

Phodopus sungorus. By Patricia D. Ross

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Phodopus Miller, 1910

Phodopus Miller, 1910:498. Type species Cricetulus bedfordiae Thomas, 1908 (a subspecies of Cricetulus roborovskii Satumin, 1903).

Cricetiscus Thomas, 1917. Type species Cricetulus campbelli Thomas, 1905 (used as a genus for Phodopus campbelli and P. sungorus only).

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciurognathi, Superfamily Muroidea, Family Muridae, Subfamily Cricetinae, Tribe Cricetini. Three species are included in Phodopus, P. sungorus, P. roborovskii, and P. campbelli (Carleton and Musser, 1993). The following key is adapted from Argyropulo (1933) and Hamann (1987):

- 1 Mid-dorsal stripe present; three posterior plantar pads suppressed; three distal pads covered in fur; major cusps and re-entrant folds on cheek teeth alternating; incisive foramina >4 mm in length, longer than upper tooth row; interparietal broader than long; cranium rectangular in dorsal view
Mid-dorsal stripe absent; posterior and distal plantar pads coalesced into one large tubercle covered with fur; major cusps and re-entrant folds of cheek teeth directly opposite; length of incisive foramina <4 mm, shorter than upper tooth row; interparietal shaped like isosceles triangle; cranium rounded in dorsal view
2 Mid-dorsal stripe wide; summer coat gray; blackish patches on crown of head, shoulder, and flanks; ventral pelage white with occasional black hairs; winter pelage pure white
Mid-dorsal stripe narrow; summer coat with a yellowish tinge, lighter than P. sungorus; no black patch on crown of head; shoulder patch paler; ventral pelage white with a slate gray base; winter pelage light gray without any yellowish brown tinge

Phodopus sungorus Pallas, 1773

Siberian Hamster

Mus sungorus Pallas, 1773:703. Type locality (die Barabinische Steppe—Argyropulo, 1933:136), and (Gratschefskoi, [Gratschevsk], 100 km west of Semipalatinsk, "Siberia" [= Kazakhstan]; Ellerman and Morrison-Scott, 1951:627).

Mus songarus Pallas, 1778:269. Renaming of Mus sungorus Pallas, 1773. The spelling "sungorus" was given priority by Argyropulo (1933).

Phodopus sungorus, Hollister, 1912:3. First use of current specific name combination.

CONTEXT AND CONTENT. Context as in generic summary above. Currently there are no recognized subspecies (Carleton and Musser, 1993).

DIAGNOSIS. Phodopus sungorus (Fig. 1) is distinguished from its closest Mongolian relative, P. campbelli, by white winter pelage, fur on the underside which is often white to the base, a dark head patch and side streak, and the absence of a buffy or beige wash on the sides and under parts of summer pelage (Hamann, 1987). At its narrowest point, the mid-dorsal stripe is 3.5 mm wide, at least 1 mm wider than that of P. campbelli. The cranium (Fig. 2) is rounder in dorsal view and the skull has a greater average length, width, and depth than P. campbelli (Ross, 1992).

GENERAL CHARACTERS. The trunk is short, compact, and robust. Ranges in external measurements (in mm) are as follows:

length of head and body, 70-90; length of tail, 5-15; length of hind foot, 11-15; and length of ear, 11-16 (Kryltsov and Shubin, 1964; Vinogradov and Argiropulo, 1941). Body mass ranges from 19 to 45 g in males and from 19 to 36 g in females (Kryltsov and Shubin, 1964).

In summer, the face is gray brown, slightly lighter in the area of the mouth, mystacial pads, and ears. The rest of the head is dark brown to black, the outer surface of the ears and a rim around each eye, black. A black-brown mid-dorsal stripe runs from a dark patch on the pate of the head to the base of the tail. A streak of brown-black hairs forms a sinuous line of demarcation between the dorsal and ventral fur. The feet, tail, throat, and abdomen are whitish, the white of the underparts extending upward to form three reentrants on the shoulders, sides, and hips. The back is ash gray to dark brown, occasionally with a light brown tinge (Figala et al., 1973). The white winter coat sometimes has a gray tinge on top of the head. The front feet have four digits with a rudimentary pollex (Pallas, 1773). The three posterior plantar pads on the hind feet are absent and the soles of the feet are densely furred. Large internal cheek pouches extend back to the shoulders when full.

The greatest length of skull is 23-25 mm (Vinogradov and Argiropulo, 1941), and the occipitonasal length, 25-27 mm (Ross, 1992). The auditory bullae are flattened and small, each with a slightly tube-shaped antero-medial projection which extends to the hamular (Ellerman, 1941; Vinogradov and Argiropulo, 1941). Like other species in the genus, the stapedia foramen is tiny, the stapedia artery does not extend anterior to the auditory bulla, and the squamosoalisphenoid groove and sphenofrontal foramen are absent (Carleton and Musser, 1984).

DISTRIBUTION. Phodopus sungorus inhabits the steppes of western Siberia, eastern Kazakhstan, and the Hakisi and Minusinsk Steppes of the Krasnoyarsk Region of Russia along the Yenisey River (Fig. 3). The distribution is discontinuous (Vorontsov et al., 1967). In 1876, the species was common at lower altitudes throughout Turkestan with the exception of the Zarevshan Districts and the area around Hodget (Severtzoff, 1876).

FOSSIL RECORD. Fossils identified as P. sungorus are known from the Late Pleistocene of Hungary, Switzerland, and Germany. Several fossils of P. sungorus may have been misidentified as Cricetulus (Schaub, 1930).

