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Phodopus campbelli.

By Patricia D. Ross

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Phodopus campbelli (Thomas, 1905)

Djungarian Hamster

Cricetulus campbelli Thomas, 1905:322. Type locality "Shaborte, N.E. Mongolia (about 46°40'N., 114°E)." Corrected by Thomas, 1908:107, to "42°40'N; 116°20'E." Allen (1940) gave coordinates of 42°40'N; 110°00'E.

Phodopus crepidatus Hollister, 1912:3. Type locality "Chuisaya Steppe (8 miles [13 km] south of Kosh-Agatch), Altai District, Siberia; 7300 ft [2225 m]."

P[hodopus] campbelli, Hollister, 1912:3. First use of current name combination.

Cricetiscus campbelli Thomas, 1917:703.

Phodopus songorus campbelli, Argyropulo, 1933:136. Name combination.

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciurognathi, Superfamily Muroidea, Family Muridae, Subfamily Cricetinae, Tribe Cricetini (Carleton and Musser, 1993). Vinogradov and Argiropulo (1941), Ellerman and Morrison-Scott (1951), Corbet (1978), and Pavlinov and Rossolimo (1987) included *P. crepidatus* in *P. s. campbelli.* Sokolov et al. (1990*a*) recognized *P. c. crepidatus* as a western subspecies of *P. campbelli.*

DIAGNOSIS. *Phodopus campbelli* (Fig. 1) is distinguished from the closely related striped hairy-footed hamster, *P. sungorus,* by smaller ears, the lack of a dark patch on the crown of its head, and by the suffusion of yellow or buffy on the dividing line between the dorsal and ventral pelage (Hollister, 1912; Thomas, 1905). The mid-dorsal stripe of *P. campbelli* is narrower and more sharply defined. The fur on the underside of *P. campbelli* is slate gray basally, that of *P. sungorus* white to the base (Allen, 1940). Unlike *P. sungorus, P. campbelli* does not turn white in winter. The Chuisaya Steppe population differs from the more eastern forms by its buffy tail, the shortness of its mid-dorsal stripe that ends about 2.5 cm above the root of the tail, slightly grayer coloration, and darker edges on the lateral margins of the dorsal pelage. The skull is smaller and more slender than that of *P. sungorus,* with larger auditory bullae, and a greater interorbital breadth (Allen, 1940; Hollister, 1912).

GENERAL CHARACTERS. *Phodopus campbelli* is one of the dwarf hamsters. Ranges in external measurements (in mm) of eight specimens from Mongolia (Allen, 1940) and of one specimen from the Chuisaya Steppe (in parentheses; Hollister, 1912) are: length of head and body, 80–103 (102); length of hind foot, 12–18 (13.5); length of tail, 4–14; and length of ear, 13–15.

The lips and cheeks are creamy white. The rest of the face, head, and upperparts are gray-buff to grayish wood-brown tipped with black, the underfur slate gray. A well-defined mid-dorsal stripe runs from the nape of the neck to the base or up to 2.5 cm anterior to the base of the tail. The throat, underparts, and legs are creamy buff, the buff of the underparts extending upward to form three convex patches on the shoulders, sides, and hips. The upper surface of the hands and feet are silvery white. The palmar and plantar surfaces, with the exception of the interdigital, large hallucal, and small medial carpal pads on the forefeet, and the three small distal pads on the hind feet, are thickly furred (Thomas, 1905). Large internal cheekpouches extend back to the shoulders when full.

There are few available data on the body mass of this species in the wild. The average body mass of four males and one female captured near Manzhouli and Dalai Nor was 23.4 g (Zimmerman, 1964).

Ranges of cranial measurements (in mm) of 10 specimens from Mongolia (Allen, 1940) and one specimen from the Chuisaya Steppe (in parentheses; Hollister, 1912) are: greatest length of skull, 22.6–26.5 (27.0); nasal length, (11.1); interorbital breadth, (3.7); basal length, 19.2–22.7; condylobasal length, (25.0); palatal length, 10.8–12.9; zygomatic breadth, 11.8–14.3 (13.0); breadth across mastoids, 9.9–11.1; width across molars, 4.6–5.2; length of upper cheek teeth row, 3.2–3.9 (4.0); and length of lower cheek teeth row, 3.5–3.8.

DISTRIBUTION. *Phodopus campbelli* inhabits the steppes and semi-deserts of central Asia: the Altai Mountains, Tuvinskaya Autonomous Region (Tuva), Transbaikalia, Mongolia, Nei Mongol (Inner Mongolia), and the adjacent parts of Heilungkiang and Hebei provinces in northeastern China (Vorontsov et al., 1967; Zimmerman, 1964; Fig. 2). The northern boundary of the species in Tuva is the Khandagayt-Samagaltay line (Yudin et al., 1979).

FOSSIL RECORDS. Fossils referred to the genus are known from the Pleistocene (Flint, 1966). Some Early Pleistocene fossils identified as *Cricetulus* from Somerset Cave in Britain and from other localities in Europe were assigned to *Phodopus* by Schaub (1930).

