

*Ovis ammon*. By Alexander K. Fedosenko and David A. Blank

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**Ovis Linnaeus, 1758**

*Ovis* Linnaeus, 1758:70. Type species *Ovis aries* Linnaeus, 1758. *Capra* Linnaeus, 1758:70. Part.

*Aries* Brisson, 1762:12. Renaming of *Ovis* Linnaeus.

*Musimon* Pallas, 1776:8. Type species *Musimon asiaticum* Pallas, 1776 (= *Capra ammon* Linnaeus) by monotypy.

*Musmon* Schrank, 1798:78. Renaming of *Ovis* Linnaeus.

*Ægoceros* Pallas, 1811:230. Renaming of *Ovis* Linnaeus.

*Ammon* Blainville, 1816:76. Renaming of *Ovis* Linnaeus.

*Caprovis* Hodgson, 1847:702. Type species *Aegoceros musimon* Pallas, 1811 (= *Ovis musimon* Schreber) by monotypy.

*Argali* Gray, 1852:174. Type species *Aegoceros argali* Pallas (= *Capra ammon* Linnaeus) by monotypy.

*Pachyceros* Gromova, 1936:84. Type species *Ovis nivicola* Eschscholtz, 1829.

**CONTEXT AND CONTENT.** Order Artiodactyla, suborder Ruminantia, infraorder Pecora, family Bovidae, subfamily Caprinae, tribe Caprini, genus *Ovis*, subgenus *Ovis* (Baryshnikov 1981). Distinctive features of *Ovis* compared with *Capra* are presence of preorbital, inguinal, and 4 fully functional interdigital pedal glands and lack of beard, knee calluses, and odoriferous tail gland (Lydekker 1912; Pocock 1910). From 1 to 7 species are recognized: 1 species (*O. ammon*—Haltcnorth 1963), 2 (*O. ammon* and *O. canadensis*—Heptner et al. 1961; Tsalkin 1951), 5 (*O. ammon*, *O. canadensis*, *O. dalli*, *O. nivicola*, and *O. orientalis*—Valdez 1982), 6 (*O. ammon*, *O. aries*, *O. canadensis*, *O. dalli*, *O. nivicola*, and *O. vignei*—Wilson and Reeder 1993), 6 (*O. ammon*, *O. canadensis*, *O. dalli*, *O. gmelini*, *O. nivicola*, and *O. vignei*—Workshop on Caprinae taxonomy, Ankara, Turkey, 8–10 May 2000), or 7 (*O. ammon*, *O. canadensis*, *O. dalli*, *O. musimon*, *O. nivicola*, *O. orientalis*, and *O. vignei*—Nadler et al. 1973). A key to 7 species (Nadler et al. 1973) follows (Geist 1971; Ludwig and Knoll 1998; Revin et al. 1988; Sokolov 1959; Valdez 1982):

- 1 Length of head and body for males < 130 cm; shoulder height < 95 cm; body mass < 80–90 kg (male); skull length < 30 cm; skull weight < 5.5 kg; horns of adult males variable, length < 105 cm, girth at base 28–30 cm; neck ruff > 12 cm; bib present in some species; most winter pelage with dorsal saddle patches ..... 2
- Length of head and body for males > 130 cm; shoulder height > 95 cm; body mass > 80–90 kg (male), skull length > 30 cm; skull weight > 5.5 kg; horns of adult males homonymous, length > 105 cm, girth at base > 28–30 cm; neck ruff < 10–12 cm or absent; bib absent; saddle patches absent ..... 3
- 2 Shoulder height > 80 cm; greatest length of skull usually = 240 mm (less only for Iranian moufflons); females with horns; body color light; front edge of choana ahead of front edge of orbits when bony palate horizontal ..... 4
- Shoulder height < 80 cm; greatest length of skull < 240 cm; females commonly without horns; body color blackish; front edge of choana on same level as front edge of orbits when bony palate horizontal ..... *Ovis musimon*
- 3 Shoulder height < 100 cm; body mass of adult males usually < 120–130 kg; length of horn < 130 cm; length of horn core in adult males always < girth at base and < skull length; skull length < 300 mm; skull width < 155 mm; upper tooth row < 80 mm; ruff absent; rump patch small and distinct; lower portion of legs usually dark, but if not dark, then entire body completely white; tail broad and dark; 2n = 52, 54 ..... 5
- Shoulder height > 100 cm; body mass of adult males usually > 120–130 kg; length of horn length > 130 cm;

- length of horn core in adult males always > girth at base and > skull length; skull length 300 mm; skull width > 155 mm; upper tooth row > 80 mm; in winter males have light ruff (< 10–12 cm), which encircles neck, rump patch large and not distinct, lower portion of legs usually white; tail thin and light; 2n = 56 ..... *Ovis ammon*
- 4 Skull length < 260 mm; bib absent; ruff black, long or short but does not reach head; saddle patch white; 2n = 54 ..... *Ovis gmelini* (was *Ovis orientalis*)
  - Skull length 260–287 mm; bib present; ruff white or black, long and reaches head; saddle patch black and white or absent; 2n = 58 ..... *Ovis vignei*
  - 5 Girth at horn base < 36–38 cm; length of upper tooth row < 80–85 mm; nasal bone < 105 mm; tail stripe divides rump patch; rump patch does not extend far above tail base ..... 6
  - Girth at horn base > 38 cm; length of upper tooth row > 80–85 mm; nasal bone > 105 mm; tail stripe does not divide rump patch; rump patch extends far above tail base ..... *Ovis canadensis*
  - 6 Body mass < 100 kg; greatest length of skull < 270 mm; orbital width < 120 mm; horn length > 100 cm; 2n = 54 ..... *Ovis dalli*
  - Body mass > 100 kg; greatest length of skull > 270 mm; orbital width > 120 mm; horn length < 100 cm; 2n = 52 ..... *Ovis nivicola*

***Ovis ammon* (Linnaeus, 1758)**

**Argali**

*Capra ammon* Linnaeus, 1758:70. Type locality not given, see “Remarks.”

*Musimon asiaticum* Pallas, 1776:8. Type locality “Upper Irtysh River,” Siberia (Ellerman and Morrison-Scott 1951:414).

*Ovis ammon*: Erxleben, 1777:250. First use of current name combination.

*Ovis argali* Boddaert, 1785:147. Type locality “Altai.”

*Ægoceros argali*: Pallas, 1811:230. Name combination.



FIG. 1. An adult male *Ovis ammon collium* (November 1998) in the Kazakhskiy Melkosopochnik (central Kazakhstan tableland near Big Semyzbug mountain). Used with permission of the photographer A. P. Berber, Karaganda State University.

- Ovis nayaur* Hodgson, 1833:135. Part. Type locality "Tibet."
- Ovis sculptorum* Blyth, 1840:12. Nomen nudum (Ellerman and Morrison-Scott 1951:416).
- Ovis poli* Blyth, 1840:62. Type locality "West of Lake Zorkul," "near sources of Syr Daria, Pamir Plateau, Russian Turkestan" (Ellerman and Morrison-Scott 1951:415).
- Ovis hodgsoni* Blyth, 1840:65. Type locality "Tibet, probably on Nepal frontier."
- Ovis hodgsonii* Blyth, 1841a:863. Unjustified emendation of *Ovis hodgsonii* Blyth, 1840:65.
- Ovis polii* Blyth, 1841b:195. Unjustified emendation of *Ovis poli* Blyth, 1840:62.
- Ovis ammonoides* Hodgson, 1841:230. Type locality "Himalayan region."
- Caprovis (Argali) argali*: Gray, 1852:174. Name combination.
- Caprovis bambhera* Gray, 1852:174. Type locality "Nepal."
- Musimon argali*: Gervais, 1855:191. Name combination.
- Ovis karelini* Severtzov, 1873:84, 86. Type locality "Alatau of Semirechya, between the Ili River and Issyk Kul, Russian Turkestan" (Ellerman and Morrison-Scott 1951:415).
- Ovis heinsii* Severtzov, 1873:84, 87. Type locality "Tomak district, north-west of Issyk Kul, Russian Turkestan" (Ellerman and Morrison-Scott 1951:415).
- Ovis nigrimontana* Severtzov, 1873:84, 87. Type locality "Karatau Province of Syr Daria, on east bank of Syr Daria, Russian Turkestan" (Ellerman and Morrison-Scott 1951:415).
- Ovis argali altaica* Severtzov, 1873:154. Type locality "Southern Altai Mountains" (Ellerman and Morrison-Scott 1951:414).
- Ovis argali daurica* Severtzov, 1873:154. Type locality "To the east of Baikal Lake," Russian mountain ranges.
- Ovis argali mongolica* Severtzov, 1873:154. Preoccupied by *Ovis aries mongolica*.
- Ovis blythi* Severtzov, 1873:154. Type locality "Tibet."
- Ovis collium* Severtzov, 1873:154. Type locality "Kirghiz Steppe, north of Lake Balkash, North-Eastern Russian Turkestan" (Ellerman and Morrison-Scott 1951:415).
- Ovis brookei* Ward, 1874:143. Type locality "Ladakh."
- Ovis jubata* Peters, 1876:177. Preoccupied by *Ovis aries jubata* Kerr, 1792.
- Ovis darwini* Przewalskiy, 1883:260. Type locality "Southern Gobi, Mongolia" (Ellerman and Morrison-Scott 1951:414).
- Ovis dalai-lamae* Przewalskiy, 1888:274. Type locality "Gorge of River Zaysan-Saytu, approximately 38° N., 89° E., Sinkiang," China (Ellerman and Morrison-Scott 1951:414).
- Ovis henrii* Milne-Edwards, 1892:672. Type locality "Tibet."
- Ovis ammon typica* Lydekker, 1898:177. Renaming of *Ovis ammon* Linnaeus, 1758:70.
- Ovis poli typica* Lydekker, 1898:192. Renaming of *Ovis poli* Blyth, 1840:62.
- Ovis poloi* de Pousargues, 1898:141. Incorrect subsequent spelling of *Ovis poli* Blyth, 1840:62.
- Ovis sairensis* Lydekker, 1898:185. Type locality "Sair Mountains, Zungaria," Kazakhstan and China (Ellerman and Morrison-Scott 1951:415).
- Ovis sairensis littedalei* Lydekker, 1902:83. Type locality "One of the tributaries of the Ili, south-east of Kuldja, Chinese Turkestan" (Ellerman and Morrison-Scott 1951:415).
- Ovis ammon adametzi* Kowarzik, 1913:439. Type locality "Lob Nor district, Chinese Turkestan" (Ellerman and Morrison-Scott 1951:416).
- Ovis ammon humei* Lydekker, 1913:6. Type locality "North-west of Kashgar, Tien Shan Mountains" (Ellerman and Morrison-Scott 1951:415).
- Ovis kozlovi* Nasonov, 1913:621. Type locality "Yabara Mountains, Southern Gobi, Mongolia" (Ellerman and Morrison-Scott 1951:414).
- Ovis polii karelini* var. *melanopyga* Nasonov, 1914a:699. Type locality "Tien Shan."
- Ovis severtzovi* Nasonov, 1914b:761. Type locality "Nura-Tau Mountains, Kizil-kum, Russian Turkestan" (Ellerman and Morrison-Scott 1951:416).
- Ovis comosa* Hollister, 1919:46. Replacement name for *Ovis jubata* Peters, 1876:177.
- Ovis ammon comosa* Sjölander, 1922:134. Incorrect subsequent spelling of *Ovis comosa* Hollister, 1919:46.
- Ovis ammon severtzovi* Nasonov, 1923:65. Incorrect subsequent spelling of *Ovis severtzovi* Nasonov, 1914:761.
- Ovis ammon przewalskii* Nasonov, 1923:118. Type locality "Saylyugem Range, Altai Mountains" (Ellerman and Morrison-Scott 1951:415).
- Ovis polii nassonovi* Laptev, 1929:76. Type locality "Talasskiy Alatau Range" western Tien Shan.
- Ovis ammon intermedia* Gromova, 1936:82. Type locality "Nain Bogdo Range, central Gobi, Mongolia."

**CONTEXT AND CONTENT.** Content as above. Type localities from Russian are translated. Nine subspecies of *Ovis ammon* are recognized (Bunch et al. 1990, 2000; Geist 1991; Shackleton 1997; Shakula et al. 1994).

*O. a. ammon* (Linnaeus, 1758:70), see above; *altaica* Severtzov, *argali* Boddaert, *argali* (Pallas), *asiaticus* (Pallas), *daurica* Severtzov, *mongolica* Severtzov, *przewalskii* Nasonov, and *typica* Lydekker are synonyms.

*O. a. collium* Severtzov, 1873:154, see above; *sairensis* Lydekker is a synonym.

*O. a. darwini* Przewalskiy, 1883:260, see above; *argali* Przewalskiy, 1876, *comosa* Hollister, *intermedia* Gromova, *jubata* Lydekker, *kozlovi* Nasonov, and *mongolica* Lydekker are synonyms.

*O. a. hodgsoni* Blyth, 1840:65, see above; *adametzi* Kowarzik, *ammonoides* Hodgson, *argali* (Adams, 1858:527), *bambhera* (Gray), *blythi* Severtzov, *brookei* Ward, *dalai-lamae* Przewalskiy, *henrii* Milne-Edwards, and *hodgsonii* Blyth are synonyms.

*O. a. jubata* Peters, 1876:177, see above; *comosa* Sjölander is a synonym.