FORM. Winter molt in captive animals maintained under natural conditions begins in mid to late September and is complete

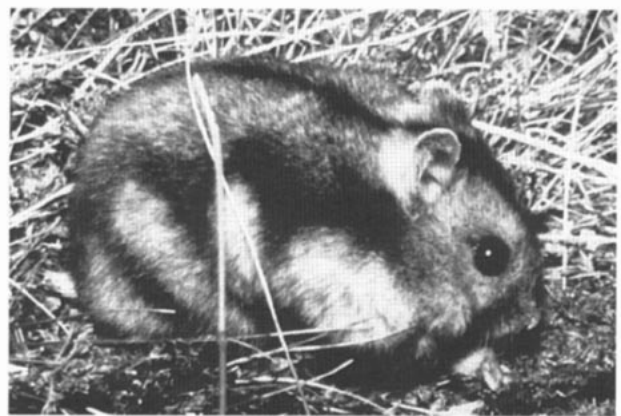


FIG. 1. Phodopus sungorus from Siberia in summer pelage. Photograph by Katherine E. Wynne-Edwards.

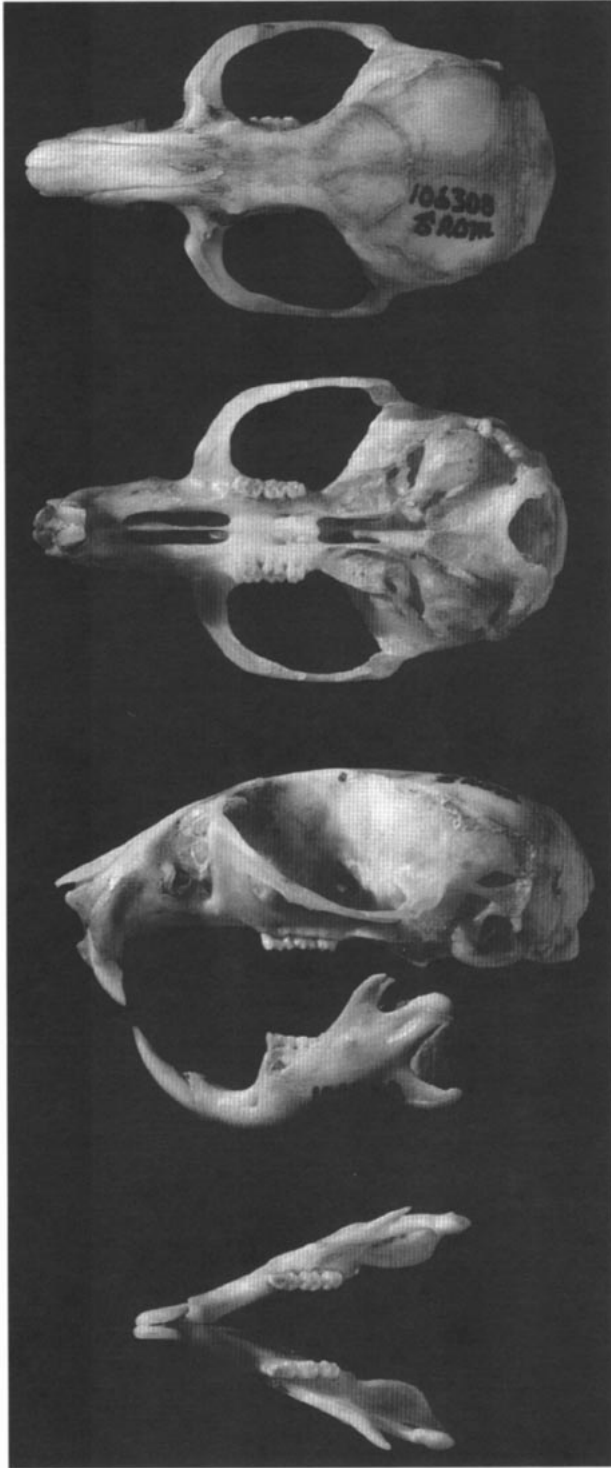


FIG. 2. Dorsal, ventral, and lateral views of the cranium and lateral and occlusal views of the lower jaw of a captive (male, Royal Ontario Museum 106308) *Phodopus sungorus*. Greatest length of skull is 26.1 mm. Photographs courtesy of the Royal Ontario Museum.

by mid-November. Molt into summer pelage begins mid-January to early February and is complete by March (Figala et al., 1973). Both molts proceed from spots on top of the head and the hind part of the back to the sides, extremities, and underparts (Veselovsky and Grundova, 1964). The average length of fur on the back is 10 mm in the summer and 10.2 mm in the winter (Heldmaier and Steinlechner, 1981a).

The Harderian gland, a yellow-brown, two- to three-lobed tub-

uloalveolar structure in the posterior part of the orbit, is made up of two types of epithelial cells. Type I cells are cylindrical with numerous small (0.8–2 μm) vacuoles. Type II cells are relatively broad with larger (2.5–5 μm) vacuoles. There are four times as many membranous structures of unknown function in the Harderian glands of female as in male *P. sungorus* (Schreckenberger and Reuss, 1993).