FORM AND FUNCTION. The skull is short, and the braincase is proportionately large and rounded (Thomas, 1905). The incisive foramina are parallel sided, and the tympanic bullae are small and flattened, with funnel-like bony eustachian tubes (Fig. 3). The stapedial foramen is tiny, and the stapedial artery does not extend anterior to the bulla. The squamosoalisphenoid groove and the sphenofrontal foramen are absent (Carleton and Musser, 1984).

In captivity under natural outdoor conditions, males began to become larger than females at 45 days of age, and had a statistically significant greater body mass by 145 days of age (Herberg et al., 1980). Under uniform laboratory conditions, males were significantly larger than females by 35 days of age (Sawrey et al., 1984).

Wild male and female hamsters use scent marks for home range delineation and conspecific communication. Both males and females use urine and feces, Harderian glands, skin glands behind the ears, and a mid-ventral sebaceous gland to scent mark (Wynne-Edwards et al., 1992).

At sexual maturity in both sexes, the mid-ventral gland consists of a large number of acini separated by connective tissue interlayers (Sokolov et al., 1988). The mid-ventral gland enlarges during the reproductive season (Vorontsov and Grutovoi, 1959), and is larger in males by 14 days of age (Sokolov et al., 1990*b*). In mature males

FIG. 1. Photograph of *Phodopus campbelli* from Erzin, Tuvinian Autonomous Republic, USSR, taken by K. E. Wynne-Edwards.

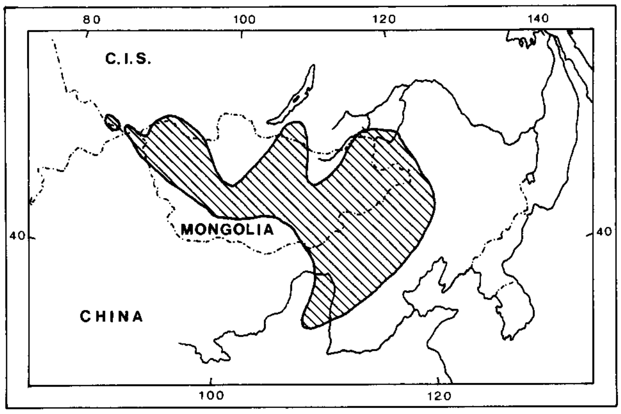

FIG. 2. Geographic distribution of *Phodopus campbelli* in Asia (adapted from Vorontsov et al., 1967).

3–9 months of age maintained under a 14 L:10 D photoperiod, this gland averaged 4.1 mm long (anterior-posterior) and 3.5 mm wide. In mature females, the gland averaged 1.1 mm long and 1.0 mm wide, or less. The average mass of the gland in males 180 days old ($n = 20$) was 68.8 mg, in females of the same age ($n = 20$), less than 1.0 mg. In males, the mid-ventral gland has a posteriorly opening pocket of skin that contains sebaceous material. There is only a small area of sebaceous material on female glands (Reasner and Johnston, 1987). Cells of these glands respond to hormonal stimulation, and in males produce both progesterone and testosterone (Sokolov et al., 1992). Deposition of the mid-ventral gland's secretion is facilitated by longitudinally grooved hairs with spatulate bases that grow on the periphery of the gland (Heisler, 1984).

In captive hamsters, the secretion does not seem to have a deterrent effect on conspecifics, but appears to be used for orientation (Müller-Sultemeyer and Klingel, 1984). The secretion also contains a factor which accelerates the sexual maturation of female young and delays the sexual maturation of male young (Sokolov et al., 1990*b*).

In common with *P. sungorus*, but not *P. roborovskii* or other hamsters, the glandular field at the corner of the mouth surrounds the opening of a sac-like structure located between the skin of the cheek and the cheek pouch. The saccule is formed during ontogenesis by a complex epidermal transformation of muscular and connective tissue and is completely developed by 20 days of life (Sokolov and Demina, 1992). The external wall of the saccule is formed of two layers of fibrous elastic connective tissue separated by a thin layer of striated muscle fibers. The internal wall consists of a multilayered epithelium with an exfoliating lining. Dense sheets of dead cells are shed into the cavity of the saccule and form part of the secretory substance, a whitish yellow substance with a sharp odor. The opening of the saccule is surrounded by a ring of long strands of striated muscle fibers. The saccules had an average mass of 7.5 and 8.4 mg and the contents of the saccules weighed 4.1–20.5 and 5.7–10.1 mg in three males and three females, respectively. The contents of the saccules may be used with the secretions of the sebaceous glands at the corners of the mouth to mark contents of cheek pouches or for defense (Sokolov et al., 1991).

