Ammotragus Blyth, 1840


CONCEPT AND CONTENT. Order Artiodactyla, Suborder Ruminantia, Infraorder Pecora, Family Bovidae, Subfamily Caprinae, Tribe Caprini. The genus Ammotragus consists of one species, as treated below.

Ammotragus lervia Pallas, 1777

Barbary Sheep; Aoudad, Audad, Udad, Arui; Mouflon à Manchettes; Mähnenpringer; Muflone Berbere; Arrui

Antilope lervia Pallas, 1777:12. Type locality "Afrique borealei prorsa."

Ovis tragelaphus Afzelius, 1815:216. Type locality "Mauritania."

Ovis ornata I. Geoffroy Saint-Hilaire, 1827-284. Type locality "pays des monts de la ville du Caire" (=Caire, Egypt).

Ammotragus lervia Thomas, 1902:13, first use of current name combination.

CONCEPT AND CONTENT. Context noted in generic summary above. Six subspecies are recognized (Allen, 1939) as follows:

A. l. lervia (Pallas, 1777:12). Type locality restricted to the "Department of Oran, western Algeria" by Harper (1940:327). A. l. ornata (I. Geoffroy Saint-Hilaire, 1827-264), see above.

A. l. saharinensis (Rothschild, 1913:459). Type locality "Oued Mya" between El-Golea and In-Salah, 2903 N, 3 E, Algerian Sahara.

A. l. malini (Rothschild, 1913:460). Type locality "Border of Donqola Province and Kordofan," Anglo-Egyptian Sudan.

A. l. anguis (Rothschild, 1921:75). Type locality "Tarrouaji Mt., Asben, 3,100 ft.," French West Africa.

A. l. fassini (Lepri, 1930:271). Type locality Garian range, northeastern Libya.

DIAGNOSIS. The following combination of gross morphological characteristics is diagnostic for Ammotragus: presence of true horns, subcaudal gland, ventral neck mane, and chap hair on front legs of adults (particularly evident on males); absence of preorbital, interdigital, or inguinal glands, and inter-rimal chin beard.

GENERAL CHARACTERS. Pelage is rufous or tawny brown with occasional dark brown areas about the head and forequarters. The chin, belly, and inside of legs are whitish, and a circular spot of white hairs frequently occurs on the head between the horns. A fringe of long hair, the mane, extends from under the throat down the front of the neck to the brisket. This hair then bifurcates and continues down the forelegs of mature animals, where it is termed chaps. Although a mane is found on other wild sheep, chaps are peculiar to aoudads. A short erect fringe is present on the back of the base of the neck to just behind the withers.

The head is relatively long with narrow, evenly tapered ears and a small black nose. Eyes are large and distinctive; a horizontal pupil is surrounded by a yellow iris.

True horns (Fig. 1), present on both sexes, are relatively large and moderately long, with a moderately high spiral angle (small radius). They are elliptical and keeled in cross section, with a fairly broad frontal surface, exhibit heteromyum winding, and have numerous shallow and uniform sulci (rings) as well as periodic growth checks or annuli (Ogren, 1962, 1963; Geist, 1966; Schaffer and Reed, 1972). Horn points are directed inward, or inward and downward. Horn lengths and basal circumferences rarely exceed 840 and 355 mm in males, and 510 and 205 mm in females.

The neck is robust and the forequarters are more massive than the hind, particularly in males. This appearance is accentuated by the topline which slopes from the withers. The legs appear to be short and stocky, and hooves are large, blunt, and well developed. Dew claws are usually hidden by chap hair. The tail is 175 to 205 mm long, tufted on the terminal half, and naked underneath (McClellan, 1955). Preorbital, interdigital, and flank glands are absent.

Dimensions of the largest males harvested in New Mexico (Ogren, 1965) were: total length, 190 cm; height, 112 cm; girth, 137 cm; weight, 145 kg. The largest females measured 165 cm, 94 cm, 112 cm, and 63.5 kg. These are significantly larger measurements than have been reported for type specimens from Africa, which were from 94 to 99 cm in height (Clark, 1964).