The mid-ventral sebaceous gland is oval or circular in shape and is larger in males, particularly during the breeding season (Vorontsov and Gurtovi, 1959). In males under long photoperiods, the gland has an average length of 7.6 mm and mass of 48.1 mg, and under short photoperiods, an average length of 2.4 mm and mass of 21.7 mg. Closely packed acini form lobules of assorted size and shape with common excretory ducts. Connective tissue containing a dense capillary network surrounds the lobules. Regions of the endothelial wall of the capillaries facing sebocytes of the acini or duct epithelium are 50–80 nm thick and fenestrated with groups of two to five 30–80 nm fenestrations, each closed by a 5–7 nm membrane (Sunderkötter et al., 1990). Nuclear receptors for the steroid hormone vitamin D (soltriol) are associated with basal cells, cells of the outer hair sheath, hair bulbs, and epidermis (Stumpf et al., 1993).

In common with *P. campbelli*, but not *P. roborovskii* or other hamsters, an epidermal pocket, or sac-like structure, is formed between the skin of the cheek and the opening of the cheek pouch during ontogenesis by a complex transformation of muscle and connective tissue. The outer layer comprises two layers of fibrous elastic connective tissue separated by a layer of striated muscle fibers. The inner layer is multilayered epithelium with an exfoliating lining. Sheets of dead cells shed into the sacculle form part of the secretory material, a whitish-yellow substance with a sharp odor. Both the mass of the sacs and amount of secretion is greatest in breeding females (Sokolov et al., 1994).

The cheek pouches are an extension of the adoral cavity (Vorontsov, 1979). The size of the entrance to the pouch through an opening in the diastema is controlled by five components of the buccinatorius muscle. The internal surface of the pouches is characterized by folds and numerous cone-like dermal papillae. Dense continuous bands of elastic fibers in the dermis aid the expansion and contraction of the pouch. Well-developed retractor muscles originate from the lumbar vertebrae and insert into the posterior one-quarter of the pouch (Ryan, 1986).

The dental formula is i 1/1, c 0/0, p 0/0, m 3/3, total 16. The anterocone and anteroconid are divided into two well defined cusps (Fig. 2). The endoloph joining the main cusps is straight and parallel to the longitudinal axis of the tooth row (Wahlert, 1984). Each molar decreases in size posteriorly so that each is two-thirds the size of the one in front (Vinogradov and Argiropulo, 1941). The length of the upper tooth row is variously 3.4–3.7 mm (Vinogradov and Argiropulo, 1941) and 3.6–4.0 mm (Ross, 1992). There are 6 L, 3 S, and 10 Ca vertebrae (Pallas, 1778). Numbers of Ce and T vertebrae are not recorded.

The nucleus, mitochondria, Golgi apparatus, endoplasmic reticulum, and secretory granules of almost all the acinar cells in the parotid (salivary) gland contain cytoplasmic crystalloids. At least four kinds of secretory granules are present (Suzuki et al., 1983). The length of the tongue is ca. 12.8 mm, the width, 3.7–4.2 mm. A shallow sulcus medianus linguae extends to the end of the tongue, the sulcus semilunaris is absent, and the torus linguae is weak. Taste buds are associated with papillae fungiformes on the dorsum and tip of the tongue, a single row of papillae foliatae on the lateral margin of the tongue opposite the cheek teeth, and a papilla circumvallatus (490 μm by 280 μm) in the root of the tongue (Vorontsov, 1958, 1979). The stomach is two-chambered, consisting of a left corneous fore-stomach and a right glandular stomach separated by a narrow isthmus (Vorontsov, 1979). At birth the mucosa in the glandular portion is characterized by large folds with a few glandular pits. Individual cells are not well defined. The cellular surface is densely covered by short microvillae, and some cells have long shaggy microvillae at the entrance to the pits. The fundic and pyloric regions can be differentiated by 1 week of age. By 4 weeks of age, the mucosa folds have regressed, some cell surfaces are completely free of microvillae, and the long shaggy microvillae are absent. Adult cells are well defined and rounded with large pits open to the surface (Ercan et al., 1986). The cecum consists of a small bulbous ampulla ceci and a voluminous corpus ceci. The walls of the corpus ceci are smooth when filled with