The large cheek pouches, like those of other hamsters, are an extension of the adoral cavity (Vorontsov, 1967). Food and other substances enter the cheek pouch from a hole in the diastema. The size of the pouch opening in *P. campbelli* is controlled anteriorly by the buccinatorius pars orbicularis oris muscle and posteriorly by a combination of the buccinatorius pars intermaxillaris, buccinatorius pars mandibularis anterior and other buccinatorius muscles. The cheek pouch retractor muscle, derived from a slip of the trapezius muscle, originates from the spines and lumbodorsal fascia of the lumbar vertebrae and inserts into the medial and lateral walls of the posterior one-fourth of the pouch. The pouch epithelium consists of a highly keratinized 30 µm-thick stratum corneum and a well-developed stratum germinativum, four to five cells thick. The internal wall of the pouch consists of folds and numerous cone-like dermal papillae. A peninsula of highly folded tissue extends into the empty pouch, and becomes part of the wall structure when the pouch is full (Ryan, 1986). By 11 days of age the cheek pouches are big

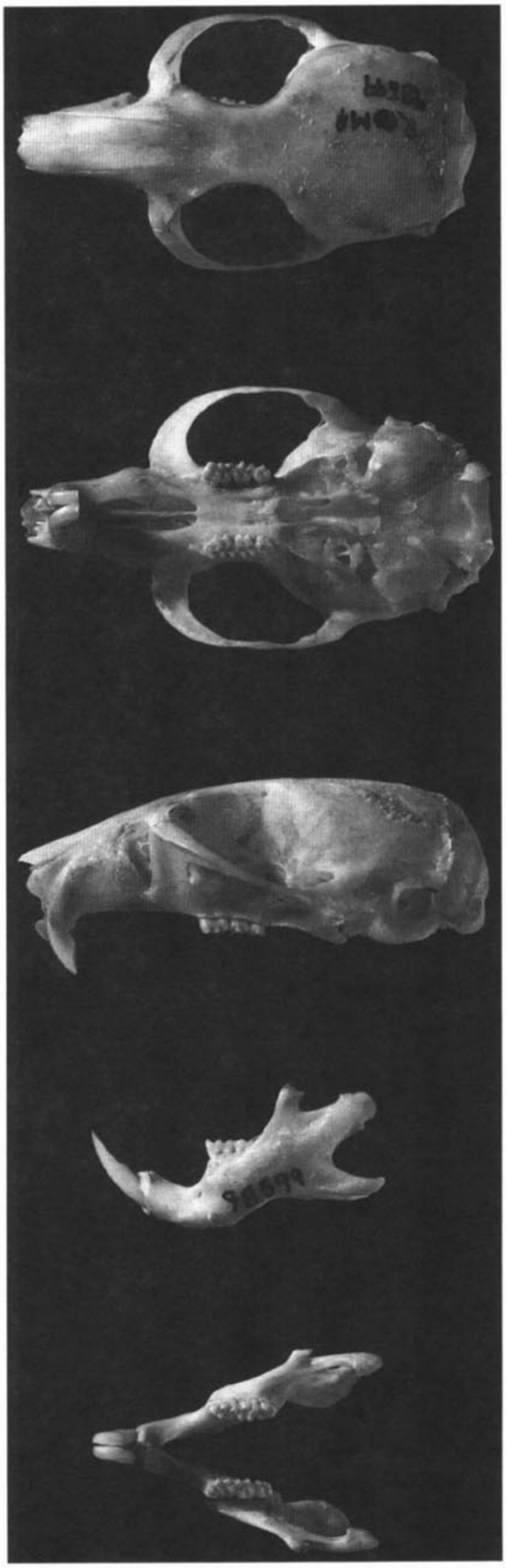

FIG. 3. Dorsal, ventral, and lateral views of the skull, and lateral and dorsal views of the mandible of a captive adult female *Phodopus campbelli* (Royal Ontario Museum 98599). Greatest length of skull is 25.4 mm.

enough to contain a sunflower seed (Ross and Cameron, 1989). Food is collected in one pouch at a time and, when full, the pouches extend back beyond the shoulders, restricting movement of the shoulder and the shoulder blade (Vorontsov, 1967).

The dental formula is i 1/1, c 0/0, p 0/0, m 3/3, total 16. The size of the molars decreases posteriorly such that each molar is only two-thirds as long as the preceding tooth (Vinogradov and Argiropulo, 1941). The first, second, and third upper cheekteeth occupy approximately 45, 30, and 25% of the upper toothrow, and the three lower molars occupy approximately 40, 31, and 29% of the lower toothrow, respectively (Wahlert, 1984; Fig. 3).

The islets of Langerhans in healthy pancreatic tissue are few, small, and well granulated. Most are innervated by unmyelated nerve fibers which terminate on all three major cell types, a central mass of insulin producing B-cells surrounded by a rim of A and D cells that produce glucagon and somatostatin, respectively. In *P. campbelli* that develop hyperglycemia, pancreatic cells become degranulated and glycogen is deposited until only the Golgi complexes and nuclei are free (Herberg et al., 1980; Voss et al., 1978). The stomach, like that of all true hamsters, is two chambered, with a corneous forestomach and a glandular stomach (Vorontsov, 1957).