DISTRIBUTION. Lhote (1957:88) designated the range as being all the hills of the Sahara, but particularly the Hoggar, Tassili, Ayr, and Tibesti mountains. Barrett (1967) summarized the biogeographic distribution, indicating that the species inhabited all the major mountain massifs of North Africa above 15° latitude (Fig. 2), citing Bigourdan and Pruniere (1937), Rode (1943), Brouin (1950), Malbrard (1952), and Edmond-Blanc (1957). Joleaud (1927) also delineated the distribution.

Barbary sheep were present in some European zoological gardens during the last half of the previous century (Ogren 1965;5). were introduced into the Teutoburger Forest of West Germany (Strasson, 1916), and onto Italian game preserves (Zamponi, 1930). The first importations from Europe to the US occurred about 1900 (Ogren, 1965:5). Barbary sheep readily reproduce in confinement, and surplus zoo stock was eventually sold to private parties. Wild populations in the southwestern United States were derived from groups which were released or escaped from private herds. The larger wild populations are located in Palo Duro Canyon of the Texas Panhandle, the Canadian River Gorge, Canyon Largo, and Hondo Valley of New Mexico, and Santa Lucia mountains of west-central California.

FOSSIL RECORD. Fossil sheep remains recovered from Tertiary deposits in Europe were referred to as Ovis tragelaphus fossils by Serres (1848:149), and O. magna and O. primigena by Gervais (1852:76). Lydekker (1912:310) commented that these “sheep were akin to the modern arui of North Africa.” Osborn (1910:433), writing of the Pleistocene in North America, mentioned a “wild sheep (Ovis paleotragus) very similar to the existing Barbary sheep.”

McBurney (1967) found remains of Ammotragus in Haua Fteah, a large natural cave on the northern coast of Cyrenaica Libya, in a number of deposits which ranged in antiquity from about 85,000 to 2000 years B.P. Bate (1955) discussed the vertebrate faunas, including Barbary sheep, from Quaternary deposits in Cyrenaica. Vaufrey (1955) noted the species among the Pleistocene fauna in the Maghreb (Atlas massif), and Arambourg et al. (1934) recorded the taxon at Beni Segoua.

FORM. The skin is relatively thick, cutaneous glands are rare, and special dermal glands absent (Bourdelle, 1924). Females possess one pair of inguinal mammas.

In general, osteological characteristics are more nearly like those of goats than sheep (Bourdelle, 1924). Sexual dimorphism in horn size, sinuses, and associated cranial morphology is pronounced. Horn bases are displaced behind the orbit. Schaffer and Reed (1972) made the following observations on the cranial morphology of Ammotragus. The male skull is considered to be of an advanced shape among Caprini—that is, the foramen magnum is located beneath the horn bases and the back of the skull is more nearly vertical, so that the inclusive angle formed by the intersection of a plane along the parietal and supraoccipital bones with the plane of the palate is greater than 70°, and the ratio of
parietal length to ventral skull length approximates 0.15. In the aoudad this configuration has been achieved by a ventrad rotation of the brain case (Fig. 1). The frontal sinuses are extensive and the septa complex in males, moderately extensive and moderately complex in females; the cornual sinuses are extensive and septa complex in males, extensive and moderately complex in females. The vertebral formula is C 7, T 13, L 6, S 4; Cd 14 (Lydekker, 1913). Incisors are typically goat-like, whereas molars are more nearly sheep-like (Bourdelle, 1924). The dental formula is i 0/3, c 0/1, p 3/3, m 3/3, total 32.

The structure of the hemoglobin (Hb) α polypeptide chain from this species consists of two forms, and both α' and α'' chains closely resemble those of the domestic goat (Huisman, 1974); the βα chain is apparently unique among the Caprini. The Amm-B Hb chain of Barbary sheep was shown to be related to but not identical with Hb B of the domestic sheep, and the Barbary sheep Amm-βα chain was similar to the sheep βα chain (Huisman et al., 1968). The Hb of Barbary sheep was compared with Hb-I and Hb-II from Dutch Texel sheep and found almost identical to Hb-I in electrophoretic mobility, but of intermediate solubility between Hb-I and Hb-II in a series of phosphate buffers (pH 6.5) of graded molarities (Huisman et al., 1958). Hb-II has a greater affinity for oxygen, originated—in domestic breeds—from sheep living at high altitudes, and may be of adaptive significance; Hb-I is characteristic of breeds living at sea level. In an examination of blood proteins by electrophoresis in acrylamide and starch gel, Ammotragus was found to have five distinctly sheep-like biochemical characteristics, seven characteristics in common with both sheep and goats, and 10 unique characteristics (Manwell and Baker, 1977). Barbary sheep serum cholinesterase may be more primitive than either sheep or goat cholinesterase since it is more active on butyrylthiocholine and α-naphthyl acetate.