*O. a. karelini* Severtzov, 1873:84, 86, see above; *heinsii* Severtzov, *humei* Lydekker, *littedalei* Lydekker, 1909, *melanopyga* Nasonov, and *nassonovi* Laptev are synonyms.

*O. a. nigrimontana* Severtzov, 1873:84, 87, see above.

*O. a. poli* Blyth, 1840:62, see above; *polii* Blyth, *polii* (Brehm), *poloi* de Pousargues, *sculptorum* Blyth, and *typica* Lydekker are synonyms.

*O. a. severtzovi* Nasonov, 1914b:761, see above; *severtzov* Nasonov is a synonym.

**DIAGNOSIS.** *Ovis ammon* (Fig. 1) is the largest species in the genus (ranges of maximum values for adult males are: total length, 177–200 cm; height at shoulder, 106–135 cm; body mass, 110–182, maximum 216 kg—Fedosenko 2000). Horns of *O. ammon* are longest, thickest (except of *O. nivicola*), and heaviest of wild species of sheep (maximum values are: length along anterior surface, 192 cm; girth at base, 59 cm; span, 186 cm; mass with skull, 32 kg). Argali horns have 2 full circles of spiral, with tops always directed sideways; this pattern is distinct from that of other *Ovis* species. In *O. ammon*, horn surface is heavily corrugated as compared to *O. nivicola*, horn color is lighter than in *O. vignei*, and females have horns in contrast to *O. musimon*. Occiput of argali protrudes little beyond rear margins of horn cores and drops almost vertically; occiput is considerably shorter in *O. ammon* than in *O. musimon* and *O. gmelini*. Greatest height of skull is behind eye sockets. Facial part of skull of *O. ammon* is elongated, with length >60% of entire skull. Horn core of *O. ammon* is thicker than that of *O. musimon* and *O. vignei*, but thinner than that of *O. nivicola*. Girth of horn core at the base is >70% of its length in *O. ammon*. All argali, except *O. a. ammon* and *O. a. darwini*, have a long throat ruff (8–12 cm), which almost completely surrounds the neck. Ruff of argali is significantly smaller than ruff of *O. vignei* (Fedosenko and Kapitonov 1983; Geist 1991; Heptner et al. 1961; Sapozhnikov 1976; Sokolov 1959; Sopin 1982).

**GENERAL CHARACTERS.** Argali are stout-bodied, but not heavily muscled with a short body, thick neck, and lightly boned, but robust legs. Leg bones are long; lengths (in mm) are: front leg, 680 (59% length of vertebral column); hind leg, 1,085 (72% length of vertebral column); metacarpus, 218; radius, 259; ulna, 231; metatarsus, 233; shin, 332; femur, 282. Hooves are relatively small; size of hooves (in mm) from front legs and hind legs, respectively, is: length, 70–78, 59–67; height, 41–45, 37–43. Line of back is straight with an incline down to front; height of sacrum exceeds height of shoulder by 2–7 cm. Tail is short. Head is massive with thick horns and a slightly hook-nosed profile. Ears are 9–13 cm long. Females are more lightly built than males and have

a thin, straight muzzle and lighter color. Legs and neck of ewes are long and thin (Heptner et al. 1961; Schaller 1977; Sokolov 1959).

*Ovis ammon* is the most sexually dimorphic of species of wild sheep. Some skull indices of males are up to 32.1% larger than those of females (Revin et al. 1988). External measurements (mean  $\pm$  SE, where available, and ranges, in cm) of adult (> 5 years of age except where indicated) males and females, respectively, are: total length of body,  $176 \pm 2.2$ , 172–180 ( $n = 4$ ),  $170.5 \pm 2.0$ , 167–174 ( $n = 3$ ) for *O. a. ammon*;  $177.5$ , 165–199 ( $n = 19$ ), 145.9, 136–160 ( $n = 10$ ) for *O. a. collium*;  $167.5$ , 158–190 ( $n = 6$ ) for *O. a. karelini* (males > 2 years old);  $171.9$ , 160–180 ( $n = 4$  males > 4 years), 143.5 ( $n = 4$  females > 2 years) for *O. a. polii*; slanting length of body (length from lowest point of chest to highest point of rump), 106.6, 89–121 ( $n = 19$ ), 98.9, 89–110 ( $n = 8$ ) for *O. a. collium*; 111, 103–112 ( $n = 4$  males 2–3.5 years) for *O. a. karelini*; 101.5, 98–105 ( $n = 3$ , > 4 years), 90.5 ( $n = 2$ ) for *O. a. polii*; shoulder height,  $117 \pm 1.0$ , 115–120 ( $n = 4$ ),  $108 \pm 4.0$ , 100–114 ( $n = 3$ ) for *O. a. ammon*;  $117.2$ , 108–135 ( $n = 21$ ), 95.9, 85–100 ( $n = 9$ ) for *O. a. collium*;  $108.3$ , 103–112 ( $n = 4$  males 2–3.5 years) for *O. a. karelini*;  $111.9$ , 101.5–120 ( $n = 4$ , > 4 years), 87.2 ( $n = 4$ , > 2 years) for *O. a. polii*; sacral height,  $119 \pm 0.65$ , 117–120 ( $n = 4$ ),  $112 \pm 3.9$ , 105–118 ( $n = 3$ ) for *O. a. ammon*; 113, 112–118 ( $n = 4$ ), 101, 87–108 ( $n = 9$ ) for *O. a. collium*; 116, 115–117 ( $n = 2$  males 2.5–3.5 years) for *O. a. karelini*; 103.5, 101–106 ( $n = 3$ , > 4 years), 91 ( $n = 4$ , > 2 years) for *O. a. polii*; chest girth,  $135 \pm 3.0$ , 126–140 ( $n = 4$ ),  $114 \pm 2.3$ , 110–118 ( $n = 3$ ) for *O. a. ammon*; 135, 128–152 ( $n = 21$ ), 107.3, 102–116 ( $n = 9$ ) for *O. a. collium*;  $126.5$ , 118–133 ( $n = 4$  males 2–3.5 years) for *O. a. karelini*; 112, 108–116 ( $n = 3$ , > 4 years), 102.7 ( $n = 4$ , > 2 years) for *O. a. polii*; length of tail,  $11 \pm 0.35$ , 10–12 ( $n = 4$ ),  $10.7 \pm 0.7$ , 9.5–12 for *O. a. ammon*; 13.3, 10–17 ( $n = 21$ ), 10.3, 7–16 ( $n = 9$ ) for *O. a. collium*; 12, 12–12 ( $n = 3$ , 2.5–3.5 years) for *O. a. karelini*; 10.3, 8.5–11.3 ( $n = 3$ , > 4 years), 9.2 ( $n = 4$ , > 2 years) for *O. a. polii*; length of ear,  $13 \pm 0.35$ , 12–14 ( $n = 4$ ),  $11 \pm 0.58$ , 10–12 ( $n = 3$ ) for *O. a. ammon*; 12, 9–14.5 ( $n = 23$ ), 12.6, 10–14 ( $n = 9$ ) for *O. a. collium*; 11.7, 11–12 ( $n = 3$  males 2.5–3.5 years) for *O. a. karelini*; 10.4, 10–10.7 ( $n = 3$ ), 10.6 ( $n = 4$ , > 2 years) for *O. a. polii*; body mass (in kg),  $134 \pm 11$ , 101–160 ( $n = 4$ ),  $90 \pm 5.8$ , 80–100 ( $n = 3$ ) for *O. a. ammon*; 139.1, 108–157 ( $n = 20$ ), 52.3, 43.2–62 ( $n = 8$ ) for *O. a. collium*; 113, 97–152 ( $n = 4$ ), 54.2, 47–66.1 ( $n = 13$ ) for *O. a. karelini*; 111.9, 100–123.7 ( $n = 2$ ), 55.3, 48.5–61.5 ( $n = 3$ ) for *O. a. polii* (Berber and Kalmykov 1994; Fedosenko 2000; Sapozhnikov 1976; Savinov 1975; Sopin 1975). Length (in mm, range) of vertebral column of *O. ammon* is 1,155 (1,095–1,221) for males and 1,007 (982–1,049) for females. Lengths (in mm) of select regions of the vertebral column are: thoracic, 421 for males and 405 for females; lumbar, 254 for males and 212 for females. Proportions of total length of vertebral column for select regions are: thoracic, 36.4% for males and 37.3% for females; lumbar, 23.4% for males and 23.5% for females. Measurements (in mm) of pelvic bones in males and females, respectively, are: length of ischium, 130, 111; length of ilium, 155, 140; width of ischium, 163, 148; width of ilium, 144, 134 (Revin et al. 1988).

Body color varies but is never pure white or blackish brown. During winter, color of male's back and sides is from dark, gray brown to light reddish brown or pale gray brown. Back is darker than sides, which gradually brighten downward. A black-brown stripe lies between darker color of sides and golden-yellow or dirty-white belly and groin; this stripe is sometimes indistinct or comprised of black spots closer to front and hind legs. Saddlelike white spots on back occur only in *O. a. darwini* and *O. a. ammon*. Tail, buttocks, and sometimes area above tail are yellowish white. Forehead and occiput are darkest areas on head, which has yellowish-gray to yellowish-brown tints. A black-brown ring may be present around eyes. Lower parts of neck, lips, and top of muzzle are light yellowish white, sometimes almost pure white. Males > 8 years have a very light, or sometimes pure white, "dickey" or "bib." Ears are gray brown on outside and dirty white on inside. Upper exterior parts of legs to carpal and metatarsus joints are the same color as the body or darker. Inside of legs is white and lower parts are dirty white to yellowish. Females are slightly lighter in color than males. During summer, males and females have a short, usually brown, pepper-and-salt-colored coat. Summer pelage has more reddish tones, and a distinct black-brown stripe appears in the middle of the back and neck. Young argali are a light gray-yellow color with

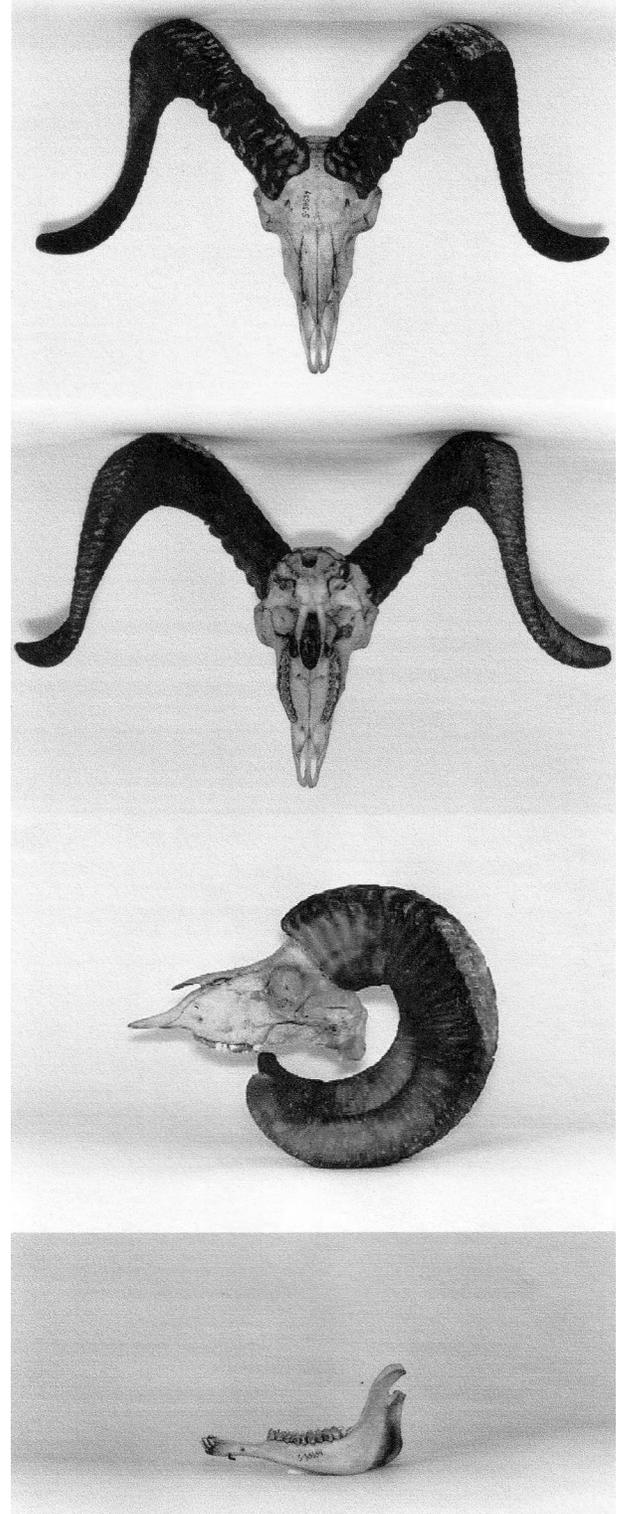


FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of a 5-year-old male *Ovis ammon karelini* (Zoological Museum of the Moscow Lomonosov State University S-39634) from Terskey Alatau Range, Tien Shan. Greatest length of skull is 317 mm, orbital breadth is 173 mm, and length of horn is 901 mm. Photographs by A. V. Antropov.

a darker gray-brown head. Coat of young begins to darken at 5–6 months, and pelage characteristic of adult males has developed by 6 years (Geist 1991; Sokolov 1959).