Phodopus campbelli, like *P. sungorus* and *P. roborovskii*, has a highly effective renal mechanism for conserving water, is capable of cation concentration, but has no unique mechanisms for the excretion of excess salts. In an ambient temperature of 18°–20°C and a relative humidity of about 60% with water freely available, the mean osmotic urine concentration was 2,627 mOsM (n = 20). When water was withheld, urine concentration rose to 5,550 mOsM (n = 15). Four hours after water loading (30 μl/g), *P. campbelli* had excreted more of the load (70%) than *P. roborovskii* (43%) and less of the load than *P. sungorus* (87%). Approximately 80% of excess potassium chloride and salt were excreted after salt loading, almost twice as much as in *P. roborovskii* (45%—Mescherskii and Klishin, 1990).

The efferent ducts of male *P. campbelli* are made up of three functionally different types of cells. The most frequent, as in most mammals, are principal or nonciliated cells. The apical cystoplasm of these cells contains coated vesicles, pits, and several classes of tubular profiles. The apices are covered with dense fields of microvilli. The lateral plasma and basal membranes are elaborately interdigitated, and dense populations of mitochondria and fenestrated capillaries adjacent to the basal interdigitations suggest intercellular transport. Nonciliated cells, like those of the rat (*Rattus norvegicus*), are involved in fluid-phase and absorptive endocytosis. The number of lysosomes in the cytoplasm, however, are far fewer than in the rat. Two types of columnar cells extend from the basal lamina to the lumen. The first has many microvilli and few cilia, the second has many cilia and few microvilli. The latter cell type contains multivesicular bodies, lysosomes, and lipofuscin granules. Neither cell type has tubular complexes (Nagy, 1990).

In summer, the average basal metabolic rate (±*SE*) is 1.88 ± 0.57 $cm^3O_2g^{-1}h^{-1}$ and the rectal temperature is 34.3 ± 1.7°C. In winter, the average basal metabolic rate falls to 1.63 ± 0.38 $cm^3\,O_2g^{-1}h^{-1}$ and the rectal temperature is 35.7 ± 1.3°C. Maximum oxygen consumption in winter (14.56 ± 1.96 $cm^3O_2g^{-1}h^{-1}$) is higher than in the summer (12.93 ± 1.68 $cm^3O_2g^{-1}h^{-1}$—Weiner and Heldmaier, 1987).

Phodopus campbelli is less well adapted to cold temperatures than *P. sungorus*. The lowest ambient temperatures tolerated in summer and winter, measured by maximum rates of oxygen consumption, are −31.8°C and −44.6°C, respectively, 6–10°C higher than in *P. sungorus*. Thermogenic response to cold is not linear, as in *P. sungorus*. As the ambient temperature is lowered, the basal metabolic rate increases rapidly and, at −10°C, the body temperature shows a sudden drop to 23.7°C (Weiner and Heldmaier, 1987). Pup survival is high (95%; n = 107) in litters (n = 19) raised by both parents at an ambient temperature of 21°C, but drops significantly (32%; n = 78) in litters (n = 16) raised by both parents at 4°C (Wynne-Edwards and Lisk, 1989).

Phodopus campbelli is prone to genetically determined abnormalities in the metabolism of carbohydrates and lipids (Herberg et al., 1980; Voss et al., 1978). *P. campbelli* has a tendency to develop spontaneous tumors of the mammary glands, squamosal skin cells, lungs, uterus, ovary, and reticulum tissue. Tumors can also be induced by exposure to chemical carcinogens (7,12-diemthylbenz[*a*]anthracene, 3-methylcholanthrene, diethylnitrosamine, and methylnitrosourea) and oncogenetic viruses (Rous sarcoma virus, simian adenovirus, and human adenovirus). *P. campbelli* is resistant to urethan and, in common with the Chinese hamster, *Cricetulus griseus*, but not the Syrian hamster, *M. auratus*, simian virus 40 (Pogosianz, 1975). Structural changes in the X chromosome and autosomes have been demonstrated in the karyotypes of cells from chemically induced tumors (Sokova and Pogosianz, 1989). For these reasons and because of small size and the ease with which it can be maintained and bred in captivity, *P. campbelli* has proved to be a useful subject for cancer and cytogenetic studies (Cantrell and Padovan, 1987; Pogosianz and Sokova, 1977; Sokova and Pogosianz, 1989). Captive hamsters are succeptible to obesity and ringworm, *Trichophyton mentagrophytes* (Pogosianz, 1975; Young, 1974).

Slow locomotion, a lack of noticeable response to bright lights and human observers, open habitat, and low population densities enable field studies of entire populations. Individual hamsters were tracked using interperitoneal implants (Wynne-Edwards et al., 1992).

ONTOGENY AND REPRODUCTION. The breeding season in Tuva begins in the middle of April (Flint and Golovkin, 1961), in Mongolia at the end of April or the beginning of May (Bannikov, 1954), and in Transbaikalia at the end of April or the beginning of May (Nekepilov, 1960). It ends in September or early October throughout the range (Meyer, 1967). Captive animals breed throughout the year (Flint, 1966; Meyer, 1967), but a greater number of offspring are born during the summer (Jordan, 1971; Pogosianz, 1975). In Transbaikalia, females that are capable of reproducing weigh at least 14 g, and spermatogenesis in males from this locality begins in males weighing 20 g. Three or four litters are produced during the summer. Female offspring of breeding stock captured in this locality had their first litters at about 48 days of age (Meyer, 1967). In contrast, females descended from a Tuva population had their first litters at 35 days of age.