The uterus is bicorbinate and the semideciduous placenta cotyledonary; an unusual type of corpora luteal scar that Ogren (1965:65) described sperm structure and Steklenov (1972) compared sperm morphology with other representatives of the Caprinæ.

A number of general morphological features can be used to separate Onis from Capra, and Payne (1968) indicated that Ammotragus shares six of the nine characteristics he inventoried with Capra. Linear body measurements were listed by Rode (1943), Brouin (1950), and Panouse (1957).

**FUNCTION.** Brady and Ullrey (1975) presented serum biochemical and hematological parameters of weaned juvenile Barbary sheep fed an exotic ruminant diet. Serum biochemical and hematological values of captive adults more closely resembled values for white-tailed deer, Odocoileus virginianus, than those of cattle or sheep, and activities of three serum enzymes assayed were also similar to those reported for white-tailed deer (Tumbleson et al., 1970). Meyer (1967) and Huisman et al. (1968) also listed hematological values for Ammotragus, and Huisman and Miller (1972) demonstrated that Hb-B is replaced by another hemoglobin type (Hb-C) during bloodless anemia whereas a Hb-C-like variant, Hb-C(low), present in certain nonanemic Barbary sheep, cannot be replaced when the animal is made severely anemic.

Average daily gain in weight of weaned juveniles was not significantly affected by dietary protein level and the only significant dietary effect on blood parameters was on plasma urea nitrogen (Brady and Ullrey, 1975). The dietary protein requirement for weaned animals did not exceed 13.1% under study conditions, and levels up to 19.6% did not appear to be harmful.

Nouvèl et al. (1969) reported the effect of an intramuscular injection of 12 ml of Sédalaide (= Halo-anisone), fluoro-methoxyphenyl-piperazine butyrophenone, on a male; and Hampe (1978) immobilized three males with M99 (etorphine) using M50-50 (diprenorphine) as the antagonist drug.
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ONTOCENY AND REPRODUCTION. Sperm is abundant in the epididymis of older males year-round (Ogren, 1965:64). Most matings are accomplished during an autumn rut, from September through November, but some take place throughout the year. The gestation period is 22 to 23 weeks (Brown, 1936; Lobanov and Treus, 1971), and up to 84% of births occur from March through May (Flower, 1932; Zuckerman, 1963; Lobanov and Treus, 1971). Fourteen mature females collected in New Mexico during the late autumn of 1957 had a total of 17 embryos (1.2 per female); the ratio was 1.6 embryos per female for seven mature females taken in the late winter of 1959 (Ogren, 1965:50). Of 67 females shot during the first eight hunts in Palo Duro Canyon, Texas, 44 (65.6%) were pregnant with 57 fetuses (1.3 per female). One female had triplets, 14 had twins, and 29 contained single fetuses (DeArment, 1971). Fetal sex ratio was 19 males:21 females, with 17 unknowns.

Twins are produced once in every six or seven births under conditions of confinement (Zuckerman, 1953; Blunt, 1963). The sex ratio at parturition is unity and birth weights average 4.5 kg (Blunt, 1963). The neonate is precocial and able to negotiate moderately rugged terrain almost immediately after birth (Ogren, 1965:69). Concurrent lactation and gravidity indicates that lactation overlaps the estrous cycle in some females.

Age of puberty is variable. Ogren (1965:65) found sperm in an 11-month-old male, but not in a 15-month-old male, and a known-age female produced an offspring when only 13 months, 12 days of age (Blunt, 1963). On two occasions a 10-month-old female has produced offspring twice in less than 7 months, and one had three single births within 13 months, 4 days (Blunt, 1963). Ogren (1965:59) regarded all females at least 19 months old as being sexually mature.