Cranial dimensions (mean  $\pm$  SE, where available, and ranges, in mm) of adult males ( $n = 44$ ) are (Fig. 2): basilar length, 323.8

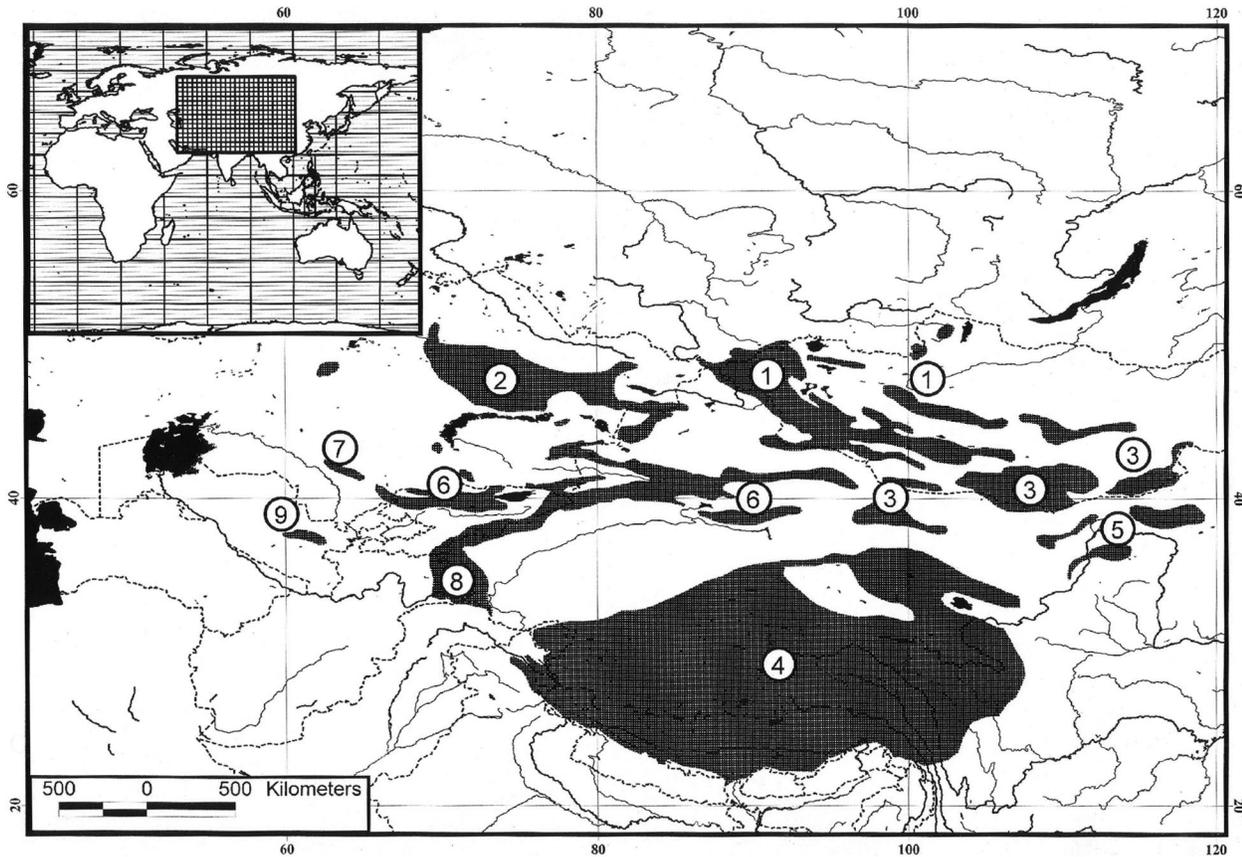


FIG. 3. Geographic distribution of *Ovis ammon* in central Asia and southern Siberia. Type localities of subspecies: 1, *O. a. ammon*; 2, *O. a. collium*; 3, *O. a. darwini*; 4, *O. a. hodgsoni*; 5, *O. a. jubata*; 6, *O. a. karelini*; 7, *O. a. nigrimontana*; 8, *O. a. polii*; 9, *O. a. severtzovi*. Precise boundaries between subspecies are unknown. Adapted from Fedosenko (2000) and Shackleton (1997).

$\pm 33.22$ , 233–374; greatest breadth of skull (orbital),  $175.2 \pm 17.91$ , 126–202; length of upper toothrow,  $87.5 \pm 10.38$ , 61–112; length of incisive bone,  $120.7 \pm 17.5$ , 65–150; orbital diameter,  $54.1 \pm 3.26$ , 46–60. Basilar length (range, in mm) in females is 232–318. Part of skull housing brain (from acrocranium to back edge of socket) is short and comprises 46% (range, 40.7–46.7%) of length of skull and 58–69% of length of muzzle (from prosthion to front edge of socket). External hearing duct (meatus auditorius externus) sits under base of horn cores. Facial part of skull is long and constitutes >64% (up to 75%) of length of skull. Nasal bones are narrow, with a width of 33–43% of their length. Knitting of skull sutures occurs early and is complete (Ludwig and Knoll 1998; Sokolov 1959).

*Ovis ammon* has large, helical, yellowish-gray horns with homonymic winding and distinct wrinkles. Horn measurements (mean  $\pm SE$  or mean or range, in cm) in adult males and females (> 5 years of age), respectively, are: length of horn,  $109 \pm 2.9$ , 82–132 ( $n = 25$ ),  $47 \pm 1.6$ , 40–56 ( $n = 10$ ) for *O. a. ammon*; 119.6, 94.5–137.5 ( $n = 24$ ), 29.1, 26–32 ( $n = 8$ ) for *O. a. collium*; 113.8, 69–148 ( $n = 50$ ), 30.2, 26–34 ( $n = 17$ ) for *O. a. karelini*; 130.1, 89–164 ( $n = 126$ ), 39, 33–49.5 ( $n = 5$ ) for *O. a. polii*; horn girth at base,  $43 \pm 0.9$ , 34–50.5 ( $n = 25$ ),  $18 \pm 0.4$ , 16–19 ( $n = 10$ ) for *O. a. ammon*; 38.5, 32.3–43 ( $n = 23$  males) for *O. a. collium*; 37.5, 32–47 ( $n = 116$ ), 14.7, 13.5–16.0 ( $n = 3$ ) for *O. a. polii*; horn span, 73.4, 63–87 ( $n = 9$ ), 17.4, 17–18.5 ( $n = 6$ ) for *O. a. ammon*; 75.3, 50–94 ( $n = 25$  males) for *O. a. collium*; 102.4, 69–130 ( $n = 75$ ), 34.2, 25–43.5 ( $n = 3$ ) for *O. a. polii*; horn mass (with skull and without lower jaw, range, in kg, for males only), 18.5–22 for *O. a. ammon*; 11–14.75 for *O. a. collium*; 7.7–14.4 for *O. a. polii* (Berber 1999; Berber and Kalmykov 1994; Fedosenko 2000; Sapozhnikov 1976; Savinov 1975; Sopin 1975). Length of first 4 segments of horn (growth of 5 years) ranges from 67 to 115 cm, with a volume reaching 2,500 cm<sup>3</sup>. Girth of horn at base ranges from 28.5 to 50 cm (very rarely <30 cm) and from 25.2% to 54.9% of total length of horn. Largest diameter of horn in cross section ranges from 65 to 138 mm. Horns are bent in an

extended spiral. In extreme cases, horns make 2 spirals, with their tops directed straight out laterally. Horns become flat on top and have 3 edges at base. Cross section of horn is an isosceles triangular with rounded sides and a more acute angle at back edge. Cross section of horn varies from a triangular base with sharp-angled edges in argali from Pamir to an increasingly rounder shape in argali from extreme northern Tien Shan and Mongolia (Fedosenko and Kapitonov 1983; Heptner et al. 1961; Sokolov 1959; Valdez 1982).

Horns of ewes are significantly smaller and thinner than those of males and are laterally compressed with a saberlike form and tops directed backward and out. Some measurements (range, in cm) of horns of ewes are: length, 23–53; girth at base, 16–19; and tip-to-tip spread, 43–45. Two distinct ribs occur on horns of ewes (internal and hind) and both are rounded. Horn color is a light yellowish gray or black brown. Horns of young males are similar to those of ewes (Heptner et al. 1961; Sokolov 1959).

Argali have proportionately the shortest tails among the Caprinae. Their tails are round, not flat, and terminate in a small dark tuft of hair. Ears are small and round. Legs are relatively long (Geist 1991; Schaller 1977).

**DISTRIBUTION.** *Ovis ammon* lives in southern Siberia and in the mountains of Central and Middle Asia, from central Kazakhstan in the west (to 67°E) to Shansi Province of China in the east (to 110–113°E), and from Altai in the north to Himalayas in the south (Fig. 3).

**FOSSIL RECORD.** The 1st records of true sheep are from the early mid-Pleistocene of Europe and China (Herre and Kesper 1953). These sheep were large, argalilike in form, and ranged throughout the steppe foothills of Eurasia. Sheep decreased in size over time (Gromova 1948). In the Pleistocene Epoch (1.8 million to 10,000 years ago), ice sheets and vegetative barriers (forests) isolated northern wild sheep (Argaliforms) from southern sheep (Moufloniforms—Geist 1971; Kurtén 1968). Eurasian sheep form

an “*ammon* cline,” starting with the most primitive form of *Amotragus lervia*, through mouflons to *O. a. hodgsonii* (ruffed argali), and further to *O. a. polii*, and *O. a. karelini*, culminating in *O. a. ammon* (Geist 1971).

Sediments from 440,000 years ago in the Caune de l'Arago cave, France, contain fossils of *O. ammon antiqua* (Rivals and Deniaux 2003). Fossil bones of argali (*Ovis* cf. *ammon*) were found in the Quaternary strata in the Caucasus (Verestsagin 1959). Argali-like forms were noted in the Oshelskian and Orin'iakskian stratum layers in Crimean caves. A tooth of a large argali was found in the Quaternary loam of western Iran (Sapozhnikov 1977). Remains of sheep, described as *Ovis* cf. *ammon* occur in the Chustskiy settlement (Uzbekistan—Verestsagin 1959) from the Bronze Age (2000 BCE—Ishunin 1961).

**FORM AND FUNCTION.** Pelage of *O. ammon* has 3 types of hair during winter: slightly wavy, coarse brittle guard hairs; intermediate summer hairs; and thin fluff (88%). Diameter of guard hair is 37.5–315  $\mu\text{m}$  and diameter of fluff hair is 7.5–21  $\mu\text{m}$  (Fedosenko and Kapitonov 1983). Newborns have mainly guard and intermediate hairs with a density of 1,552 hairs/cm<sup>2</sup>; density of hair decreases with age and guard hairs become base of pelage. Guard hairs of adult argali are softer on neck, back, and sides of body and thicker and coarser on belly and croup near tail (Sokolov 1959). In summer, hair is longest on back of body (18 mm), shorter on legs and neck (9–10 mm), and shortest on belly, flanks, and hindquarters (4–5 mm). Summer hair density is 373–776 hairs/cm<sup>2</sup>. In winter, longest guard hairs are on upper (80 mm) and lower (70 mm) parts of neck, shorter hairs are on back and sides of body (40–45 mm), and shortest are on hindquarters (30 mm), belly (20 mm), and legs (11 mm). Winter hair density can reach 1,300 hairs/cm<sup>2</sup> for females and 732 hairs/cm<sup>2</sup> for males. The large core cavity of guard hairs yields high thermoinsulation and easy evaporation of moisture (Sapozhnikov 1976).

The most common color for wild argali is gray brown, with differing intensities. Color is determined by presence of black and red pigments. Black pigment occurs in granular form mainly in the cortical layer of the hair and red pigment occurs in diffuse form in the core layer. Predominance of 1 pigment over the other, variation in thickness of hair, and degree to which cortical and core layers are developed produce gray-brown tints that range from light gray brown to black brown. Color along a single hair is uneven, with a lighter base and tip, and black brown in between (Revin et al. 1988). Argali develop a “worn-out” winter coat as hairs become abraded and shortened due to damage from the elements or from rubbing against the ground. Such damage causes diffusion of once sharp borders between pelage color fields and winter coats become light in color (Geist 1991).

Molting occurs once a year from mid-March to early August. Start and end of molt vary geographically. Molting occurs earliest in warm southern mountains (April–mid-May) and later in more northern or higher and colder mountains (end of May–June—Antipin 1947; Fedosenko 2000; Sapozhnikov 1976; Sopin 1975). The latest molt occurs in coldest mountains of Mongolia (early July—Dorogostaiskiy 1918) and central Tien Shan (end of July—early August—Fedosenko et al. 1995b). Timing of molt varies with individual condition; females with young finish molting 20–25 days later than others. The molt begins with older hairs on groin, belly, and lower chest, then moves to shoulders, muzzle, and sides of body, and finally to occiput, upper neck, back, legs, and tail. During peak of molt, winter coat is shed in entire layers (Antipin 1947; Dorogostaiskiy 1918; Sapozhnikov 1976). A feltlike covering of winter guard hairs mixed with matted underwool may be present until midsummer (Geist 1991). Winter pelage begins to grow late summer–early autumn, before the rut. Argali have their winter coat by mid-October, although hairs continue to grow into November (Fedosenko and Kapitonov 1983; Heptner et al. 1961). First changes in juvenile pelage occur by 15–20 days of age and young argali have their complete summer pelage by 2 months old. Guard and fluff hairs of young continue to grow, so that by December–January their coat does not differ from that of adult argali (Sapozhnikov 1976).