The average number of offspring per litter in females from Transbaikalia was 8.2 (Meyer, 1967). One gravid female captured near Manzhouli in Inner Mongolia had nine embryos (Zimmerman, 1964). Females in laboratory colonies have from 1 to 18 litters with 1–9 offspring per litter (Pogosianz, 1975).

Parturition is followed immediately by a fertile post-partum estrus (Wynne-Edwards and Lisk, 1984). The gestation period of captive females has been reported as 17.5–18.5 days (Daly, 1976), 18–19 days (Ross and Cameron, 1989), and as 20–22 days (Flint, 1966; Flint and Golovkin, 1961; Meyer, 1967). The minimal gestation period in captive females was 13 days (Herberg et al., 1980).

At birth (day 1), young are hairless and have a body mass of approximately 1.5 g. Incisors and claws are present, but the digits, eyes, and ear pinnae are sealed. Rates of morphological development differ by about a day in different parts of the species' range. Ear pinnae on young from Tuva begin to separate from the head on day 1 and separation is complete by day 3. The same process in young from Transbaikalia occurs on days 2 to 4. Fur first appears on the head, then the back, sides and abdomen. Young from Tuva and Transbaikalia are completely furred by day 7. Digits on the forefeet of most young from Tuva are completely separate on day 5, but not until a day later on young from Transbaikalia. The eyes of most young from Tuva are open by day 9, and those of young from Transbaikalia, by day 10 (Meyer, 1967).

Increase in the mass of young born in captivity, and the growth rates of the length of head and body, length of tail, length of hind foot, and length of the ear were most rapid just after birth. By 28 days of age young attained 63.5% of their adult mass of 32.1 g, 85% of their adult (102.1 mm) total length, 96% of adult (15.3 mm) hind foot and tail (11.8 mm) lengths, and 92% of their adult (14.8 mm) ear length. These young were weaned by 17 days of age (Ross and Cameron, 1989).

Captive females become sexually mature at about 2 months of age. Vesicular follicles form at least 16 days prior to the first spontaneous ovulation. Weanling female *P. campbelli* exposed for 10 days to males or to endogenous androgens in male urine have larger uteri, ovaries, adrenal glands, and vesicular follicles, and are younger at first ovulation than those housed alone or with sisters (Gudermouth et al., 1992; Reasner and Johnston, 1988). In captivity, most (85–88%) sexually mature females show regular 4-day estrous cycles; the remaining have 5-day or a mix of 4- and 5-day cycles (Wynne-Edwards et al., 1987*a*).

The time of behavioral receptivity of captive females at the beginning of the dark phase of the light cycle, and the time of ovulation, a little after the mid point of the dark phase, are consistent with those observed in the golden hamster, *Mesocricetus auratus.* The 17 β-estradiol concentration rises from a baseline of 54 pg/ml on the morning of estrus over the first 48 h after ovulation to a high of 187 pg/ml about 12 h before ovulation, then falls rapidly to the baseline concentration. Unlike in *M. auratus*, progesterone plays no part in the behavioral receptivity of the female. The level of serum progesterone peaks during the early afternoon of diestrous day 2 at 8,046 pg/ml and is only present in a concentration of 2,504 pg/ml at the time of peak receptivity. Primary follicles measure, on average, 83 ($n = 32$; range, 39–123) μm in diameter, preovulatory, or Graffian follicles, 455 ($n = 35$; range, 257–658) μm in diameter. Fewer than 100 follicles are in the ovary, and the ovulated follicles (new corpora lutea) are blood filled. At ovulation, 5–8 ova are shed (Wynne-Edwards et al., 1987*a*).

ECOLOGY. The burrow consists of four to six vertical and horizontal tunnels. The tunnel leading to the nest chamber can be as deep as 1 m below the surface of the ground, but most are only 25–30 cm deep (Flint, 1966; Veselovsky and Grundova, 1964). The nest is built of dry grass (Flint, 1966) and sheep's wool (Yudin et al., 1979).

The species also shares the paths, tunnels, and burrows of *Ochotona daurica* in the high steppes and semi-deserts of the Barga Upland in northern Manchuria, and the burrows of *O. mantchurica* in the rocks and cliffs of the Great Khingan Range (Loukashkin, 1940). On the Mongolian Plateau about 100 miles north of Kalgan (Zhangjiakou), *P. campbelli* shares the burrows of *Meriones* in preference to digging its own (Allen, 1940; Thomas, 1908).

Population densities are low and stable. In various habitats in Transbaikalia, *P. campbelli* accounted for only 0.01–6.0% of the rodents captured during yearly rodent censuses from 1944 to 1958. These were caught in traps baited with bread soaked in vegetable oil (Flint, 1966). In Tuva, *P. campbelli* made up 0.2–4.5% of the small rodents captured in various habitats during 1958 and 1959; the highest numbers were trapped on *Potentilla-Artemisia* (cinquefoil-wormwood) and grass-wormwood steppes (Flint and Golovkin, 1961). The habitat by Lake Tere Xol on the Mongolian border is characterized by open sand dunes and *Artemisia* and *Potentilla* steppe with *Caragana* bushes 0.2–3.0 m in diameter. Here, each female hamster's 3.5-ha home range contains just over 1,000 bushes (Wynne-Edwards et al., 1992).