Dental maturity is apparently achieved rather late. Irruption of the permanent canine, an incisiform tooth, was observed in 65 and 68 months in two known-age animals (Ogren, 1965:31). Longevity has exceeded 20 years in zoos (Ogren, 1965:6), but longer in the wild probably rarely exceeds 10 years.

Although Gray (1954:60) indicated that no live births resulting from matings of Ammotragus males to female domestic goats (Capra hircus) had been produced, a viable female from this mating combination was reported by Petsch (1957) and this hybrid was successfully backcrossed to a Barbary sheep male. Brentjes (1968) suggested that this provides a possible interpretation for the presence of goat-like animals in ancient Egyptian pictographs, and that such hybrids may have been relatively common because of the wide geographic distribution of Barbary sheep.

ECOLOGY. This species inhabits arid and semiarid lands from sea level to at least 945 m in elevation within its endemic North African range (Rothschild, 1921:75) and canyonslud with gorges to 505 m in deep at elevations up to 1829 m in the southwestern United States (Ogren, 1965:31). It favours utilising the greatest in areas of precipitous topography (Evans, 1967; Hampy, 1978).

The major spring food plant in New Mexico was mountain mahogany, Cercocarpus breviflorus (54.3% rumen content by volume), followed by grasses (25%), forbs (13.8%), and other browse (5.6%). Summer foods included C. breviflorus (31.5%), wavyleaf oak, Quercus undulata (30%), grasses (26%), forbs (8.8%), and other browse (3%). The autumn diet featured Q. undulata (54.3%), grasses (29%), forbes (12.4%), and other browse (4.1%), whereas the principal winter food category was grass (86%) supplemented by small amounts of browse (10.9%) and forbs (2.4%) (Ogren, 1962, 1965). Mountain mahogany and wavyleaf oak accounted for half the total volume of 79 plants identified. An analysis of stomach contents from 109 animals collected in late autumn or early winter hunting seasons in Palo Duro Canyon, Texas, from 1963 through 1970 (DeArment, 1971) revealed the following woody plants to be important dietary components during this season: sand shinnery oak, Quercus havardii (contained in 66.9% of the stomachs); honey mesquite, Prosopis glandulosa (53.2%); yucca, Yucca angustifolia (24.9%); mountain mahogany, Cercocarpus montanus (33.9%); juniper, Juniperus sp. (24.8%); netleaf hackberry, Celtis reticulata (13.8%); and black willow, Salix nigra (13.8%). Principal forbs were western ragweed, Ambrosia psilostachya (13.8%) and buffalobur, Solanum rostratum (10.1%); and grasses, little bluestem, blue grama, and indropus, schwienbergii (18.4%), silver bluestem, A. saccaroide (15.6%), and blue grama, Bouteloua gracilis (14.7%). Research in progress at Palo Duro Canyon, based primarily on fecal pellet analysis, suggests that mountain mahogany is the most important coarse class in the diet (53% relative frequency), summer (68%), and fall (48%), while browse (42%) and grass (43%) are equally important during winter months (Simpson et al., 1978). Forbs were the preferred forage of a tame animal whose food habits were observed on the Edwards Plateau of Texas (Ramsey and Andergassen, 1972).

A few animals from an introduction at Palo Duro Canyon, Texas, dispersed up to 32.3 km (20 mi) from the release site within 5 to 7 months (DeArment, 1971). The home range of radio-collared adults in Palo Duro Canyon (Hampe, 1978) was 0.98 km² (0.38 mi²) and 2.64 km² (1.02 mi²) for one male during the winter as determined by minimum convex polygon (MCP) and home range (THR) methods, respectively. Summer THR size was 19.26 km² (7.44 mi²) and summer THR was 30.85 km² (11.91 mi²). Two adult females exhibited a mean winter MHR of 2.09 km² (0.81 mi²) and THR of 4.57 km² (1.76 mi²); and these two plus one additional female had a mean summer MHR of 12.98 km² (5.01 mi²) and THR of 16.69 km² (6.44 mi²). Abrupt seasonal movements of as much as 23.4 airline km (14.5 mi) were also observed. Interspecific competition has not been documented but it is likely that Ammotragus would have an advantage over most other ungulates in regions where such interactions are possible. Concern has been expressed for the future of the desert bighorn sheep (Ovis canadensis) in southwestern United States should Barbary sheep invade much of the desert bighorn's range (Barrett, 1967; Simpson et al., 1978). Predation does not appear to have a significant impact upon populations within its exotic range (Ogren, 1965:54, 1971:15).