Argali have meibomian, preorbital, groin, and interdigital glands and secretory fields on nose-patch, nostril wing, and around vagina and anus. *O. ammon* may have preputial glands and secretory fields under tail and in external acoustic meatus (Sokolov and Chernova 1988).

Color of hooves is almost black in males, dark gray in females, and dark brown in young. Body mass loading on hooves is 1,016 g/cm<sup>2</sup> in males and 660–700 g/cm<sup>2</sup> in females (for *O. a. polii*). High loading on hooves prevents argali from digging food from under snow that is more than 20–25 cm deep (Heptner et al. 1961).

Milk of argali consists of 83.67% water and 16.33% solids, of which 0.68% is ash, 3.26% is protein, and 6.00% is fat (Ishunin 1961). A ewe's investment in neonatal development is high and reaches 5.0 g of neonatal mass per kilocalorie of maternal basal metabolism (Geist 1991). Dental formula is i 0/3, c 0/1, p 3/3, m 3/3, total 32 (Sapozhnikov 1976).

Argali are adapted for fast running over long distances. Distal parts of legs are longer than proximal parts. In *O. a. polii*, ratio of length of leg to the summed length of thoracic and lumbar regions of the vertebral column is as follows: femur, 39.7%; tibia, 49.0%; hind foot, 59.2%; humerus, 29.0%; forearm, 45.0%; front foot, 48.0%. Front part of body is lower than sacrum. Ratio of height at withers to height at sacrum is 94–96% in *O. a. karelini* and 100% in *O. a. polii* (Gambarian 1972; Revin et al. 1988; Sapozhnikov 1976). Some argali (5 of 23) have a rudimentary 5th bone of metacarpus (Sapozhnikov 1977). Running argali elevate their heads and throw up their hindquarters similar to domestic sheep. *O. ammon* can run for as long as an hour and can reach speeds of 50 km/h (adult males) and 60 km/h (females and young males—Meklenburtsev 1948). At high speeds, *O. ammon* has a jumping run (Gambarian 1972).

The ratio of slanting length of body to length of front leg below metacarpus is lower for species adapted for speed; this index is 136.0 for *Ovis a. ammon*, 142.0 for *O. a. karelini*, and 158.0 for *O. a. polii*. The ratio of metacarpus girth to length of front leg below the metacarpus is also lower for faster species and is 14.0 for *O. a. ammon*, 15.3 for *O. a. karelini*, and 17.0 for *O. a. polii*. The ratio of slanting length of body to height of withers is lower for faster species and is 81.5 for *O. a. ammon*, 95.5 for *O. a. karelini*, and 96.0 for *O. a. polii*. The ratio of height of front leg to elbow to slanting length of body is higher in faster species and is 73.1 in *O. a. ammon*, 62.2 in *O. a. karelini*, and 63.0 in *O. a. polii*. Thus, *O. a. ammon* is the fastest runner (longest legs and shortest body) and *O. a. polii* is the slowest (Revin et al. 1988).

*Ovis ammon* has the largest horns and atlas among *Ovis*. Length (in mm) of atlas is 90 for males and 71 for females; width (in mm) of atlas is 116 in males and 84 in females. Atlas of *O. ammon* has the largest ventral arch of *Ovis* species (44 mm in length and 70 mm in width). Dorsal and ventral tubercles of atlas are well developed. Vertebrae of male argali are more massive than those of females. In male argali, the foramen magnum lies beneath horn bases, allowing the whole neck to absorb blows involving frontal head and horn bashes (Revin et al. 1988; Schaffer and Reed 1972).

Horns consist of keratinized epidermis. Although horns grow throughout life, the most rapid growth occurs during the first 3 years. Horns grow over bony ossicones on frontal bones. A new sheath grows each year on the horn core inside the preceding sheath; this results in a series of cones stacked one inside the other. Some new annual growth is partially hidden beneath growth from the previous year. Growth of horns stops in winter because of nutritional and hormonal factors, and then resumes each spring; thus, a growth ring or annulus is deposited each year (Valdez 1982). For males, mass of horns, including skull, may reach 13% of live body mass, whereas the entire skeleton accounts for ca. 8% of live body mass (Geist 1971).

Horns of argali suffer damage, and tips are often broken or splintered. This type of damage is called brooming, and older rams with the longest horns display the most extensive brooming. Brooming results from the clash posture of fighting rams. When 2 rams clash they twist their heads and horns in such way that the horn tips come in contact with the opponent's horn base, and tips are damaged. Degree of brooming also depends on tightness of curl of horns and degree of divergence of horns from the head (horn spread). Greater curl diameter and horn spread reduce the probability that horn tips will contact the opponent's horn base and consequently decrease brooming (Shackleton and Hutton 1971). Other damage to horns, such as when they occasionally snap off near the end of cores, may be received in atypical clashes when the horn between the tip and base receives a direct hit from an opponent (Schaller 1977).

During fighting, *O. ammon* (175 kg) has the greatest closing

velocity (up to 26.9 m/s) and the most power of the relative impact force (1.00 Fi) among Caprini species. Relative torque during fighting of *O. ammon* is 0.68 Ts and mass of neck muscles is 0.09 cm<sup>2</sup>/kg in the lateral area and 0.10 cm<sup>2</sup>/kg in the basioccipital area (Schaffer 1968).

Meat is the most valuable product from argali. Carcass mass (without head and lower parts of legs) of an adult male ranges from 55 to 96 kg and that of female ranges from 34 to 36 kg. Yield of pure meat is 56–63.6% of live weight of rams, 49.2–54.8% of ewes, and 63.5% of young. Composition of argali meat is 84.0% protein, 6.26% fat, 4.52% minerals, and 5.22% extra-active nonnitrogenous substances. Hypodermic fat is not developed in argali; other major fat deposits are found inside breast and abdominal cavities. Argali fat is refractory, and its melting temperature is from 48 to 53°C (Sokolov 1959).

Argali have keen eyesight (Valdez 1982). They notice humans and carnivores at a distance of 1 km, and sometimes up to 2–3 km away. Argali avoid timbered mountainsides where visibility is limited (Valdez 1982). Sense of smell in *O. ammon* is acute and they can detect human scent at a distance of 1 km under favorable conditions (Antipin 1947; Geist 1971; Sokolov 1959).

**ONTOGENY AND REPRODUCTION.** Argali reach sexual maturity by 2.5–3 years of age. Males begin to show interest in females when 1.5 years old, display full courting behavior at 2.5 years, and mate when 4–5 years old. Testes of *O. ammon* do not contain sperm at 1.5 years of age. In mature males, each testis weighs 62–85 g (mean, 73 g) in spring and summer; size of testis increases 2–3 times during rut (December). Females usually have their 1st young when 3 years old (Fedosenko and Kapitonov 1983; Sapozhnikov 1976). One captive female gave birth at 2 years (Berber 1999).

Rut extends from October to mid-January, lasting longer in the lower mountainous regions than in the highest zones of Altai, Tien Shan, Pamir, and Tibet. Rut is earliest in Mongolia (September–October), and later (October–November) in Nan Shan (China), Tien Shan, central Kazakhstan, and in the Nuratau Range, Uzbekistan (Bannikov 1954; Berber 1999; Fedosenko 2000; Shakula 1989). Rut occurs later (November–December) in Altai (Fedosenko 1989) and Pamir (Fedosenko 2000; Meklenburtsev 1948; Sapozhnikov 1976), and still later (mid-December–January) in Tibet (Schaller 1977, 1998). Mating occurs 2–3 weeks after the rut begins.

Gestation lasts ca. 160–165 days. Lambing begins earliest (late March and April) in the warmer lower mountain ranges and their spurs and latest in the highest habitat of Pamir and Tibet (late May–June—Berber 1999; Fedosenko 2000; Lvov 1981; Sapozhnikov 1976; Savinov 1975; Schaller 1998; Shakula 1989).

Each year, some ewes may be barren: *O. a. nigrimontana*, 9.1% ( $n = 33$ ); *O. a. ammon*, 12.5% ( $n = 115$ ); *O. a. collium*, < 23.5% ( $n = 68$ ); *O. a. karelini*, 26.9% ( $n = 31$ )—Fedosenko 1989; Fedosenko and Zhiriakov 1987; Savinov 1975). Proportion of barren females increases after hard years; 34.1% of ewes of *O. a. karelini* were barren in the southwestern spurs of Djungarskiy Alatau after a difficult year. Number of young per 100 ewes in Altai (*O. a. ammon*; June–July) was 67 in 1984, 59 in 1985, 67.5 in 1989, and 50.2 in 1999; in the southern Gobi (*O. a. darwini*; August 1994) was 24.7 young in the west and 53.7 in the east (mean, 36.9 young); and in central Kazakhstan (*O. a. collium*) was 86.8 (September 1989) and 58.9 (June 1990—Berber 1999; Fedosenko 1989, 2000; Kapitonov and Mahmutov 1977; Reading et al. 1997). In central Kazakhstan, more young are born in north than in south, which has bare granite massifs with poor pastures: 66.9 versus 46.4 (1990), 41.8 versus 22.0 (1996), 62.1 versus 44.7 (1997) per 100 females. In Pamir (*O. a. polii*), 32.1 (November 1995) and 45.4 young (September 1997) per 100 females occurred, with 67.3 young per 100 ewes in 1997 in the most northern habitat (Fedosenko 2000; Fedosenko et al. 1995b). In Tibet (*O. a. hodgsoni*), 41–55 young per 100 females were reported (Harris 1993; Schaller 1998). Females of *O. a. ammon*, *O. a. polii*, and *O. a. hodgsoni* always bear 1 young (Fedosenko 1989; Fedosenko et al. 1995a; Harris 1993; Schaller 1998). Twins occurred in *O. a. hodgsoni* in Ladakh (Ward 1924), and a captive *O. a. polii* gave birth to a litter of 5 young, followed 2 years later by triplets (Lambden 1966). Populations of *O. a. karelini* in Tien Shan had 65% singles, 33% twins (from 66 females), and 1 ewe had 3 young (Antipin 1947); in Djungarskiy Alatau, 10% of ewes had twins. *O. a. nigrimontana* in Karatau Range (western Tien Shan) had 13.3%

twins ( $n = 30$  females). Captive *O. a. collium* had 76.5% twins ( $n = 17$  females), and wild females had 16.7–33.3% twins ( $n = 41$  females) for typical years and 1.9% ( $n = 52$  females) for difficult years. Twins also were noted for *O. a. severtzovi*. Twins are absent in the highest habitats (Altai, Pamir, and Tibet), which are characterized by short summers and cold snowy winters (Fedosenko 2000; Ishunin 1967; Meklenburtsev 1948; Savinov 1975).

Rate of growth increases significantly during the last months of gestation; in an *O. a. polii*, body mass of a male fetus was 1,130–1,350 g in mid-April and 4.5 kg before birth at the end of May (Fedosenko 2000). Body masses (in kg) of individual females of *O. a. severtzovi* at different ages are: 2.65 and 3.7 (newborns), 5.25 (1 month), 10.0 (2 months), and 25.1 (6 months—Shakula 1989). Young of *O. a. darwini* weighed 3–4 kg at 10–15 days of age and 13–14 kg at 1–1.5 months of age (Lvov 1981). Newborn *O. a. collium* at the Karaganda Zoo weighed 3–4.5 kg. At 50 days of age, a ram from northern central Kazakhstan weighed 16.5 kg, and a ewe at 80 days from the southern part of this region weighed 25.3 kg (Berber 1999; Fedosenko and Kapitonov 1983). Additional body mass data on young of different ages and subspecies are available (Rumiantsev et al. 1935; Savinov 1975). During the 1st year of life, males and females gain body mass at the same rate and achieve a mass 9–10 times their birth mass. During their 2nd year, females increase their body mass by only 1.3 times, and increases in subsequent years are insignificant. In contrast, males increase body mass during their 3rd and 4th years. At 4 years of age, a male may reach 92–94 kg, whereas a female is 55–60 kg. Rate of growth for males slows after 4 years (Sapozhnikov 1976). Young from high-elevation populations and subspecies grow more rapidly than those from lower elevations, and subspecies with larger adults (Altai and Pamir argali) have larger yearlings (Sapozhnikov 1976; Savinov 1975; Sopin 1975). External measurements (in cm) for males at birth, 2 months, 1 year, and 4 years of age, respectively, are: length of body, 62, 92, 127, 168; height of shoulder, 57.5, 64.4, 80.5, 106; height of sacrum, 56.5, 71, 93, 106; girth of chest, 46.6, 70, 91, 116 (*O. a. polii*—Sapozhnikov 1976). The largest male *O. a. polii* found in Pamir had a body length of 168 cm and a shoulder height of 106 cm. External measurements (in cm) of 2 females at 1 year, 2 years, and 4 years, respectively, are: length of body, 133, 148.4, 138.5; height of shoulder, 90, 95.3, 79; height of sacrum, 97.5, 99.5, 82.5; girth of chest, 94, 107.3, 98; length of ear, 10, 10.4, 10.7; length of tail, 7, 10.5, 7.8. The largest female *O. a. polii* in Pamir had a body length of 148.5 cm, a shoulder height of 95.3 cm, and a sacrum height of 99.5 cm. Proportions of body frame are formed during the 1st year of life, giving yearlings frame indices close to those of adults. Proportion (in %) of different body parts of a male yearling, an adult male, and an adult female, respectively, are: ratio of slanting length of body to length of foreleg, 142, 154.6, 156; girth of metacarpus to length of foreleg, 17.3, 17.6, 16.4; slanting length of body to height of shoulder, 97, 99.2, 100.5; length of head to length of body, 25.1, 26.3, 23.8; body mass to height of shoulder, 6.8, 8.8, 6.64; height of shoulder to height of sacrum, 86.5, 100.4, 92.3 (*O. a. polii*—Sapozhnikov 1976).