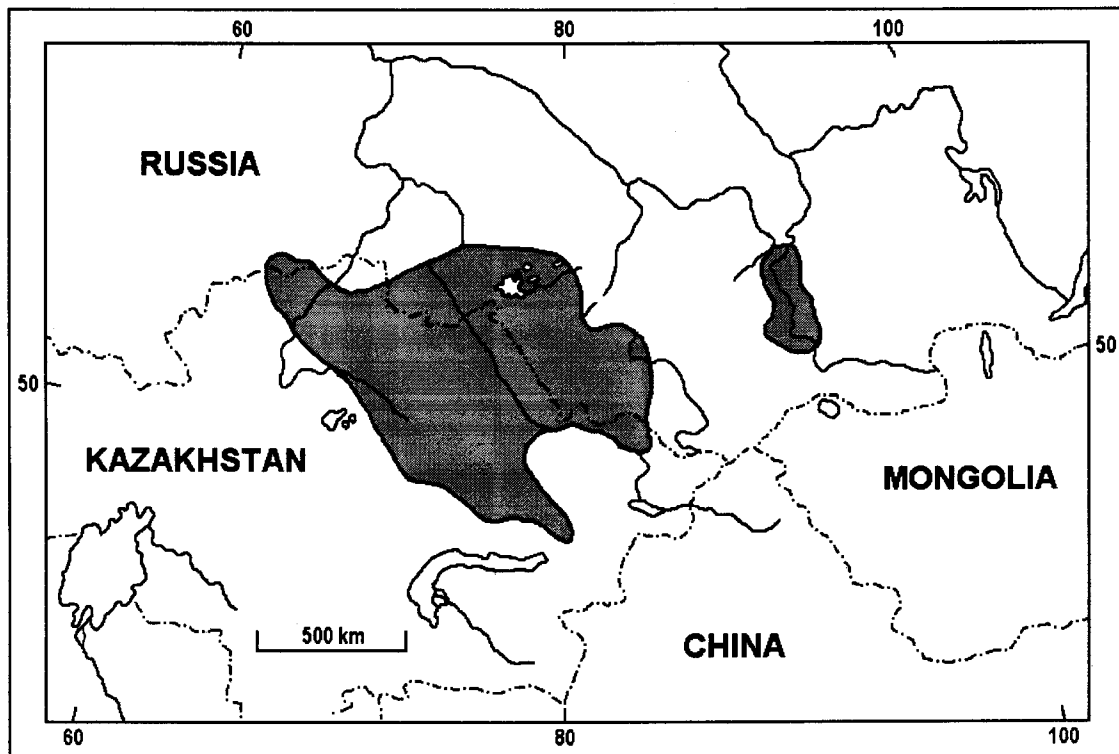


FIG. 3. Distribution of *Phodopus sungorus* in central Asia. *P. sungorus* is found in both delimited areas. Modified from Vorontsov et al., 1967.

intestinal content. A well-developed microvillar epithelial border suggests an active absorption of nutrients (Snipes, 1979). The small intestine, large intestine, and cecum account, respectively, for 60, 27, and 13% of the total length of the intestine (Vorontsov, 1962).

Mean measurements of the reproductive system of males raised in long days (16L:8D) and (short days—8L:16D) are: mass of testes, 945 mg (36 mg); mass of seminal vesicles, 684 mg (109 mg); diameter of seminal vesicles, 200 μm (70 μm —Schlatt et al., 1995); number of Sertoli cells, 1.38×10^7 (1.14×10^7 —van Haaster et al., 1993), area of Sertoli cell nuclei, 23 μm^2 (10 μm^2); area of Leydig cells, 40 μm^2 (24 μm^2); and size of Leydig cell nuclei, 11.6 μm^2 (9.5 μm^2 —Kliesch et al., 1991). The diameter of maturing oocytes increases from ca. 10.5 μm in nongrowing follicles on day 8 postpartum to 67.4 μm in preovulatory follicles by day 28. Mature follicles are characterized by a thecal layer which is almost as wide as the granulosa layer (Theuring and Hansmann, 1986).

FUNCTION. *Phodopus sungorus* displays an annual morphological and physiological cycle controlled by the action of photoperiod (Heldmaier and Steinlechner, 1981a) on the pineal gland and the circadian rhythm of melatonin secretion (Goldman and Darrow, 1983). Photoc information reaches the pineal gland by means of a multisynaptic neural pathway which includes the retina, suprachiasmatic nucleus, paraventricular nucleus of the hypothalamus, intermedial horn of the spinal cord, and the superior cervical ganglia where postsynaptic neurons send projections directly to pinealocytes (Bartness and Wade, 1985). Melatonin binds to the pars tuberalis of the pituitary, the nucleus reuniens and the paraventricular nucleus of the thalamus, and the suprachiasmatic nucleus of the hypothalamus which represents the biological or circadian clock which regulates the synthesis and secretion of melatonin (Carlson et al., 1991). *P. sungorus* has a Type C melatonin pattern with prolonged peak activity during most of the dark phase (Lerchl and Nieschlag, 1992). The duration (Goldman et al., 1984) and amplitude (Niklowitz et al., 1994) of the melatonin pulse during the dark phase provide information on ambient day length and season. The melatonin signal can be enhanced by exposure to cold and reduced food (Stieglitz et al., 1991). A pulse of light during the dark phase can inhibit melatonin synthesis for the duration of the dark period, and exposure to red light 2 h before the beginning of the light phase is sufficient to reset the morning oscillator of the

circadian clock (Klante and Steinlechner, 1995). Oxidation of melatonin precursors (pineal serotonin) in aging hamsters reduces the amount of melatonin secreted (Lerchl, 1994). Melatonin synthesis and metabolism in the retina is independent of pineal melatonin synthesis and peaks may occur at variable times of the day and night in different seasons. Melatonin released into the blood from the retina or other organs is sufficient to cause gonadal atrophy in pinealectomized *P. sungorus* several weeks after pinealectomy. This suggests a long-term feedback mechanism which informs the retina or other organs that are capable of releasing melatonin that melatonin from the pineal is absent (Steinlechner et al., 1995).

Exposure to decreasing day length in the autumn or short (8L:16D) photoperiods initiates gonadal regression, molt into winter pelage, increased thermogenic capacity, daily bouts of torpor, decreased food intake, and reduction of body mass (Figala et al., 1973; Hoffmann, 1973), all of which contribute to survival in a severe climate over the winter. The degree of photo responsiveness is variable, genetically controlled, and under the control of a different functional system than the circadian system (Lynch et al., 1989). Siberian hamsters that do not respond to short day length lack a short-day melatonin rhythm (Puchalski and Lynch, 1986), display a different pattern of neuronal activity in the suprachiasmatic nucleus (Margraf et al., 1991), and remain reproductively active (Kliman and Lynch, 1992).

Vitamin D (solatriol) acts on spleen and thymus cells (Stumpf et al., 1990) and functions in *P. sungorus* as a seasonal regulator in response to changes in day length. It has specific effects at the level of the blood-brain barrier (Bidmon and Stumpf, 1992), as well as on cell groups involved in the regulation of motor, sensory, autonomic, neuroendocrine, metabolic, and immune functions (Stumpf et al., 1992). It affects the regulation of follicle-stimulating hormone on Sertoli cell function and testicular growth (Majumdar et al., 1994).