Phodopus campbelli was common along the caravan route from Kalgan to Taboul (Thomas, 1908). Nine specimens of *P. campbelli* were collected during six expeditions to Mongolia between 1963 and 1968: a male on an open *Caragana* steppe (1,400 m), a male on an *Artemisia* steppe (600 m), a female on a mountain steppe partially covered with stone and rock near a marmot burrow (1,650 m), and five males and one female on a gravel steppe with sandy, gravel, and grassy areas (Topál, 1973). In Manchuria, *P. campbelli* is found in association with *Pitymys brandti, Microtus gregalis, Cricetulus barabensis,* and *Allactaga sibirica* (Loukashkin, 1940). *P. campbelli* also inhabits areas of human habitation, and is found in Mongolian yurts and more substantial buildings, particularly during the winter (Flint, 1966). In the northwestern part of its range, *P. campbelli* is found in association with four other species of hamsters, *P. roborovskii, Cricetulus barabensis, C. curtatus,* and *C. longicaudatus.* The diets of the four hamster species are sufficiently different to avoid competition (Flint and Golovkin, 1961). Although the range of *P. campbelli* shows a considerable overlap with that of *P. roborovskii* (Flint, 1966), the two species do not come into direct contact (Vorontsov, 1967). *P. campbelli* occupies stable ground (Vorontsov, 1960), or clay areas that are avoided by the desert hamster (Flint, 1966), and is found in semi-desert and steppe regions, as well as the periodically dry mud flats of Mongolia (Argyropulo, 1933; Flint, 1966; Hamann, 1987; Schmid et al., 1986).

The diet of *P. campbelli* varies among different parts of its range. Fifty-one species of plants have been identified in the diet of the Transbaikalia population, the most important including *Stipa capillata, Allium, Iris ruthenia,* and *I. flavisima.* In contrast, only 10 species of plants have been identified in the diet of the Tuva population. Two of the most important are *Potentilla* and *Aneurolepedium* (Flint, 1966). The cheek pouches of a male *P. campbelli* captured near Manzhouli contained 120 seeds and the proboscis of a beetle (*Pacephorus umbratus*; Zimmerman, 1964). In captivity, these hamsters eat wheat grain, sunflower seeds, dandelions, locusts, and citrus fruit (Jordan, 1971; Yudin et al., 1979).

Predators include the eagle owl (*Bubo bubo*), the steppe eagle (*Aquila nipalensis*), the kestrel (*Falco tinnunculus*), the saker falcon (*F. cherrug*), and the corsac fox (*Vulpes corsac*) (Brom, 1952; Lipajev and Tarrasov, 1952; Peshkov, 1957). In southeastern Transbaikalia, *P. campbelli* remains accounted for 7.7% of the stomach contents of 52 steppe foxes during the summer, and 2.6% of the stomach contents of 38 steppe foxes during the winter (Heptner and Naumov, 1974).

Ectoparasites include *Amphipsylla longispina, A. anceps, A. schelkovnikovi, Paradoxopsyllus naryni, Wagneria tecta, W. schelkovnikovi,* and *Neopsylla,* none of which are exclusive to *P. campbelli* (Flint, 1966). No internal parasites have been reported.

In a captive breeding colony, *P. campbelli* lived in mated pairs with their current litter and displayed a well-defined dominance hierarchy. Each pregnant female built a new nest with the help of the male prior to parturition. Siblings and offspring were driven off. The α-male of the litter remained in the nest to mate with an immigrant female, and the other young dispersed. Strange conspecifics were attacked by both dominant males and females. Immature males were bitten, injured, and occasionally castrated or killed. Young animals remained sexually inactive, and sexual development in young males was retarded (Müller-Sultemeyer and Klingel, 1984).

Support for obligate monogamy in captive *P. campbelli* is given by Wynne-Edwards (1987) who found that mated pairs raised litters more successfully than did lone females or pairs of sibling females in spite of the fact that the female was lactating and gestating her next litter. Females did not become pregnant if mated in the presence of two or more males (Wynne-Edwards and Lisk, 1984), and showed pregnancy block if housed with an unfamiliar male or abandoned by their mate at a critical period after mating and before implantation (Wynne-Edwards et al., 1987*b*).

In all natural populations, females are more numerous than males. Males are at higher risk due to their greater mobility (Meyer, 1967). In Tuva, the home ranges of females do not overlap, but may overlap an area visited by more than one male (Wynne-Edwards et al., 1992). Males may visit one or more females to mate (Meyer, 1967; Wynne-Edwards et al., 1992).

The average life span of *P. campbelli* in captivity was 278 days for nine males, and 356 days for six females. The oldest male lived 654 days and the oldest female 618 days (Herberg et al., 1980). Captive Djungarian hamsters born in late summer or early autumn survived through the following two winters, living an average of 2–2.5 years (Hamann, 1987).