Horn growth begins 15–20 days after birth, with small knobs on frontal bones. Horn measurements (mean, range, where available, in mm and angle in degrees; sample size provided unless  $n = 1$ ) of male *O. a. polii* at 2 months, 7–8 months, and 1, 2, 3, 4, 5, 6, 7, 8, 9, and 10 years of age, respectively, are: length of horn, 45; 220; 362, 230–500 ( $n = 7$ ); 550, 450–700 ( $n = 5$ ); 773, 570–990 ( $n = 13$ ); 893.3, 700–1,075 ( $n = 11$ ); 1,013.6, 720–1,180 ( $n = 24$ ); 1,130.8, 890–1,300 ( $n = 21$ ); 1,234, 1,060–1,420 ( $n = 13$ ); 1,238.8, 1,140–1,460 ( $n = 6$ ); 1,280, 1,240–1,320 ( $n = 2$ ); 1,412.2, 1,200–1,640 ( $n = 9$ ); girth of base, 75; 130; 199, 140–225 ( $n = 5$ ); 262, 230–305 ( $n = 5$ ); 298.7, 280–325 ( $n = 13$ ); 331.7, 280–370 ( $n = 11$ ); 347, 225–380 ( $n = 24$ ); 363.3, 335–400 ( $n = 21$ ); 373, 320–395 ( $n = 14$ ); 380.3, 360–390 ( $n = 6$ ); 350 ( $n = 1$ ); 380.5, 360–410 ( $n = 9$ ); tip-to-tip spread, 100; 285; 505, 300–605 ( $n = 5$ ); 586, 465–650 ( $n = 5$ ); 836.4, 620–1,030 ( $n = 7$ ); 828.5, 695–930 ( $n = 5$ ); 965.9, 810–1,080 ( $n = 11$ ); 955, 700–1,210 ( $n = 9$ ); 1,048, 820–1,230 ( $n = 5$ ); 1,087.5, 1,000–1,140 ( $n = 4$ ); 1,118, 980–1,240 ( $n = 5$ ); 163.3, 1,050–1,300 ( $n = 9$ ); angle between horns, 65; 60; 58, 50–70 ( $n = 5$ ); 60.6, 55–67 ( $n = 5$ ); 67.8, 60–75 ( $n = 7$ ); 69.2, 60–75 ( $n = 4$ ); 71.8, 60–83 ( $n = 8$ ); 76.8, 60–90 ( $n = 8$ ); 66.7, 60–75 ( $n = 4$ ); 70 ( $n = 1$ ); 76.5, 65–88 ( $n = 2$ ). In males, average annual increment in horn growth is greatest during the 1st year. Coefficient of length of horn increases between 1st and 2nd years (K1) is 1.3, between 2nd

and 3rd years (K2) is 1.5, K3 = 1.0, K4 = 1.2, K5 = 1.0, K6 = 1.1, K7 = 1.0. Length (mean, range, in mm) of 1st, 2nd, 3rd, 4th, 5th, 6th, 7th, 8th, 9th, and 10th segments, respectively, are: 180 (150–240, *n* unknown), 225 (125–330, *n* = 41), 239 (100–300, *n* = 43), 203 (130–290, *n* = 43), 147 (100–240, *n* = 39), 110 (60–170, *n* = 34), 89 (40–130, *n* = 24), 65 (45–100, *n* = 12), 53 (30–70, *n* = 3), and 80 (*n* = 1). Maximum length of horn for *O. a. polii* was 1,640 mm for a 12- to 13-year-old male. Rate of increase in thickness of the horn is greatest during the 1st and 2nd years of life. In *O. a. polii*, girth of horn can reach 410 mm. Tops of horns are directed upward, backward, and somewhat outward in a 2-month-old male and are directed backward, outward, and somewhat downward in an 8-month-old male. Horns of males become homonymous by 19–20 months of age. Greatest increase in tip-to-tip spread occurs between the 2nd and 3rd years (K = 1.4); in *O. a. polii*, tip-to-tip spread can reach 1,300 mm in a 12- to 13-year-old male. Angle between horns is least in young males, and varies among adult males (from 60° to 90°). Mass (mean or range, in g, *n* = 2) of both horn covers of male *O. a. polii* at 1, 2, 3, 4, 5, 6, 7, 8, and 9 years of age, respectively, are: 519; 484–800; 1,600–2,600; 1,600–2,100; 2,600–6,000; 5,600–6,000; 7,000–7,200; 9,100; 9,000–12,000. Mass of both horn covers varies (Fedosenko 2000; Fedosenko et al. 1995a; Sapozhnikov 1976). Horn indices in male *O. a. karelini* are smaller than those of male *O. a. polii*: length of horn by 18.4%, girth of horn base by 5.3%, and tip-to-tip spread by 29.6% (Zhiriakov and Fedosenko 1983).

Horn measurements (mean, range, where available, in mm and angle in degrees) of female *O. a. polii* at 1, 2, 4, 5, 6, and 8 years of age, respectively, are: length of horn, 232.5 (215–250, *n* = 2), 298.7 (270–325, *n* = 4), 313 (290–360, *n* = 7), 390 (*n* = 1), 350 (*n* = 1), 355 (330–390, *n* = 3); girth of base, 112.5 (110–115, *n* = 2), 130 (125–135, *n* = 4), 139 (135–155, *n* = 6), 150 (*n* = 1), 145 (*n* = 1), 147.5 (135–160, *n* = 2); tip-to-tip spread, 275 (255–295, *n* = 2), 330 (270–360, *n* = 4), 330 (300–480, *n* = 5), 330 (*n* = 1), 250 (*n* = 1), 387.5 (340–435, *n* = 2); angle between horns, 47.5 (45–50, *n* = 2), 46.2 (45–50, *n* = 4), 52.6 (45–63, *n* = 5), 40 (35–45, *n* = 2), 37 (*n* = 1), 47.5 (45–50, *n* = 2). Horns of female *O. a. karelini* are smaller than that of female *O. a. polii*: by 16.6% for length of horn, by 11.8% for girth of base, and by 14.7% for tip-to-tip spread. In females, increase in length of horn is most intense up to 2 years of age. Girth of horn base changes insignificantly, and tip-to-tip spread increases very slowly in adult ewes. In females, tips of horns are always directed outward, and angle between horns is always less than that in males and shows almost no change with age (Sapozhnikov 1976; Zhiriakov and Fedosenko 1983).

Skull proportions stabilize by 8–12 months, although rapid growth in size continues until 3 years with little growth after 5 years of age. External measurements (in mm) and mass (in g; *n* = 1, 1, 1, 5, 4, 5, 3, 4, and 3, respectively) of skull (with horn cover) in male *O. a. polii* at various ages are: greatest length, 146 (2–3 weeks), 187 (2 months), 238 (7–8 months), 241–283.5 (1 year), 280.5–305.5 (2 years), 306–327 (3 years), 336 (4 years), 337 (6 years), up to 340 (7 years); basilar length, 231 (7–8 months), 236–281 (1 year), 276–300.5 (2 years), 294–321.5 (3 years), up to 325.5 (4 years); orbital breadth, 61 (2–3 weeks), 76.5 (2 months), 93 (7–8 months), 93–112 (1 year), 105–118 (2 years), 111–127 (3 years), up to 122 (4 years); length of horn core, 235 (1 year), 280–415 (3 years), 315–320 (4 years), 420–430 (5 years), 390–430 (6 years), 420–450 (7 years); skull mass, 59 (2–3 weeks), 122 (2 months), 400 (7–8 months), 807 (1 year), 2,300 (2 years), 7,400 (5 years), 10,700 (6 years), 9,200 (7 years), up to 11,000 (8 years); mass of lower jaw, 17 (2–3 weeks), 40 (2 months), 122 (7–8 months), 177 (1 year), 239 (2 years), 292 (6 years). The same measures (*n* = 3, 2, 4, 4, and 5, respectively) in female *O. a. polii* at 6–8 months, 1, 2, 4, and 5–8 years, respectively, are: greatest length, 212–233.5, 254–260, 262.5–282.5, 293–307, 303.5; basilar length, 206–227, 246–251.5, 255–273.5, 285.5–298, 292; orbital breadth, 84–93, 94.5–96, 95–105, 111–118, 117; mass of skull, 268, 500, 566, 762, 700–850; mass of lower jaw, 116, 141–170, 211, 236, 173–249 (Sapozhnikov 1976).

By 20 days of age, young have all milk incisor teeth (crowns incompletely formed), premolars have erupted through gums, and 1st crowns of molars are distinct in jawbone. Canine teeth do not appear until 6 months. Yearlings have worn milk incisors and premolars with smooth masticatory surface; M1 shows wear and M2 erupts. At 2 years, milk incisors (I<sub>d1</sub> and I<sub>d2</sub>) have been replaced

by permanent teeth, and replacement of premolars has begun. Tooth development and replacement is complete by 5 years, after which wear occurs. Argali 10–13 years age have incisors and canines that are worn down to dental neck. Masticatory surfaces of premolars and 1st molar are worn completely smooth and their crown height is one-half of normal; only M2 and M3 keep their lunulae (Sapozhnikov 1976).

Ewes stop nursing lambs in August for *O. a. karelini* from the desert spurs of Djungarskiy Alatau (Antipin 1941), in October for *O. a. severtzovi* from the Nuratau Range (Shakula 1989), in December and sometimes May of the following year for *O. a. ammon* from Altai (Anchiforov and Faleev 1993; Fedosenko et al. 1995a), and in February for *O. a. polii* (Meklenburtsev 1948). Lambs of *O. a. ammon* 1st attempt to eat vegetation 12–16 days after birth and exhibit constant grazing by 18–19 days of age (Anchiforov and Faleev 1993). Lambs of *O. a. severtzovi* 1st attempt to eat vegetation 2–3 days after birth and display constant grazing by 1.5–2 months of age (Shakula 1989). Argali can reach 13 years of age in the wild (Roberts 1977). Most skulls found in the wild belong to argali of 4–5 years and more rarely to argali 6–10 years of age (Meklenburtsev 1948; Tsalkin 1951).

**ECOLOGY.** Argali live in mountains from 300 to 5,750 m above sea level. They prefer gently sloping open areas with soft broken terrain. Females stay in precipitous areas only during the short period of lambing and for 2–3 weeks thereafter. Argali are very rarely found on the vast flatlands, and only during migrations. They avoid forested slopes, except in central Kazakhstan, where poaching and livestock force argali into unusual areas such as high forests of *Betula* and *Populus* in the Ermentau Range (year-round), and among *Juniperus* and *Pinus* in Baianoulskiy, Kent, and Bachtay ranges (summer only). In Tien Shan, Altai, and Pamir, livestock force argali to live in precipitous regions with rock cliffs, scree, and narrow canyons with trees and bushes at the base (Fedosenko 2000; Fedosenko and Kapitonov 1983; Ishunin 1960; Schaller 1977). Argali prefer high mountains with both steep slopes and low gentle slopes; high mountains are used in summer and low ranges in winter (Fedosenko and Kapitonov 1983). Argali prefer well-drained soil with little or no snow, or areas with winds that blow snow off the slopes and plateau (Heptner et al. 1961). Argali segregate by sexes. Males climb to upper, more severe mountainous zones earlier in spring than females, and leave those zones later in autumn (Fedosenko 1989; Geist and Petocz 1977; Schaller 1977).

In Pamir, male argali eat 18–18.5 kg of vegetation per day and females eat 16 kg. Amount of water in the stomach is less in spring (11.6–27.8%) than in summer (36.3–62.5%, *n* = 7—Sapozhnikov 1976). Diet of argali varies with habitat and falls into 4 categories. The 1st category from high-elevation zones of mountains (Pamir, Altai, Tibet, and Tien Shan) is predominantly cereals, sedges, and forbs (mainly Papilionaceae and Asteraceae). In Pamir, cereals and sedges account for 59–99% of stomach contents (*n* = 8), and 88% in Tibet in June, <70% in July–August, and 24% in September. Leaves and sprouts from bushes are insignificant components of the diet and no vegetative parts of trees are present (Fedosenko 2000; Fedosenko and Scuratov 1990; Harris and Miller 1995; Sapozhnikov 1976; Schaller 1998). The 2nd category of diet from mid-level ranges includes greater amounts of bushes and mesophytic grasses and fewer cereals and sedges. In the 3rd diet type, from low ranges and spurs of deserts; cereals and sedges are predominant components, and desert plants replace mountain plant species. The 4th type for northern central Kazakhstan, has sprouts, leaves, flowers, and fruits from bushes and trees as significant dietary components all year-round and mesophytic species are more significant than cereals and sedges (Fedosenko 2000).