Continued exposure to a short (6L:18D) photoperiod causes the concentration of intratesticular testosterone to drop from ca. 248 to 10 ng/testis, serum testosterone from 3.8 to <1 ng/ml, pituitary follicular-stimulating hormone from 106 to 20 ng/pituitary, and serum follicular-stimulating hormone from 2.43 to 0.5 ng/ml (Schlatt et al., 1995). In females, the concentration of pituitary follicular-stimulating hormone remains at 2.43 ng/ml during exposure to a

short photoperiod, but less is released. After 18 weeks under short day length, follicular development in females (Schlatt et al., 1993) and spontaneous recrudescence of spermatogenesis up to stage of spermatids in males are initiated by follicular-stimulating hormone released from the pituitary. Both follicular-stimulating hormone and testosterone are required to restore full fertility in males (Lerchl et al., 1994). Activity of 3β -hydroxysteroid-dehydrogenase is restored in Leydig cells only after testes weigh 400 g and serum testosterone levels remain low until week 24 (Schlatt et al., 1995). Exposure to long days initiates an almost immediate surge of follicular-stimulating hormone which sends specific signals for the growth and development of testes. Thirty days later, an increase of luteinizing-hormone leads to the secretion of testosterone and stimulation of sexual activity (Wolfe et al., 1995). The critical daylength to maintain testicular function is variously ca. 13 h (Hoffmann, 1982) and 14–16 h (Duncan et al., 1985).

A decrease of serum prolactin during short days is presumed to be responsible for the growth of an unpigmented winter coat (Duncan and Goldman, 1984). Daylength must be <14 h to initiate change into winter pelage (Duncan et al., 1985).

In captivity, *P. sungorus* reduces its winter metabolic requirements by 35% by losing 30% of its body mass, and by improving its thermal insulation. Captive *P. sungorus* weighing ca. 42 g at the end of August had a body mass of only 28 g in December (Steinlechner et al., 1983). Weight loss during the first weeks in short photoperiods is due mainly to decreased fat-cell size in epididymal, retroperitoneal, inguinal, and dorsosubcutaneous white adipose tissue pads (Mauer and Bartness, 1997), initiated by both a drop in circulating androgens and a gonad-independent increase in melatonin (Bartness and Wade, 1985). Metabolic rate increases linearly with falling ambient temperature (Weiner and Heldmaier, 1987). The basic metabolic rate is lowest in July ($1.68 \text{ ml g}^{-1} \text{ h}^{-1}$; $n = 118$) and highest in January ($2.06 \text{ ml g}^{-1} \text{ h}^{-1}$; Heldmaier and Steinlechner, 1981a). In January, the average body temperature fluctuated from 36.9°C for *P. sungorus* ($n = 60$) maintained under natural conditions to an average of 20.7°C in animals ($n = 33$) which had entered spontaneous daily torpor (Heldmaier and Steinlechner, 1981b).

Torpor, food intake, and change in body mass are controlled by an internal seasonal timekeeping mechanism (Bartness et al., 1989). Under natural conditions, spontaneous winter daily torpor begins in October. Testicular regression, molt, and decrease in body weight must occur before torpor begins (Heldmaier and Steinlechner, 1981a). Torpor occurs in ambient temperatures from thermoneutrality (23°C) to -1°C , begins early in the light phase, and continues for 4–8 h (Heldmaier and Ruf, 1992; Ouarour et al., 1991). *P. sungorus* maintained in 8L:16D at 20°C exhibited the first bout of daily torpor after week 12 of exposure. Torpor was initiated by a rapid 5.7–34.1% decrease in metabolic rate. The resulting deficit in heat production caused a decline in body temperature which was correlated with ambient temperature. A constant body temperature (25 to 13°C) was maintained while in torpor. Torpor was terminated by a rapid increase in metabolic rate and elevation of body temperature to normothermic levels before the beginning of the dark phase, a process which took ca. 40 min at 10°C . The frequency of daily bouts increased during dark days and as exposure to short days increased, reaching a maximum at 130 days (Heldmaier and Ruf, 1992). After week 28, bouts of torpor ceased, even though the hamsters were kept in short days. All males entered torpor at least once during weeks 12–28, but 3 of 7 females did not. The average saving in energy was 56.8% over a period of torpor, 11.9% over 24 h, and 2.4% for males and 1% for females over the 16 weeks the hamsters entered torpor (Kirsch et al., 1991). Decreased activity levels between bouts of torpor also lowered daily energy expenditure (Ruf and Heldmaier, 1992). In nature, winter torpor ceases when the spring molt begins (Heldmaier and Steinlechner, 1981a). Testosterone and estradiol implants (Vitale et al. 1985) or ablation of the suprachiasmatic nuclei (Ruby et al., 1989) inhibit torpor in males and females, respectively. Thermoneutrality and excess food do not prevent winter torpor (Heldmaier and Steinlechner, 1981a), but a diet high in polyunsaturated fat can increase the occurrence of torpor in individuals maintained in temperatures $<18^\circ\text{C}$ (Geiser and Heldmaier, 1995). A decrease in temperature has no effect on frequency and characteristics of torpor, but low temperatures with short day length may accelerate expression of maximal torpor bouts (Ouarour et al., 1991). Summer torpor, which is not mediated by the pineal gland,

can be induced in captive *P. sungorus* by food deprivation (Ruby et al., 1993) and by blocking glucose metabolism (Dark et al., 1996).