BEHAVIOR. The Djungarian hamster is crepuscular and nocturnal, and is active throughout the year (Flint, 1966). Its locomotion is slow and sluggish (Hamann, 1987) with a maximum running speed of approximately 6.5 km h (Wynne-Edwards et al., 1992).

The first day of appearance (day 0 = day of birth), and the mean day of appearance (in parentheses) of grooming, feeding, and digging behavior in eight litters of *P. campbelli* reared under laboratory conditions were: contactless scratching, 4 (5); scratching with contact, 5 (5.5); snout grooming, 5 (7); overhead grooming, 7 (9); scratching with foot-licks, 9 (12.5); body grooming, 11 (12.5); shaking, 13 (17); mouthing food, 7 (8); eating, 8 (8); eating sitting up, 9 (12); carrying food to nest, 13 (16); forepaw digging, 9 (10); and complete digging, 13 (17.5—Daly, 1976).

The home-cage activity of 12 adult males in an air-conditioned room under a reversed 16 L:8 D photoperiod over a 24 h period was acyclic. Percentages of time spent in four catagories of behavior during the light phase and the dark phase (in parentheses) were: sleep, 71% (66%); groom, 10% (14%); eat, 9% (11%); and locomotion, 6% (4%); the overall temporal pattern of wheel running of adult males over 29 consecutive days was nocturnal although the temporal patterns of some hamsters were acyclic (Sawrey et al., 1984).

Under natural conditions, captive *P. campbelli* showed both a daily and seasonal periodicity in behavior. The greatest number of nest exits was recorded just after 1800 h, the least at 0230 h. Peak yearly activity (6.5 h/day) was observed during February, the time of least activity (< 15 min/day) observed in the sympatric desert hamster, *P. roborovskii.* Several hours of wheel running by individual hamsters on one or more nights could be followed by nights of reduced running, or by no running at all (Hamann, 1987).

Two female hamsters observed in the field (Wynne-Edwards et al., 1992) were active above ground for an average of 4.1 h on

15, and 2.6 h on eight consecutive nights, respectively, between dusk and dawn. Each female spent approximately 40% of this time travelling, 20% eating, and 12% grooming. Most ventral gland, vaginal, rolling, and urine scent marking occurred early in the evening during the first and second expeditions from the burrow. Both females distributed over 50% of their scent marks under bushes and tussock grass. Marks were also placed on sandy and open grass substrates and by burrows, but the two females differed significantly in their choice of substrates. Scent marking by males in the same area was restricted to each male's own home range, with the largest concentration at the periphery. Males sometimes marked near the burrow of a female during mating (Wynne-Edwards et al., 1992). Captive males direct their scent marks at both male and female conspecifics, discriminate between male and female odors, and investigate areas marked by males and females in a different manner (Reasner and Johnston, 1987).

The basic pattern of copulatory behavior consists of one to several discrete series of mounts, each series terminated by a brief ejaculatory lock (Wynne-Edwards and Lisk, 1984), or no lock (Sawrey et al., 1984), and separated from the next series of mounts by a refractory period. Several intromissions occur before each ejaculation (Sawrey et al., 1984; Wynne-Edwards and Lisk, 1984), at which time the male and female both fall onto their sides, the male grasping the female with his forepaws so that she is unable to escape for approximately 9 s (Sawrey et al., 1984). Intermount pursuit is slow, and lordosis is brief. Repeated thrusting is observed only as the male tires. Unreceptive females will strike a male with a snatching motion of one or both forepaws while in an upright posture (Daly, 1976). Mating may take from 4 to 6 h, and contains, on average, six complete ejaculatory series (Wynne-Edwards and Lisk, 1984). A copulatory plug is deposited after ejaculation (Sawrey et al., 1984). The measures of copulatory behavior obtained in pairs where estrus was induced by injecting the females with estradiol benzoate are not comparable to those obtained from pairs where females were in natural estrus (Sawrey et al., 1984).

In 10 min agonistic interactions with like-sexed conspecifics, dominant male *P. campbelli* were more aggressive than dominant female *P. campbelli*. The frequencies of attacks, chases, bites, and boxes during same-sex male interactions were all significantly higher than those of same-sex female interactions. Dominant males could inflict serious physical injury or death by biting the head and neck of their opponent. This behavior was not observed in *P. campbelli* females or during similar interactions between same-sexed *P. sungorus* males and females. *P. campbelli* females display less aggression towards conspecific females than *P. sungorus* females (Wynne-Edwards and Lisk, 1987).

Phodopus campbelli reacts to cold exposure by exercising vigorously, and trying to escape to shelter instead of resting in a curled posture and relying on its capacity for heat production and body insulation as does *P. sungorus*. This suggests that *P. campbelli* seeks refuge from extreme cold despite the energetic cost of such activity (Weiner and Heldmaier, 1987).