Argali in high ranges have numerous watering places and regularly drink from springs and rivers. In contrast, argali inhabiting low dry mountains have sparse springs and drink less frequently. In habitats with few watering places, small basins (up to 5–10 m in diameter and 1.5 m deep) found in some granite mountains as a result of weathering are very important sources of water for argali. These basins (stone pans) fill with water during the rainy season and hold water into the dry periods that follow. If stone pans are rare or dry out, argali walk long distances for water. Argali of the southwestern spurs of Djungarskiy Alatau (southeastern Kazakhstan) go to the Ili River to drink, crossing a desert flat of 3–15 km. Such movements cease temporarily only after a rare rain, when wild argali again have water in the stone pans. In the desert spurs of

Gissaro-Alai Range (Uzbekistan), springs are especially rare and occupied by livestock; here, *O. a. severtzovi* drinks only from rock pans, which contain water until the beginning of summer. Once the pans dry out, these argali manage without water until autumn rains. In winter, argali eat snow for water (Fedosenko and Kapitonov 1983; Ishunin 1960; Zhiriakov 1977).

Eating saline soil is typical for *O. ammon*. They constantly visit wet and dry sites of saline soil during all warm seasons. On cloudy and rainy days, argali visit sites of saline soil rather than watering places and show the opposite pattern on sunny days (Fedosenko 2000). In Altai, 3 types of saline sites are small pits on gentle slopes, which were gnawed out by argali (0.5–2 m in diameter and 30–50 cm in depth), caves and niches in precipices, and wet sites of saline soil. In northern Tien Shan and Djungarskiy Alatau, sites of saline soil are rare (Fedosenko and Kapitonov 1983). In central Kazakhstan, argali eat salt soil year-round, and their pellets consist almost entirely of clay (Kapitonov and Mahmutov 1977; Savinov 1975). In Pamir, sites of saline soil are unknown, but *O. ammon* eat the thin coating of salt that covers the soil (Sapozhnikov 1976). Sites of saline soil are also unknown for low desert mountains (Fedosenko and Kapitonov 1983; Ishunin 1961).

Proportions of adult females, adult males, and young (males and females), respectively, are: *O. a. ammon*, 40–53%, 14–40%, 19–33% ( $n = 2,025$ ); *O. a. collium*, 42%, 37.7%, 22.1% ( $n = 446$ ); *O. a. darwini*, 53.3%, 14.3%, 19.7% ( $n = 673$ ); *O. a. karelini*, 45.9%, 37.9%, 16.2% ( $n = 1,059$ ); *O. a. nigrimontana*, 35.3%, 32.4%, 32.4% ( $n = 139$ ); *O. a. polii*, 48.7%, 27.8%, 23.5% ( $n = 5,953$ ); *O. a. hodgsoni*, 50.5%, 29.5%, 20.5% ( $n = 202$ ). During the year, structure of herds changes, with most adult males leaving groups of females early in the spring and migrating either higher in elevation or from south to north slopes (Fedosenko 1989; Reading et al. 1997; Sapozhnikov 1976; Schaller 1998).

Competition with other wild species is not significant for *O. ammon* in most parts of its natural habitat. Argali are sympatric with Siberian ibex (*Capra sibirica*), but usually have different habits and prefer different pastures on the same ridges (Fedosenko and Kapitonov 1983). Only in Tibet do wild ungulates considerably influence argali populations. Here, argali diet overlaps significantly with males of chiru (*Pantholops hodgsoni*, 0.956), wild yak (*Bos mutus*, sex not specified, 0.920), bharal (*Pseudois nayaur*, sex not specified, 0.846), and white-lipped deer (*Cervus albirostris*, sex not specified, 0.814). Competition with Tibetan gazelle (*Procapra picticaudata*, 0.473–0.502) and kiang (*Equus hemionus kiang*, 0.305) is not significant (Harris and Miller 1995). Domestic ungulates are serious competitors with argali. In Altai, argali are forced either to migrate to higher elevations or graze inside yak herds (Fedosenko 2000). In the Enigoi Valley of Tibet, 7,100 individuals of various ungulate species and >3,000 domestic goats and argali stay year-round in an area of 100,000 ha. In this area, argali comprise only 3.4% of wild ungulates. Competition with livestock also occurs in nature reserves of Mongolia and China (Schaller 1998). During summer, argali compete less with livestock than during winter because domestic ungulates are dispersed throughout vast areas in summer. Competition increases in winter, when pasture areas decrease in size and quantity and quality of fodder decreases. Argali also become infected with diseases and parasites from livestock (Harris and Miller 1995; Schaller 1977, 1998).

Wolves (*Canis lupus*) are the main predators of *O. ammon*. In Altai, predation by wolves is the 3rd leading cause of death (17.7%), behind poaching (45.9%) and starvation (36.3%). In Djungarskiy Alatau Range, predation by wolves (36.4%) follows poaching (63.6%) as leading causes of death, and 40–73% of argali losses in central Kazakhstan were due to wolves. In Aksai River basin (Kirgizia), 145 skulls and other bones of *O. a. polii* were found, 37.5% of these individuals had been killed by wolves; those killed included 78% rams >5 years of age and 42.5% >7 years (Fedosenko 2000; Fedosenko et al. 1995a). Wolves hunt *O. ammon* more often in winter, when rodents (*Marmota*) disappear under snow cover or hibernate. Hunting by wolves is especially successful during winters with deep snow cover or other unusually hard climatic conditions for argali (Berber 1999; Fedosenko and Sludskiy 1981; Schaller 1977; Sopin 1976; Vyrypaev 1983). In Mongolia, wolves prefer hunting argali near the rarely found watering places (Fedosenko 2000). In Tibet, argali are rare prey for wolves, with only 3.4% of wolf excrement containing argali hairs (Schaller 1998).

Snow leopards (*Uncia uncia*) sometimes hunt *O. ammon*;

hunting by leopards has been reported in Altai, Tien Shan, and Pamir (Fedosenko 2000; Heptner et al. 1961). Isolated cases of wolverines (*Gulo gulo*) chasing and killing *O. ammon* have been recorded (Fedosenko 1986; Sopin 1976). Lynx (*Lynx lynx*) hunt argali in Tien Shan and in central Kazakhstan; foxes (*Vulpes vulpes*) chase argali young, as do dogs of shepherds (Baidavletov 1995; Fedosenko and Kapitonov 1983). Rarely, argali remains have been found in the excrement of bears (*Ursus arctos*; 0.6%—Schaller 1998). Large birds of prey (cinereous vulture [*Aegypius monachus*], golden eagle [*Aquila chrysaetos*], and lammergeier [*Gypaetus barbatus*]) have been seen flying in low circles over herds of ewes with young, and even diving on them. Although no successful catches have been observed, remains of 2 argali young were found under the nest of a golden eagle (Fedosenko 1989; Kapitonov and Mahmutov 1977).

Argali are prone to pasteurellosis infection, with such an epizootic occurring in 1886–1887 in Pamir. Also in Pamir, an epidemic of rinderpest was recorded, as well as malignant anthrax, resulting in deaths of argali over several years (1895–1898); infections were introduced by flocks of domestic sheep (Meklenburtsev 1948). In Altai, pasteurellosis and tuberculosis were noted in the lungs of argali; test samples demonstrated 100% invasiveness in 1889. *Sarcocystis gusevi* n. sp. (Coccidiida, Sarcosporidia) was reported in cardiac muscle of *O. a. polii* (Sapozhnikov 1976). In Altai, argali have 86–108 enteric helminthes per gram of excrement (Anchiforov and Faleev 1993). Foci of microceliosis (*Dycoelium*, Trematoda) and echinococcosis (*Echinococcus*, Cestoda) have been noted for *O. a. collium*; argali are primary hosts for the trematodes and intermediate hosts for the cestodes. Invasiveness by microceliosis was 76% of individuals with an intensity of 110–2,100 parasites per host. Invasiveness by echinococcosis was 23.3% of individuals with an intensity of 1–18 bubbles per lung. One argali with echinococcosis was reported from 4 tested in 1995, 2 from 9 individuals in 1996, and 3 from 6 in 1997, with a maximum intensity of 18 bubbles per argali. For *O. a. collium*, invasiveness by some endoparasites can reach 100% (Beliakova and Baidavletov 1994).

Of 21 *O. a. karelini* from Chu-Iliskiy Range, 3 from Djambulgora and Baigora (region of Balhash Lake, southeastern Kazakhstan), and 2 from Talasskiy Alatau (western Tien Shan) had 34 nematodes, of which 21 are found in cattle and 8 in humans (Boev et al. 1962). Argali can be infected experimentally with *Multiceps multiceps* in the larval form (Bondareva et al. 1960). In Pamir, 500 argali were checked for parasites and all had *Marshallagia dentispicularis*, 400 had *Ostartagiella circumcincta* and *Nematodirus oiratianus*, and much smaller numbers had *Avitellina contripunctata*, *Moniesia benedeni*, *Moniesia*, *Trichostrongylus axei*, and *T. columbiformes* (Pustovoi and Lvov 1972). Several *Trichocephalus skrjabini* were found in *O. a. severtzovi* (Mambetzhumayev 1974). Most helminthes are parasites of the alimentary canal, fewer live in the lungs, and still fewer inhabit the liver, muscles, and brain (Fedosenko 2000).

Ticks (*Acarus siro*) were reported on *O. a. karelini* from Tien Shan in 1968–1972 (Kusov et al. 1976). The following species of ticks are most commonly noted on argali: *Dermacentor marginatus*, *D. pavlovskyi*, *Hyalomma plumbeum*, *Ixodes persulcatus*, *I. crenulatus*, *Rhipicephalus rossicus*, *R. pumilio*, and *Haemophysalis warburtoni*. Ticks have been recorded on neck, inside ears, armpit, groin, and around anus and genitals (Galuzo 1948; Ushakova et al. 1976). Fleas (*Vermitisylla alacurt*) were found on *O. a. karelini* from Djungarskiy Alatau (Kusov 1957), and *V. dorcadia* parasitized *O. a. polii* and *O. a. karelini* (Kusov 1957; Sapozhnikov 1976). Gadflies (*Tabanus*), flies from genus *Liporisia*, and louse flies (*Melophagus montanus* and *M. ovinus*, Hippoboscidae) are usually found on argali from Tien Shan and Pamir (Doszhanov 1980). The most common warble flies (Hypodermatidae) on argali are from the genus *Cruvella*; some argali have so many larvae that the skin on their back is similar in texture to a sieve. In Pamir, larvae of warble flies (*Cruvella silens*) were found on 10 of 30 argali (7.6 larvae per argali), and 3 of the individuals checked also had *Oestrus ovis* (1.3 larvae per argali—Sapozhnikov 1976). *Oestrus ovis* also was noted on argali from Tien Shan (3 from 15) and *Rhinoestrus tshernyshevi* was noted in Kazakhstan (Grebenuk 1966; Grebenuk and Sartbaev 1955; Grunin and Sludskiy 1960).

Magpies (*Pica pica*) often examine argali and peck off ticks. Over an hour, 2 magpies removed ticks from 7 adult rams. One ram stood quietly while he was checked for 20 min; the other males

waited until receiving similar treatment from the birds and then returned to their grazing. Choughs (*Pyrrhocorax pyrrhocorax* and *P. graculus*) often sit on argali, especially during spring when they gather fur for their nests (Fedosenko and Kapitonov 1983; Sapozhnikov 1976).

Highest mortality for argali occurs during the 1st months of life. For *O. a. ammon* from Altai, 11.9–37% of young died during their first 3–4 months and only 25% of young survived until 2 years of age (Fedosenko 1989). For *O. a. collium* in central Kazakhstan, 1st-year losses accounted for 42.5% in the northern region and reached 70% in the central region (Berber 1999). For *O. a. karelini* from Tien Shan, up to 35.7% of young died during their 1st year and 38.5% died in the Djungarskiy Alatau spurs. In Pamir and Tien Shan, mortality of young is higher in *O. a. polii* than in *O. a. karelini*, 67.2 and 56.7%, respectively (Fedosenko 2000; Fedosenko et al. 1995a). Among adult argali the highest death rate is for individuals 4–5 years of age (33%,  $n = 51$ ). Death rates are slightly lower for individuals 6–8 years of age (21%) and >8 years (21%). Adult argali with broken legs live for a short time, but soon grow thin and die or become prey to carnivores (Antipin 1947; Fedosenko and Kapitonov 1983; Fedosenko and Zhiriakov 1977).

Argali are sensitive to deep snow cover, especially in combination with low temperatures. Populations of argali disappeared entirely in the Transbaikalian ranges (eastern Siberia, Russia) and in Chentee Range (Mongolia) during deep snow in the winter of 1831–1832. High mortality of *O. ammon* was recorded in Kazakhstan during severe winters in 1875–1877, 1912, 1950–1951, 1963–1969, and 1973–1974 (Fedosenko and Kapitonov 1983), and in the Mongolian Altai in 1983–1984 and 1992–1993, when snow cover was >60 cm deep and temperature dropped to  $-50^{\circ}\text{C}$  (Fedosenko 2000). In western Tien Shan, bodies of 5 argali were found along a 10-km route after the snowy winter of 1975–1976 (Grachev 1981). After the severe winter of 1961–1962 in Djungarskiy Alatau Range, 15 dead argali were found in a 100-km<sup>2</sup> area (Savinov 1975), and in Tibet, number of argali decreased by one-half after the hard winter of 1996 (Harris et al. 1999). Weakened argali sometimes join herds of domestic sheep and approach human habitation (Heptner et al. 1961). Droughts cause mortality, especially of young, and number of births decreases during and after a drought. In spring of 1942, 18 argali were killed by an avalanche in western Tien Shan (Heptner et al. 1961).