Phodopus sungorus can maintain a body temperature of 36.1 – 37°C when exposed for several hours to a temperature of -35°C , partially the result of a melatonin mediated increase in mitochondrial activity and nonshivering thermogenesis in brown adipose tissue (Heldmaier et al., 1982). Maximum thermal insulation at -35°C was $1.1 \text{ g } ^\circ\text{C}/\text{mW}$ (Heldmaier, 1975). Thermal conductance remains constant throughout the year at $0.78 \text{ mW}/\text{g } ^\circ\text{C}$ (Heldmaier and Steinlechner, 1981a). The experimental cold limit in winter was -51.3°C , in summer, -42.4°C (Weiner and Heldmaier, 1987). Severe hyperthermia was induced when individuals were exposed to temperatures of 35°C . Pregnant females increase body temperature just before parturition, exhibit hyperthermia during the first nine to 12 days of lactation, and tolerate excess heat produced by young that are capable of independent thermogenesis before weaning (Scribner and Wynne-Edwards, 1994). Thermogenesis and independent thermoregulation were observed in all young by 9 and 12 days of age, respectively (Newkirk et al., 1998). The metabolic cost of running at 0.5 km/h in summer, 213 mW , decreased during the winter to 164 mW (Heldmaier and Steinlechner, 1981a).

Seasonal changes in metabolic rate are accompanied by seasonal changes in relative heart weight. There is an increase of heart weight from 4–5% of total body mass during the summer period from May to July to 7–8% of total body mass between November and March. The efficiency of oxygen transport also is enhanced in winter by an average increase of 10.2% in the number of erythrocytes (Puchalski and Heldmaier, 1986). Females metabolized an extra 20.9 MJ kg^{-1} during gestation and lactation of one litter under natural conditions and an extra 22.6 MJ kg^{-1} under semi-natural conditions, an increase of 37 and 24%, respectively, over normal maintenance expenditure under the same conditions (Schierwater and Klingel, 1986).

Urine, feces, and secretions from oral, Harderian, skin glands behind the ears, and the mid-ventral gland (Wynne-Edwards et al., 1992) create an "integrated odor field that serves as a potent regulator of populational mechanisms" (Sokolov et al., 1994:146). The function of the mid-ventral gland is regulated by testosterone, vitamin D, and perhaps estradiol (Stumpf et al., 1993). Fenestrated capillaries in the vascular network facilitate the supply of fluids and nutrients to the sebaceous acini and the production of sebocytes (Sunderkötter et al., 1990). Specialized grooved hairs with spatulate bases that grow around the periphery of the gland aid in deposition of secretions from the gland (Heisler, 1984). Secretions from additional saccules are specific to individual hamsters, can be differentiated by conspecifics, and may be used to communicate sex, age, and social status, and, in combination with secretions of sebaceous glands at the corners of the mouth, to mark pelage and stores of food (Sokolov et al., 1994).

The Harderian gland is presumed to be involved in corneal lubrication, pheromone and thermoregulatory lipid production, photoreception, or in a pineal-pituitary-gonadal axis. Receptors for vitamin D on myoepithelial cells and 5.5–19% of the alveolar cells suggest that the functions of the Harderian gland may be partially under the control of this hormone (Pérez-Delgado et al., 1993).

Phodopus sungorus uses cheek pouches to transport food to storage areas in burrows. Inflating cheek pouches with air enhances buoyancy while swimming (Vorontsov, 1979). The species is highly tolerant of water deprivation and will regain body weight and fat lost during a 3 month period of deprivation in <3 weeks (Schierwater and Klingel, 1985). A positive water balance is maintained during periods of water deprivation by reducing body mass by up to 40%, by reducing evaporative water loss from >3 to $<2 \text{ mg H}_2\text{O g}^{-1} \text{ h}^{-1}$, and by concentrating urine. During water deprivation, the osmolarity of the urine rose from $1,518.9$ ($n = 200$) to $2,852.3 \text{ mOsmol/kg H}_2\text{O}$, the concentration of sodium in the urine decreased from 105.8 to 67.7 mMol/l , the concentration of potassium increased from 183.6 to 192.3 mMol/l , the concentration of chlorine decreased from 48.3 to 7.5 mMol/l , and the pH decreased from 7.8 to 5.8 . Urine output fell from 0.69 to $0.20 \text{ ml}/24 \text{ h}$ (Trojan, 1979).

ONTOGENY AND REPRODUCTION. The reproductive season begins in April–May and extends to September (Flint, 1966). In Kazakhstan, up to 60% of the females may reproduce during the winter (Kryltsov and Shubin, 1964). Captive females have had litters in temperatures as low as -20°C (Veselovsky and

Grundova, 1964). In Krasnoyarsk, pregnant females weighed at least 20 g. Female offspring of captive females from this locality produced their first litter at 4–5 months of age (Meyer, 1967). At ovulation, a mean of 4.8 oocytes (range, 1–7) are released. No polar bodies are evident and chromosomes aligned on a metaphase plate equidistant from a bipolar spindle indicate that development is arrested in meiosis I (Murray and Laprise, 1995).