Thirteen helminth parasite species were reported from two Barbary sheep (Allen et al., 1956), and 17 helminth species were recovered from seven host animals (Allen, 1960), all collected in New Mexico. Only three helminth species were found in five hosts from Palo Duro Canyon, and worm burdens were light (Gray et al., 1978). Experimental cross-transmission of the abomasal worm, Haemonchus, suggested that the strain from wild Barbary sheep is less pathogenic than the strain from domestic sheep (Allen et al., 1958; Samson et al., 1964). A louse, Bextelia neglecta, described from zoo animals, is apparently host-specific for Ammotragus (Keller, 1942:77; Werneck, 1950:81). The winter tick (Dermapterot alplicita) was also taken from New Mexico hosts (Allen et al., 1956; Allen, 1960).

Five of seven adult males from New Mexico showed positive reactors to the agar precipitin test for bleutongue (BT) (Trainer and Jochum, 1969); and serologic reactors to infectious bovine rhinotracheitis (IBR), BT, and epizootic hemorrhagic disease (EHD) were found in three, six, and three individuals, respectively, of 12 from the Palo Duro Canyon population (Hampe et al., 1970). Fifteen fatal cases of mycoplasmosis were recorded from Barbary sheep in the Franklin Zoo (Brack, 1966; Erns et al., 1972). Naturally occurring coronary and aortic atherosclerosis was discovered during necropsies of two adults which died at the St. Louis Zoo (Wallach and Middleton, 1970), and the lesions were more extensive than those reported to be naturally occurring in most other species. Seven animals died of Johne's disease, paratuberculosis (causative agent Mycobacterium para-
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Schmidt, 1972). An alpha male also may intimidate conspecifics by raising the fringe hair over the withers, licking his lips, and uttering a low guttural growl. Intraspecific aggressive behavior is typically ritualized and of two major types (Katz, 1949; Haas, 1959; Schaffer and Reed, 1972:12). One, the head-on charge, is ordinarily confined to interactions between males and may involve a closing velocity up to 80.7 km/hr (50 mph) (Schaffer, 1968), with both animals remaining quadrupedal on impact. The other involves close butting and head shoving, or hooking the horns, neck, flanks, or belly of the conspecific from a parallel position, followed by twisting or gouging motions (Fig. 3). The torque caused by such rotational movements has probably contributed to adaptive selection for musculature which resists rotation of the head (Schaffer, 1968), producing disproportionate development of the neck and forequarters in males. Fighting of both types was also common among females, but rarely involved charging an adversary. Displaced aggression was common, frequently continued chainwise to other individuals, and was influenced by physical proximity and lower social status of recipients (Katz, 1949).

Females defend against suitors during anestrous and are adept at striking them with their horns whether or not a male has mounted (Ogren, 1965:67). Proestrus females appear to excite males, which feed and ruminate less, sniff, or lick at female urine, puddles, and genitalia, and exhibit the typical bovid flehmen (graphically pictured in Davis, 1974:262). Sexually aroused males may squat in a female posture rather than the usual erect or forward-leaning stance and may attempt to segregate a female by herding actions, and attempt mounting (Katz, 1949; Ogren, 1965:68). During estrus females sometimes lick the sides of a male, and mutual touching of muzzles is frequent. Copulation is accomplished by mouthing, forceful rapid thrusts, either immediately or several minutes after mounting, and is accompanied by male growls (Ogren, 1965:68). Copulation may be repeated up to 20 minutes later.