Conservation of argali habitat is unsatisfactory, and livestock and poachers pose problems for argali populations. Up to 70% of reported causes of argali deaths involve poaching. In Russia, a single nature reserve is in Altai, where part of the argali population is protected, although poaching and livestock occur. The current total population in the Russian Altai is estimated at 450–700 individuals (Fedosenko 2000). Mongolia has several protected areas, but grazing of livestock and poaching in these areas are common. Some argali populations remain in good condition in Mongolia (Amgalanbaatar and Mix 1999). The total population of *O. a. ammon* was reported at up to 50,000 individuals in 1970s and is estimated at 20,000 now. The population of *O. a. darwini* is estimated at 8,500–9,000 individuals (Fedosenko 2000). Kazakhstan has a single reserve (Aksu-Djabagly) in western Tien Shan where the population of *O. a. collium* is estimated at 8,000–10,000 individuals, *O. a. karelini* at <1,200–1,500, and *O. a. nigrimontana* at <250. In Kirgizia, 2 nature reserves in Tien Shan recently were created primarily for argali, but presently Pamir has no nature reserves for argali. Number of *O. a. polii* is estimated at 10,000–12,000 individuals in Pamir and 5,000 in Tien Shan. In Uzbekistan, *O. a. severtzovi* is protected in the Nuratinskiy Reserve, and the population is >2,000 individuals. In Afghanistan, protection of argali is nonexistent and no population estimates are available. India has 2 national parks, Hemis National Park (410,000 ha) in the state of Jammu and Kashmir, and Khangchendzonga, that contain habitat for *O. a. hodgsoni*. Total number of argali in Ladakh is ca. 200. In Pakistan, only Khunjerab National Park has a seasonal population of *O. a. polii*, estimated at <150 individuals. China has many nature reserves, where most subspecies of argali are protected. Population estimates in China are: *O. a. ammon*, several hundred; *O. a. darwini*, 2,100–2,800; *O. a. hodgsoni*, 29,000–36,000; *O. a. jubata*, 600–700; *O. a. karelini*, 8,000–11,000; *O. a. polii*, 1,000–3,000. Total number of argali in the world is roughly 96,500–114,600 individuals, including 20,800–21,200 *O. a. ammon*; 8,000–10,000 *O. a. collium*; 10,600–11,800 *O. a. darwini*; 29,200–36,200 *O. a. hodgsoni*; 600–700 *O. a. jubata* (or extinct,

Workshop on Caprinae taxonomy, Ankara, Turkey, 8–10 May 2000); 9,200–12,500 *O. a. karelini*; < 250 *O. a. nigrimontana*; 16,100–20,100 *O. a. polii*; >2,000 *O. a. severtzovi* (Shackleton 1997).

Argali have been hunted for meat and horns. The largest horns are sold by hunting firms or local people (Fedosenko 2000; Meklenburtsev 1948). Rarely, skins are used by local people, and only during 1930–1940s in the former United Soviet Socialist Republics did warehouses accept skins to make leather clothing. Several methods were used to hunt argali, including stealing up on an individual and killing it at close range (Valdez 1982); ambushing argali near paths, watering places, or sites of saline soil; creating traps along paths into which argali fell; and using dogs to drive them (Heptner et al. 1961; Meklenburtsev 1948). In northeastern Kazakhstan, 300 argali were shot every year at the end of the 19th century; in Zailiyskiy Alatau (Tian Shan), 50 wild argali were taken in 1886; and in northern Kirgizia, 649 individuals were killed in 1889 (Tian Shan—Smirnov 1965). The largest number of argali taken by hunters occurred in Pamir, with 3,000–4,000 individuals shot each year during the 1830s, and ca. 1,000 per year until 1885. Hunting by foreign tourists for argali trophies began in Mongolia in 1967, in Tadjikistan in 1987, and in Kirgizia and Kazakhstan in 1990. Unsuccessful attempts at trophy hunting have been reported in Afghanistan from the mid-1970s to 1979, and in Pakistan and China (Inner Mongolia) from the 1980s. In Mongolia, 1,630 argali males, most of which were *O. a. ammon*, were killed by foreign hunters during 1967–1989. The hunting allotment has been decreased in the last decade (Amgalanbaatar and Mix 1999). In Tadjikistan and Kirgizia, the yearly quota of argali of 20 and 10, respectively, represented insignificant losses to the populations. In 1998, these quotas were increased to 70 and 25, respectively (Shackleton 1997). In central Kazakhstan, argali numbers have decreased after 1995 (Fedosenko 2000).

Most subspecies of argali breed readily in captivity, with the exception of *O. a. ammon*, which has not been successfully kept in zoos. Some argali in Altai died in semicaptive conditions (Anchiforov and Faleev 1993).

**BEHAVIOR.** *Ovis ammon* is gregarious, living in groups of 2 to >150 individuals. Size and composition of argali herds change with season. Outside the rut, mature rams live in bands that average 4.4 (range, 2–9,  $n = 11$ , western Tian Shan) or 8.1 (1–27,  $n = 86$ , Altai) individuals, with some herds containing 52 rams (Tibet). Some rams are solitary. Females live in larger herds with young, subadults, and immature males; these herds average 7.2 (range, 2–16,  $n = 13$ , western Tien Shan) or 22.8 (2–92,  $n = 201$ , Altai) individuals, with up to 200 individuals reported in Mongolian Altai (Dzieciolowski et al. 1980; Fedosenko 2000; Schaller 1977). For *O. a. nigrimontana*, groups during the rut usually consist of 1 male and 1 ewe because of small population size (Fedosenko 2000). Subspecies and populations from habitats with hard broken terrain and hilly areas have smaller herds (average number of individuals, range; *O. a. collium*, 2.4, 1–12,  $n = 178$ ; *O. a. darwini*, 5.6, 1–26,  $n = 51$ ; *O. a. karelini*, 3.3, 1–15,  $n = 75$ ) than herds from open plateau (Pamir and Tibet) and gently sloping mountains (Altai; *O. a. ammon*, 18.5, 2–92,  $n = 299$ ; *O. a. hodgsoni*, 10.0, 2–31,  $n = 18$ ; *O. a. polii*, 19.7, 2–135,  $n = 275$ —Cai et al. 1989; Fedosenko 2000; Ganguli-Lachungpa 1996; Grachev 1986; Reading et al. 1997). Largest herds are formed in autumn and winter (especially during rut) when males join herds of ewes. During this period, mixed argali groups contain 4–26 ewes and 1 or more (up to 6) rams of different ages. In early spring in central Kazakhstan, herds with  $\leq 5$  individuals account for 55.2% of herds, 6–10 individuals account for 31%, 11–15 individuals for 10.3%, and 16–20 individuals for 3.4%. Most females remain alone during lambing and herd sizes increase later when they rejoin their herd (Fedosenko and Kapitonov 1983). In these mixed herds, adult ewes chase younger females, strike them with their horns, and drive them from resting places. Although younger ewes move away when threatened by an older female, ewes of similar social rank often stand their ground in a bipedal (rearing) position and butt each other. All rams, including younger individuals from 2 to 3 years of age, dominate females. When in herds, males often butt each other. In play fighting, opponents may be of different ages, but true fighting occurs between rams of the same age and social rank. Rams come together, rub muzzles against horns, mount each other, and then butt. Adult argali of both sexes play like lambs; they race, jump, and spin (Fedosenko 1989, 2000; Pleshak 1980).

At the beginning of the rut, adult males visually search and listen for other rams with which to perform rutting ceremonies. They gather in temporary groups of 2–7 to establish a hierarchy. In a typical interaction between 2 adult rams 6–8 years of age, each 1st assumes a low-stretch posture, and then side by side they spin, 1st in 1 direction and then in the opposite direction. One ram then steps back, runs in the bipedal position to his opponent who is either in bipedal position or standing with horns pointed forward. The rams strike each others horns (clash), creating a sharp sound that can be heard 400–800 m away (Fedosenko 1979, 2000). Rams emit grunting calls during combat and often chip their horns or cut the bridge of their nose (Roberts 1977). After clashing, the opponents face each other, holding their heads high (posture of present). Blows between rams occur several times, after which opponents graze quietly next to each other. Fighting can involve several slight bumps to an opponent and stressing with the horns (homing). Sometimes 4 or 5 rams gather in a circle and stand with their muzzles pointing inward and their rump patches pointing outward. Rams demonstrate their postures to each other for several minutes to an hour, and then disperse singly or in pairs. These postures are most often performed during the 1st week of rut, after which rams join herds of females and begin courting ewes. Younger males (<5–6 years) remain distant from the fighting adult rams, and display the following behaviors toward each another: low-stretch posture, butting horns, rubbing muzzle against horns, and sniffing prepuce followed by flehmen. When a younger male meets an adult ram, the younger male may threaten the older ram with his horns, or even stand in the bipedal position at some distance, but runs off when the adult ram approaches to within 1 m. Young males (<5–6 years) often rub their muzzles against the horns of an adult or rub their horns against the adult's muzzle (Fedosenko and Kapitonov 1983).

After establishment of their hierarchy, adult rams (>8 years) display interest in females. When such males see a herd of ewes, they run to within 7–10 m of the herd, slow to a walk in a low-stretch pose, and then sniff the genitals of each ewe in turn. Most females, especially younger ones, run off and continue grazing; a few squat and urinate. The male puts his head under the stream of urine or sniffs urine on the ground, raises his head up and displays flehmen, or lip-curl, while opening his mouth and baring his gums. If the ewe is not in estrus, the ram will leave her and check another. When most females are in estrus, adult males join the herd and constantly chase them, sniffing their vulvas and urine and displaying flehmen. A ram repeatedly approaches a ewe in the low-stretch pose, presses his chest to her, touches or kicks her flanks, belly, and legs with his front leg (front-kick), sniffs her vulva, and drives her from her resting place.

When females are in estrus, rams (>6 years) become less tolerant of younger males, and expel them from the herd. Younger rams run from older rams, sometimes producing high-pitched sounds. While in estrus, females eat less, are more tolerant of courting males, and periodically raise their tails. A single ram remains near an estrous female and is aggressive to other adult rams (Fedosenko 2000). The ram approaches the ewe, sniffs her vulva, stands close behind her with his chest slightly pressing on her, then turns his head 90°, kicks her body with his front legs, and produces wheezy rumbling sounds. If she does not move, he mounts her from behind and takes several steps with the female. After copulation (2 acts during 75 min), the ewe's tail remains raised for some time (Fedosenko 1979, 2000). The ram remains in the herd with females for 1–2 months after the rut (Berber 1999; Savinov 1975).

Each herd of females uses a consistent location for lambing. These locations are sheltered areas of broken terrain in the mountains. Females leave their herds not shortly before giving birth. Yearlings and 2-years olds remain alone or in herds that graze not far from the adult females giving birth (Fedosenko and Kapitonov 1983). Several days before lambing, a female's udder enlarges, her vulva swells, she becomes agitated, her breathing quickens, and her flanks appear sunken in front of her hips. Females paw a bed before lying down to give birth. The lamb appears headfirst with the head placed between extended front legs. The umbilical cord breaks, and the lamb, unable to stand, crawls near its mother who eats the afterbirth. During its 1st day of life, the lamb spends most of its time lying down, but by the next day begins to follow its mother and may give a "merhning" call when its loses contact with her (Roberts 1977). Over the next 2–3 weeks, ewes stay with their young in the area where they gave birth. During this period, females

in high mountains with cold conditions spend 78% of the day grazing and 22% of it resting; females in the lower mountains with warmer temperatures spend 45% of the day grazing and 55% resting. In the 2nd week, ewes with lambs start to leave the lambing areas and move to open plateau or gentle slopes, where they gather in larger herds. Lambs in these herds play by running in a circle, jumping up and down several times in place with both front and hind legs landing simultaneously, and climbing on rocks. Adult females may play with their young, racing with the lambs and jumping with spinning (Fedosenko 1977, 2000; Geist 1971; Walther 1961).

Soon after the appearance of lambs in the herd, yearlings approach them, but mothers attempt to strike the yearlings with their horns. In the case of real danger, the lamb runs 1st to the closest canyon or rock cliffs, ahead of its mother. Females defend their lambs against foxes (*V. vulpes*), golden eagles, and lammergeiers. However, if a human approaches a lamb lying down, its mother immediately runs away. During its 1st several weeks, a lamb faced with the sudden appearance of danger will hide by putting its head on the ground, but if a human or carnivore comes to within 8–10 m of its hiding place, it will get up and run after its mother (Fedosenko and Kapitonov 1983; Kapitonov and Mahmudov 1977).