The average number of embryos was 6.4 and the mean number of embryo scars was 5.1 in 19 females from Krasnoyarsk (Meyer, 1967). Mean litter size of females descended from *P. sungorus* collected in Karasuk, Siberia, maintained at 21°C with the male parent present was 5.0 and with the male parent absent, 5.3 (Wynne-Edwards and Lisk, 1989). Over a 5-year-period, 308 of 368 pairs of captive *P. sungorus* maintained under a 16L:8D photoperiod gave birth to 2,113 litters (mean of 6.0 young per litter). The average number of offspring was higher in the second litter than the first, and highest (6.8) in the third litter. The ratio of males to females after weaning was 1.0:1.1 (Lerchl, 1995). In captive *P. sungorus* maintained on a 16L:8D cycle, the mean number of offspring per litter was 4.3, and the mean number of young that survived until weaning was 3.2. The median interval between litters was 24 days (Ebling, 1994). The average metabolic cost of gestation and lactation for one litter born to captive females in seminatural conditions was 22.6 MJ/kg, an increase of 24% over normal energy expenditure (Schierwater and Klingel, 1986). The gestation period for captive females is ca. 18–19 days for first litters (Scribner and Wynne-Edwards, 1994). Females mate during a postpartum estrus and produce second litters after a gestation period of 18–25 days. Births of second litters delayed after 19 days may be the result of post-implantation embryonic diapause (Newkirk et al., 1997).

The mean body mass at birth of 15 young born in captivity was 2.4 g (Veselovsky and Grundova, 1964). Yudin et al. (1979) reported a mean body mass at birth of 1 g and an average total length of 26 mm. Young born to females from the Krasnoyarsk region were hairless at birth (day 1). Incisors and claws were present, but the eyelids, ear pinnae, and digits were sealed. Separation of the ear pinnae from the head was complete in all young by day 4. The eyes began to open on day 10, and most young could see by day 11. The digits of the forefeet and hind feet were fully separate by days 8 and 9. The pigment of the mid-dorsal stripe was not apparent until day 3. Fur first appeared on the head, followed by the sides and then the abdomen. Most young were well furred by day 8 (Meyer, 1967). The juvenile coat is lighter in color than that of adults, and has a yellowish tinge on the back (Veselovsky and Grundova, 1964). In Karasuk, Siberia, the mean mass of young dispersing from the nest was 12.3 g (range, 10.5–16.5 g—Wynne-Edwards and Lisk, 1989). Adult mass, 22–23 g, is attained by 1 month of age, and sexual maturity is reached by 40–45 days of age (Yudin et al., 1979). Captive young born before the end of May reproduced during their first summer (Hamann, 1987).

Age of sexual maturity in males is determined by both the prenatal photoperiod of the mother and the direction (increasing or decreasing) of postnatal photoperiod of the offspring (Shaw and Goldman, 1995). Photoperiodic information is thought to be transferred across the placental barrier by maternal pineal melatonin (Stetson et al., 1986). Young are most sensitive to maternal melatonin 3–5 days before birth (Carlson et al., 1991).

Seminiferous cords of captive males raised under a 16L:8D photoperiod contain only prespermatogonia and Sertoli cells for the first 10 days postpartum (Bergmann et al., 1991). Spermatogenesis begins between days 4 and 5 after birth when gonocytes first enter the S-phase (van Haaster et al., 1993). Germ cells connect to the basal lamina and differentiate into Type A spermatogonia between days 6 and 8, meiosis begins on day 11, pachytene spermatocytes are present on day 12, and lumen are visible in most tubules on day 13. On day 31, completion of the first spermatogenic wave is indicated by the release of elongated spermatids into the lumen of seminiferous tubules (Bergmann et al., 1991). Thereafter, while in reproductive condition, six generations of differentiating spermatogonia divide at regular intervals during the 12-stage cycle of the seminiferous epithelium. The duration of each cycle is 7.9 days. During short day photoperiods, the seminiferous epithelium consists of Sertoli cells, spermatogonia, and a few primary spermatocytes (van Haaster and de Rooij, 1993).

Testicular growth becomes photoperiod dependent after 15 days of age (Pratt and Goldman, 1986) and can be delayed for several months during short daylengths (Stetson et al., 1986). Testes are

the main source for testosterone and its metabolite dihydrotestosterone (Lerchl and Nieschlag, 1995). Plasma testosterone levels in captive males maintained in the absence of adult females during the summer months show a strong circadian rhythm, reaching a peak of 5.71 ng/ml at 18 h, just prior to sunset. Plasma testosterone levels in males housed in the vicinity of adult females show early evening levels 12 times that observed in the early morning (Hoffmann and Nieschlag, 1977).

Follicles became sensitive to gonadotropins on day 12 postpartum (Theuring and Hansmann, 1986). The absence of luteinizing hormone-releasing hormone receptors on the ovaries indicates that follicular maturation, meiosis, and ovulation are mediated from the pituitary (Theuring et al., 1987). The first spontaneous ovulation in females raised in a 16L:8D photoperiod occurred at 32 days of age (Theuring and Hansmann, 1986). The estrous cycle of captive females maintained in a 14L:10D photoperiod at 18°C was four days in length (Scribner and Wynne-Edwards, 1994).

ECOLOGY. *Phodopus sungorus* is widely distributed in the semideserts of central Asia (Yudin et al., 1979). This hamster has been collected from dry steppes, wheat and alfalfa fields, and small fields in the forests of the Minusinsk region (Meyer, 1967), and in the crop areas of Kazakhstan where it is also found in grassy meadows and birch stands in the northwest part of its range (Kryltsov and Shubin, 1964). The distribution is allopatric from those of *P. campbelli* and *P. roborovskii* (Vorontsov et al., 1967).

Population densities are variable. Of 151 small mammals caught in the Koibalsk Steppe during 1963, 31.8% were *P. sungorus* (Yudin et al., 1979). Predators include the weasel (*Mustela nivalis*—Zverev, 1931).

