Kirchshofer 1960b). Female urination appears to represent a rejection behavior to an approaching male when she is not receptive (Genest and Dubost 1974; Kirchshofer 1960b). Urination is part of aggressive behavior used by adult males, young males, and females in captivity when trying to gain access to food (Kirchshofer 1960b). In the field, both anal dragging and urination are more frequent during the breeding season and most commonly done by males (Taber and Macdonald 1984). Other interactions have been described for maras in captivity: tail-up rump display, rapid chase and rump biting, and head-on fighting (MacNamara 1980).

GENETICS. The diploid karyotype contains 64 chromosomes (Wurster et al. 1971). Twenty-four of the 31 autosomal pairs are metacentric or submetacentric, and 7 are subacrocentric (Wurster et al. 1971). Both sex chromosomes are metacentric, with the Y chromosome much smaller than the X chromosome (Wurster et al. 1971).

CONSERVATION. The mara has been classified as a vulnerable species (Ojeda and Diaz 1997). Historically, maras occurred from northcentral Argentina south, almost to Tierra del Fuego (Rood 1972). However, maras have been strongly affected by habitat alteration and hunting and are locally extinct in some regions, such as Buenos Aires Province (Cabrera 1953). The skins of maras are used for bedspreads and rugs (Ojeda and Mares 1982).

REMARKS. Additional vernacular epithets for *D. patagonum* are liebre criolla and Patagonian hare. The German common name is Pampashasen (Gerlach 1959; Krieg 1940).

Etymology of the genus *Dolichotis,* "long ear", is a reference to the ears, which are longer than those of other members of the family (Braun and Mares 1995; Gotch 1979; Palmer 1904). The specific epithet refers to its general distribution, i.e., Patagonia (Braun and Mares 1995; Gotch 1979).

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