Mothers give a short bleat to initiate suckling. A lying lamb runs to its mother at hearing her call; if her lamb is not nearby, then a mother searches for it by approaching and sniffing other young until she finds her own (Fedosenko and Kapitonov 1983). More rarely, lambs show the initiative to suckle. If its mother does not allow it, the lamb often runs ahead and either stands in front of her body or runs around her, preventing her from moving forward. This behavior is rarely successful. During suckling, a single young uses both nipples. Twin lambs use both nipples and do not suck simultaneously. Duration of sucking decreases with age of lamb. Sucking duration (mean  $\pm$  SE, where available, range, in s) of lambs at 1–7 days and 8–20 days, respectively, are: 64.1  $\pm$  17.9, 15–140 ( $n = 6$ ) and 31.1  $\pm$  6.3, 6–70 ( $n = 12$ ) in the southwestern spurs of the Djungarskiy Alatau Range (900 m above sea level); 52.9, 30–72 ( $n = 11$ ) and 29.2, 15–45 ( $n = 11$ ) in Talasskiy Alatau Range (2,000 m above sea level); 49.5  $\pm$  13.4, 10–140 ( $n = 11$ ) and 22.1  $\pm$  8.5, 15–35 ( $n = 7$ ) in Terskei Alatau Range (3,000 m above sea level). Intervals between suckling bouts (mean  $\pm$  SE, where available, range, in min) in the same areas, respectively, are: 42.1, 18–58 ( $n = 3$ ) and unknown; 61.0, range not available, ( $n = 4$ ) and unknown; 16.3  $\pm$  4.3, 3–45 ( $n = 9$ ) and 25.0  $\pm$  2.5, 15–30 ( $n = 5$ ). In Talasskiy Alatau (western Tien Shan), ewes do not limit feeding time of lambs during the 1st week. In the alpine zone of Terskei Alatau (central Tien Shan), 36% of ewes limited suckling during the 1st week, and in the desert spurs of Djungarskiy Alatau, females limited suckling beginning on their lamb's 1st day of life. Sucking duration (range, in s) is longest in desert populations of different subspecies: 15–140 in *O. a. karelini* and 30–128 in *O. a. severtzovi* (Fedosenko 1989). Sucking time (mean, range, in s) continues to decrease with age of lamb: for *O. a. karelini*: 21.6, 13–37 ( $n = 11$ ) at 1 month, 15.0 ( $n = 2$ ) at 1.5 months, 14.1, 7–20 ( $n = 9$ ) at 3 months, 10.3, 8–13 ( $n = 3$ ) at 3.5 months, 7.0, 5–10 ( $n = 4$ ) at 4 months (Fedosenko and Kapitonov 1983); for *O. a. ammon*: 17.7, 8.5–33 ( $n = 57$ ) at 1 month, 16, 9–23 ( $n = 27$ ) at 1.5 months, 15.1, 10–18 ( $n = 14$ ) at 2 months, 13.1, 9–17 ( $n = 8$ ) at 4 months, 10.1, 9–11.5 ( $n = 4$ ) at 5 months (Fedosenko 2000). If a lamb dies, a mother will search for it for up to 3 days (Geist 1971; Walther 1961).

Argali from severe alpine and desert conditions migrate seasonally. These migrations involve movements <1,000 m in elevation and up to 15 km in distance (Altai), and most frequently occur in response to decreased availability of fodder associated with a deep snow cover. Migrations also occur in response to drying vegetation, an overabundance of gadflies and other biting insects, poaching, and grazing of livestock. Unusual phenomena, such as severe drought or fires, also prompt argali to migrate (Fedosenko 1977, 1989; Sopin 1976). Everyday movements are associated with grazing, visiting watering places and points of saline soil, and finding day and night resting spots. Grazing argali move down along the slope in the morning and back up the slope in the evening. Locations for night resting usually provide good viewpoints and are often considerably higher than grazing areas. In spring and early summer, argali cover long distances while grazing, moving in either straight or circular directions (Fedosenko 1989; Fedosenko and Kapitonov 1983). In winter and early spring, when the weather is

still cold (<−20°C in Altai), argali stay in their resting places through the morning and then move to pasture where they graze throughout the day with only a single interval for resting and chewing cud. As the weather warms, argali graze earlier, and frequency and duration of their midday rest intervals increases. In summer, argali eat in the morning and evening and rest midday near glaciers and in mountain passes. Under cloudy conditions, they can graze the entire day, rotating periods of grazing (50–100 min) and rest (30–45 min). Argali also exhibit night grazing, particularly in pastures with large numbers of livestock and a high level of disturbance. In autumn, argali linger in their pastures later and later as the weather becomes colder. Most argali in the herd, especially the smaller ones, simultaneously lie down for resting and get up for grazing. During periods of rest, argali sleep several times, with each sleep cycle lasting 2–8 min, sometimes up to 21 min. Total portion of resting time spent sleeping is 12–20% (rarely up to 68%). Activity of argali can change due to strong wind (>7–8 m/s); most lie on their beds in the deep canyons and caves until heavy winds cease. Argali graze during light rains and snowfalls, but stop feeding and run to their beds during severe rains or snowfalls, especially those accompanied by strong winds. Argali prefer to rest on days with extreme frost and temperature <−20°C. Grazing duration decreases when biting insects are abundant. During hot summer days, the midday rest reaches its maximum for the year; this pattern is most marked in the low desert mountains (Antipin 1941, 1947; Fedosenko 1983, 2000; Fedosenko and Scuratov 1990). Argali use constant beds, scratching the ground with their front legs before resting; over time, this scratching forms a large pit with dimensions from 70 by 100 to 90 by 120 cm and a depth of from 5 to 50 cm (central Kazakhstan). Argali often defecate in their bed while resting in a laying position (Fedosenko and Kapitonov 1983).

Behavior of *O. ammon* near watering places varies with environmental conditions. In places with abundant water sources, argali approach the bank and drink quietly. When they drink from a spring that has low steep sides, ewes kneel to reach water. In areas where water sources are rare, individuals approach the watering place against the wind, often stopping to look and listen, and then begin to drink, but run off and return several times. They are most fearful near a closed spring surrounded by dense, tall (2- to 3-m) grasses. Argali also visit areas with saline soil. They stay for a long time at these locations, grazing and resting, but spend only a short time eating the saline soil. When such a point is small, rams visit it sequentially according to their hierarchy; waiting males either lie down or butt each other. Females are more tolerant of each other, and several ewes simultaneously use the saline point. Females kneel to eat saline soil from small pits. At larger saline locations with steep slopes, ewes strike the slopes with their head and horns, or scrape it with their front legs, and then eat the soil broken loose. At wet saline points, argali drink saline water, lick the mud, or eat the grasses covered by salt. Large herds stay for up to 2 h at the saline points (Fedosenko and Kapitonov 1983).

While grazing, females produce low muffled rumbling sounds that are audible at a short distance. When alarmed, males produce shrill abrupt calls, which sound like “ch-sh-sh-sh” or “p-ch-sh-i-u,” or more rarely, noted only for *O. a. collium*, a bleating “brraaa.” An alarmed ram may stamp a front leg. Females sensing danger usually squat and urinate; young males also urinate, but without squatting. After these acts of alarm, the entire herd runs away. In the case of sudden danger, argali run off immediately, but stop after some distance to look for the source of their alarm, and then continue to run. If the source of the threat is far away, an adult argali may hide in the nearby landscape, but runs when the danger approaches (Fedosenko and Kapitonov 1983; Sapozhnikov 1976). Before lying down to rest, argali visually search the surrounding slopes. Their resting places usually provide a good view of the terrain, and allow argali to be barely visible. Argali in the herd lie down facing different directions. Grazing argali frequently raise their heads to look around, and older individuals look around more frequently than do younger argali. In a typical situation in the pasture, proportion of time spent with heads raised for *O. a. ammon*, *O. a. karelini*, and *O. a. polii*, respectively, is 11.0–11.3%, 11.6%, and 14.5%. Argali in large herds look around less frequently than those in small herds, and solitary argali raise their heads most frequently and spend up to 30% of their grazing time with heads raised. Argali can run from wolves for up to 1 h at speeds of 50–60 km/h (Abramov and Faleev 1996; Fedosenko and Scuratov 1990; Meklenburtsev 1948).

Argali react strongly to biting insects such as gadflies, gnats, horseflies, and mosquitoes. Skin of a female's udder and nipples is attacked most often by these insects, and females try to drive them off by either raising a hind leg and striking it against their belly or reaching with their muzzle back toward the groin. Females interrupt nursing because of blood-sucking insects. Gadflies (Oestridae) may cause panic in ewes and lambs, but males stand with their heads very close to the ground and stomp their front legs to raise a cloud of dust. Argali scratch their bodies against large stones and along cliff walls because of ticks, and also during molt to remove their winter coat. During molting, they squeeze through thick bushes, sometimes leaving behind whole flocks of winter fur. In the alpine zone, where bushes are absent, argali use special scratching points along the walls of river cliffs, gullies, or geological prospecting shafts. At a scratching site, several argali all move forward and backward, along the cliff wall, pressing first 1 flank up against the rough surface and then the other (Fedosenko et al. 1995a).

**GENETICS.** Karyotype of *O. ammon* is  $2n = 56$ , including 2 pairs of biarmed and 25 pairs of acrocentric autosomes. The X chromosome is a large acrocentric and Y chromosome is a minute biarmed metacentric except in *O. a. nigrimontana*, in which the Y chromosome is an acrocentric (Bunch et al. 2000). Genetic distance between mtDNA haplotypes of subspecies of *O. ammon* are described by Hiendleder et al. (1998). Hybrids of argali (*O. a. nigrimontana*) and mouflon (*O. musimon*) are known from the Parvar Protected Region of northern Iran ( $2n = 55$ —Nadler et al. 1971). Other reports of hybrids include: *O. ammon* (female) × *O. orientalis (vignei) boharensis* (male—Gray 1972); *O. ammon hodgsoni* and *O. orientalis vignei* (Ward 1924); *O. a. hodgsoni*, *O. a. karelini*, *O. a. polii*, and different breeds of domestic sheep (Gray 1972); *O. a. karelini* and Kirgizian breed of fat-tailed sheep (females) by artificial insemination (Rumiantsev et al. 1935); and males of *O. a. karelini* and females of a Caucasian breed of domestic sheep (merino—Butarin 1960).

**REMARKS.** *Ovis a. severtzovi* was resurrected as an argali subspecies on the basis of karyotypic research (Liapunova et al. 1997; Shakula et al. 1994). The intraspecific taxonomy of *O. ammon* is debated, including subspecies status of *O. a. collium* (Fedosenko and Kapitonov 1983; Geist 1991; Shackleton 1997; Sopin 1982). Geist (1991) and Valdez (1982) consider *O. a. dalai-lamae* to be a synonym for *O. a. hodgsoni*, whereas others (Bunch et al. 2000) consider them to be separate subspecies. Valdez (1982) regards *O. a. jubata* as a synonym of *O. a. darwini*, whereas others (Geist 1991) consider it to be a separate subspecies.

The 1st published information on argali was from William of Rubruck, a Franciscan friar, sent to Mongolia in 1253. He described Altai argali, called artak, as a beast with the body of a ram with large crooked horns. Twenty years later (1271–1274), Marco Polo found argali in Pamir (Valdez 1982). In Siberia, Messerschmidt, in 1724, encountered argali in Dauria (Transbaikalia) near the Ingoda River (50°N, 111°E). In 1752–1753, G. Gmelin saw argali in southern Altai (east of the Irtysh River). Gmelin illustrated and described the sheep as *Rupicapra cornubus arietinis*, and gave them the common name argali (Geist 1991; Valdez 1982). In 1758, Linnaeus used Gmelin's descriptions and renamed argali *Capra ammon*. Geist (1991) suggested that Gmelin's description of *Capra ammon* in Linnaeus (1758:70) did not pertain to argali, but probably was a urial, and thus the initial description of true argali was by Linnaeus in 1766. Pallas did a detailed analysis of a female and lamb from Transbaikalia (Odon-cholon Range). He renames argali *Musimon asiaticus* (Pallas 1776:8, as cited in Geist 1991:711), and then *Ovis argali* (Pallas 1777–1780:20, as cited in Lydekker 1913:92). Europeans discounted the existence of Pamir argali until 1833, when Sir Alexander Burnes, during a mission in central Asia, reported a sheep called rass or kooshgar that was larger than a cow and smaller than a horse. In 1838, John Wood found numerous argali horns in the Wakhan Corridor of Afghanistan. A 2-year-old male argali was killed and described, and at least 1 horn and a specimen were sent to the Royal Society of London. Two years after its “discovery,” E. Blyth described this animal and named it *Ovis polii* (Blyth 1841b, as cited in Valdez 1982:32).

The name argali is Mongolian in origin and means ram or sheep. The Latin name *ammon* is the name of an ancient horned Egyptian god. English common names for subspecies include Altai

and Siberian argali for *O. a. ammon*; Kazakhstan argali for *O. a. collium*; Mongolian or Gobi argali for *O. a. darwini*; Tibetan argali for *O. a. hodgsoni*; Shasi or northern Chinese argali for *O. a. jubata*; Tien Shan argali for *O. a. karelini*; Kara Tau argali for *O. a. nigrimontana*; Marco Polo sheep or Pamir argali for *O. a. polii*; and Severtzov's sheep for *O. a. severtzovi*. Russian names are arhar and argali (mainly for *O. a. ammon*) and names for subspecies include Altai mountain sheep or argali for *O. a. ammon*; northern or central Kazakhstan archar for *O. a. collium*; Himalayan sheep for *O. a. hodgsoni*; and Kyzyl Kum sheep for *O. a. severtzovi*. Other common names are rass and koosghar or kutch-kar (central Asia), nan-yang and ta-tou-yang (China), nien (Tibet), arkar (Kazakhstan), ak-kiik, kuldja (for males) and echke (for females), kuzy and kuzhga (for young), bodo, and kizil-kiik (Tadjikistan—Fedosenko and Kapitonov 1983; Geist 1991; Sapozhnikov 1976; Valdez 1982).

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