GENETICS. The diploid number of chromosomes (2n) is 28 (Matthey, 1960) and the fundamental number is 51 (Schmid et al., 1986). Of the autosomes, 18 are metacentric, 4 are submetacentric, and 4 are acrocentric (Spyropoulos et al., 1982). The X chromosome is polymorphic (Vorontsov et al., 1967) and the Y chromosome is acrocentric. The X chromosome is about 15 μm in length and the Y chromosome is 6.0 μm, consisting of 7.3 and 2.9% of the total synaptonemal karyotype length of 205.2 μm (Spyropulos et al., 1982). With the exceptions of the 12th and 13th pairs which are acrocentric in *P. campbelli* and submetacentric in *P. sungorus*, the autosomes of *P. campbelli* are similar in size and morphology to those of *P. sungorus* (Safronova et al., 1993; Vorontsov et al., 1967). Each pair of chromosomes may be identified by size and centromeric index alone (Bigger and Savage, 1976). Nucleolar organizers (NORs) are associated with the short arms of chromosomes 5, 7, 12, and 13 in both mitotic (Bigger and Savage, 1976) and meiotic spreads (Spyropoulos et al., 1982).

Starch-gel electophoresis showed *P. campbelli* is polymorphic in a general protein, Gp-3, and two enzymes (nonspecific esterases Est-1 and Est-2), of 18 enzyme loci examined (Kartavtsev et al., 1984*a*). The average heterozygosity (H) per individual was 6.0%. Phenograms of genetic similarity and difference generated from electophoretic data from *P. campbelli* and species representing four other genera of hamsters (*Cricetus cricetus, Mesocricetus auratus, Tscherskia triton*, and *Cricetulus barabensis*; $n = 70$), suggested that *P. campbelli* is closer to *C. cricetus* and *C. barabensis* than to *T. triton* and *M. auratus*, and that *P. campbelli* diverged from *C. cricetus* and *C. barabensis* approximately 2.77×10^6 years ago (Karatsev et al., 1984*b*).

REMARKS. The generic name is derived from *phodos*, the genitive case of the Greek *phos*, meaning tubercle or blister, and the Greek *pous*, meaning foot. The species was named in honor of W. C. Campbell, who collected the type specimen in Inner Mongolia on 1 July 1902.

The specific status of this hamster has been in question since Argyropulo (1933) included it as as subspecies of *P. sungorus*. This classification was followed by Bannikov (1954), Flint (1966), Flint and Golovkin (1961), Bobrinskii et al. (1965), Meyer (1967), Gromov and Baranova (1981), and Hamann (1987). Vorontsov et al. (1967) concluded that *P. campbelli* merited specific rank as a member of the superspecies *P. sungorus* on the grounds of genetic isolation and morphological differences. Meyer (1967) found significant postnatal developmental and behavioral differences between populations of *P. campbelli* and *P. sungorus*. Cross breeding, rarely successful because of antagonism between male and female *P. campbelli* and *P. sungorus*, produced sterile male offspring (Safronova et al., 1993; Yudin et al., 1979) and female hybrids with reduced fertility (Safronova et al., 1993). Hybrid males have testes 1.5 times smaller than their male parent, and meiosis is blocked in most spermatocytes (Safronova et al., 1993). It is on the basis of the report of Yudin et al. (1979) that *P. campbelli* was elevated to its former taxonomic status (Corbet, 1984). This arrangement has been followed by Honacki et al. (1982), Corbet (1984), and Carleton and Musser (1993). Weiner and Heldmaier (1987) and Wynne-Edwards and Lisk (1987) provide physiological and behavioral evidence to support the specific rank of each species.

Several common names have been applied to *P. campbelli*: the striped hairy-footed hamster (Sokolov et al., 1988), the Djungarian hamster (Gudermuth et al., 1992; Herberg et al., 1980; Sokolov et al., 1992; Sokova and Pogosianz, 1989; Wynne-Edwards, 1987; Wynne-Edwards and Lisk, 1984, 1987; Wynne-Edwards et al., 1987*a*); the Siberian hamster (Nagy, 1990); and Campbell's hamster (Sokolov et al., 1991). Although the names striped hairy-footed hamster and Siberian hamster usually refer to *P. sungorus* (Corbet, 1978; Corbet and Hill, 1986), the term Djungarian is also used to refer to *P. sungorus* (Pilborough, 1971; Puchalski and Lynch, 1988). Unless the name *campbelli* or geographic locality are specified, it is not always possible to deduce which taxon is being discussed. Even specification of geographic locality can lead to confusion. Weiner and Heldmaier (1987) state that the *Phodopus* from east-central Mongolia (47°03'N; 107°38'E, the center of *P. campbelli*'s range) studied by Weiner and Gorecki (1982) belonged to the nominate subspecies. Information on *P. campbelli* and *P. sungorus* is sometimes combined (Cantrell and Pedovan, 1987) because of such confusion.

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Editors of this account were ELAINE ANDERSON, TROY L. BEST, J. ALDEN LACKEY, and KARL F. KOOPMAN. Managing editor was JOSEPH F. MERRITT.

P. D. ROSS, DEPARTMENT OF MAMMALOGY, ROYAL ONTARIO MUSEUM, 100 QUEENS PARK, TORONTO, ONTARIO, CANADA M5S 2C6.