Burrow construction varies in different parts of the range (Yudin et al., 1979). In Kazakhstan, the burrow is made up of vertical galleries with four to six entrances. The nest chamber is ca. 1 m below the surface of the ground (Vinogradov and Argiropulo, 1941). In Hakasia, there are several horizontal and vertical corridors linked to the main tunnel which lies ca. 35 cm beneath the surface. Nests are lined with moss in the summer and animal fur in the winter. Only one entrance is used in the winter. On the Koibalsk Steppes, *P. sungorus* occupies the burrows of marmots and other mammals and seldom digs its own (Yudin et al., 1979). Burrows constructed by *P. sungorus* under seminatural conditions were characterized by higher relative humidities and smaller temperature fluctuations than were observed outside (Schierwater and Klingel, 1986).

Diet consists mainly of the seeds of wild plants, mostly grasses, but insects, particularly grasshoppers, also are eaten (Kryltsov and Shubin, 1964). Seeds were found in the contents of 32 of 40 stomachs, vegetational parts of plants other than seeds in 11 stomachs, and insects in 15 stomachs analyzed. During winter, *P. sungorus* was observed feeding on undigested grains in horse droppings (Yudin et al., 1979). In captivity during long daylength, intake of complex carbohydrate was greater than fat, which was greater than protein. Exposure to short daylength increases the consumption of complex carbohydrate and protein, and decreases the consumption of fat (Fine and Bartness, 1996).

Females account for more than 50% of the population in all natural populations of *P. sungorus*, perhaps because of the higher mortality rate in males, which are more mobile and therefore more subject to predation than females (Meyer, 1967). The life span in captivity is reported to be 2–2.5 years (Hamann, 1987).

BEHAVIOR. *Phodopus sungorus* is nocturnal and crepuscular and is active throughout the year. During the winter, it has been observed at least 300 m from its burrow in search of food, and has been trapped at night in temperatures as low as –40°C (Flint, 1966). At temperatures <20°C, *P. sungorus* rests hunched over its hind feet with its head and forepaws hidden in its ventral fur with the pelage evenly fluffed. This posture is maintained with only sporadic bursts of activity for the duration of time the animal is exposed to cold. At temperatures >30°C, *P. sungorus* rests flat on its ventral surface with its limbs splayed out to the side. The pelage is not fluffed, but clumped, showing numerous “ventilation” gaps (Heldmaier, 1975).

Activity, measured by wheel running, indicated *P. sungorus* was most active in November, running almost 8 h/day, and least active in March, running only 2 h/day (Hamann, 1987). Activity of females during the dark phase declined sharply after parturition and

remained low until day 9 postpartum when it slowly began to increase and reach normal levels when the young were weaned (Scribner and Wynne-Edwards, 1994). General locomotion is described as slow and sluggish (Hamann, 1987). The sleep-wake pattern is similar to that of other nocturnal rodents. Seven *P. sungorus* spent 59% of the time sleeping during a 48 h period, 67% in light phase and 43% in dark phase (Deboer et al., 1994).

In paired agonistic interactions, *P. sungorus* males were less aggressive toward conspecific males than *P. sungorus* females were toward conspecific females. After dominance was established in an encounter, it was never reversed. Only dominant hamsters chased, and dominant males and females marked more often and spent more time in the home area of the subordinate (Wynne-Edwards and Lisk, 1987). Attempts to mate a *P. sungorus* male with a *P. campbelli* female resulted in the male biting the female to death (Yudin et al., 1979).

Phodopus sungorus breeds well in captivity and is easily domesticated. It also has been used as a model for depression (Crawley, 1984). The care, management, susceptibility to disease, and research uses of this species are summarized by Cantrell and Padovan (1987).

GENETICS. The chromosomes are $2n = 28$, and $FN = 51$. Chromosomes 12, 14, 15, 16 and Y are acrocentric; all other autosomes are metacentric (Schmid et al., 1986). The X chromosome comprises 9.9% of the haploid female karyotype (Haaf et al., 1987). It is almost metacentric, with two G bands on the slightly longer arm. In contrast to *P. campbelli*, C-banding shows heterochromatin in the first metacentric pair of chromosomes (Safronova et al., 1993). The short arm of the X chromosome and the entire Y chromosome are heterochromatic, and it is these regions that are involved in pairing (Vistorin et al., 1977). Nucleolar organizers are associated with the short arms of chromosomes 5, 7, 12, and 13 (Bigger and Savage, 1976; Schmid et al., 1986).

Genetic differences have developed between *P. sungorus* bred in Germany and *P. sungorus* bred in the United States. Siberian hamsters bred in the United States have fewer photoresponsive individuals, molt later, and lose body mass less rapidly than those bred in Germany (Lynch et al., 1989).

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 specific name refers to the Dzungaria Valley on the border of Kazakhstan and China.

Phodopus sungorus was originally considered to consist of two subspecies, *P. s. sungorus* and *P. s. campbelli* by Argyropulo (1933). This arrangement was followed by Ellerman (1941), Ellerman and Morrison-Scott (1951), Corbet (1978), and Gromov and Baranova (1981). Vorontsov et al. (1967) considered the two taxa to be geographically isolated and karyotypically and specifically distinct. Hybridization of the two forms produced females with reduced fertility and sterile males (Sokolov and Vasil'eva, 1994), a result of abnormal conjugation of the X- and Y-chromosomes and asynapsis in autosomes during meiosis (Safronova and Vasil'eva, 1996). Carleton and Musser (1993) support the separation into two species. The common names "Djungarian" and "Siberian" are used interchangeably for both forms in the literature, but the species under discussion may be determined by the supplier, geographic origin of the hamster, or by phrases such as "turns white in winter".

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