Juveniles exhibit a number of recognizable elements of aggressive and sexual behaviors, as well as typical maintenance and comfort postures (Haas, 1959), but these are frequently displayed in inappropriate contexts. Thus the ontogeny of behavior in this species may consist of rearranging many rather elaborate innate patterns into appropriate sequences, rather than slow development or abrupt emergence of these patterns. Temporal periodicity in behavior embraces fairly regular cycles of alternating activity and rest within the daily regimen of herd behavior, as well as distinctive seasonal behavioral changes (Katz, 1949).

GENETICS. This species has a karyotype of 2N = 58, FN = 60, composed of one pair of biramous and 27 pairs of acrocentric autosomes, a large acrocentric X chromosome and a minute biramous Y chromosome (Nadler et al., 1974). This karyotype is identical in general structure with that of Ovis aries. The centromeric pattern of the biramous chromosomes is similar to that seen from the largest biramous autosomal pair (I) of O. moschata (O. orientalis, O. canadensis, and O. moschata × O. canadensis F1 and F2 hybrids. Among the acrocentric chromosomes of Ammotragus were pairs with G-band patterns resembling those seen in biramous pairs II and III of 2N = 54 wild and domestic sheep. Buckland and Evans (1978b) noted that, with the exception of a single Robertsonian translocation, the G-band pattern is the same as the goat karyotype, and there is virtually no demonstrable centromeric heterochromatin (Buckland and Evans, 1978b). Karyotypes were published by Beck et al. (1968), Schmitt and Ulrich (1968), and Nadler et al. (1974).

The F1 hybrid from a natural breeding of a male with a female domestic goat, Capra hircus (2N = 60), was a 2N = 59 female with a karyotype containing one unpaired metacentric, two unpaired and 27 paired acrocentric autosomes, and two large acrocentric X's (Bunch et al., 1977). The phenotype incorporated features from both species. Several studies intended to clarify the phylogenetic relationship of Ammotragus to the other Caprinae may have only intensified the controversy. Serum protein analyses by Schmitt (1963) and immunoglobulin cross-reactivity studies by Curtin and Fudenberg (1973) indicated a close relationship between Ammotragus and Ovis. The amino acid sequence of various hemoglobin chains examined by Manuel and Baker (1975) showed that Ammotragus hemoglobin was more nearly similar to that from the domestic goat, Capra hircus, than that from the domestic sheep, Ovis aries, but also exhibited some unique characteristics. But an immunological technique adapted for computer analysis by Hau and Nadler (1976) demonstrated that the relationship between Ovis and Capra than between either of these and Ammotragus.
REMARKS. Ammotragus may have shared the habitat. Ophion, with Ovis ammot in ancient accounts by Pliny and others (Cuvier, 1827:359). The species was called Tragelaphus by Caius in 1561 (Cuvier, 1827:319; Scortecchi, 1957:492), and Lervew or Fisslath by Shaw (1798). Fisslath may derive from fest, bristles on the mane long, hence long mane; or from skæft, a desert, and tall, wanderer (Cuvier, 1827:320). Common native appellations include aoudad (Mauretania), kebsh (Egypt), and beddan (males only) or tedal/teytal (Nubia) (Blyth, 1839:76).

A succession of generic or subgeneric reassignments, which do not properly belong in the synonymy, may have contributed to confusion about the taxonomy of this species. This nomenclature is included here for the convenience of interested persons.

Ovis (Ammotragus) tragelaphus Blyth, 1840:13.

Ammotragus tragelaphus Gray, 1850:40.

Musimon tragelaphus Germain, 1855:192.

Aries tragelaphus Lastage, 1887:35.

Ovis (Ammotragus) lervia Lydekker, 1898:226.

Ovis lervia Anderson and de Winton, 1902:334.

Because Barbary sheep sometimes sire live hybrid offspring when bred to goats, and appear to be closer to goats in gross anatomical characteristics, Ansell (1971), Van Gelder (1977), and Corbet (1978) have placed Barbary sheep in the genus Capra. We demur from this assignment since the phylogenetic relationships are ambiguous, as noted in the section on genetics.

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E. LAWLOR.

GARY G. GRAY AND C. DAVID SIMPSON, DEPARTMENT OF RANGE
AND WILDLIFE MANAGEMENT, TEXAS TECH UNIVERSITY, LUB-
BOCK 79409.