

Oceanian type black rats in Hawaii have been reported by YOSIDA and TSUCHIYA<sup>10</sup>. DAVIS and BAKER<sup>11</sup> have also reported Oceanian type idiogram in all black rats collected in Texas, Washington, Puerto Rico and Mexico. The  $M_2$  pair of those rats was typically metacentric. The subtelocentric  $M_2$  observed in the present material has never been reported in any locality of the world. As described above, the subtelocentric has been derived from the pericentric inversion of the metacentric  $M_2$  chromo-

some. Such inversion seems to have occurred considerably more recently in California (San Lorenzo?) after the rats migrated there. All 5 rats with the subtelocentric  $M_2$  showed heterozygous pair consisting of subtelocentric and metacentric. Have the rats with the subtelocentric  $M_2$  pair become lethal? To solve this problem we are now breeding these rats in our laboratory, and the result of this study will be reported later<sup>12</sup>.

**Résumé.** Dix rats (*Rattus rattus*) d'une colonie californienne ont été examinés. Cinq sont de type océanique. Les cinq autres ont 1 paire  $M_2$  hétéromorphe, formée d'un métacentrique et d'un sub-métacentrique, ce qui implique une inversion péracentrique. Les transferrines sont du type océanique.

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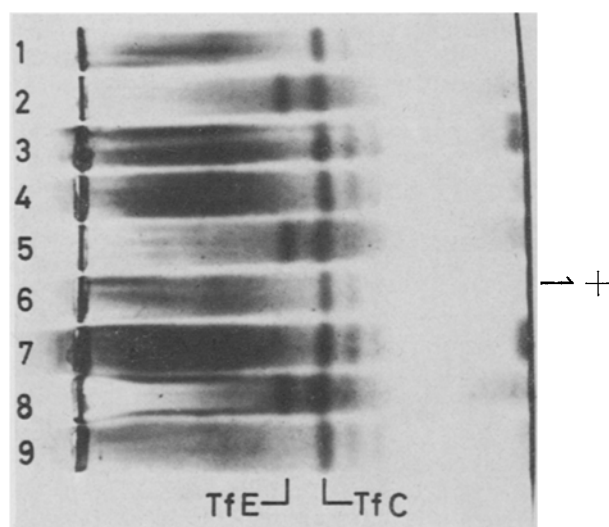


Fig. 4. Demonstration of C type serum transferrin by thin layer acrylamide gel electrophoresis combine with acrinol pretreatment<sup>7</sup>. Sample Nos. 2, 5, 8: Standard samples, TfC E. Sample Nos. 1, 3, 4, 6, 7, 9: Sera of Oceanian type *Rattus rattus* obtained from California.

<sup>10</sup> T. H. YOSIDA and K. TSUCHIYA, Rep. natl. Inst. Genet., Misima 20, 15 (1970).

<sup>11</sup> B. L. DAVIS and R. J. BAKER, Cytologia 36, 417 (1971).

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## G-Band Patterns, Chromosomal Homologies, and Evolutionary Relationships Among Wild Sheep, Goats, and Aoudads (Mammalia, Artiodactyla)

The tribe Caprini (family Bovidae) contains 5 genera<sup>1,2</sup>, among which the wild sheep (*Ovis*) and goats (*Capra*) are most closely related<sup>3</sup>. The aoudad (*Ammotragus*) of North Africa shares affinities with both, especially the latter<sup>2,3</sup>. *Ammotragus*, together with the primitive caprine, *Hemitragus*, also shares behavioral and morphological characters with the tribe Rupicapriini, from which caprines probably evolved<sup>3,4</sup>, and GEIST<sup>3</sup> postulated that *Ammotragus* resembles the form ancestral to *Ovis*, and is itself derived from rupicaprine ancestors. *Capra* presumably represents a separate evolutionary lineage derived from ancestral caprine stock. The divergence of sheep and goat lineages probably occurred no later than the early Pleistocene<sup>3,5</sup>, contrary to PAYNE's<sup>6</sup> hypothesis that *Ovis* and *Capra* were derived from a single interbreeding caprovine stock in late Paleolithic time.

Chromosome analyses of these 3 genera demonstrated a common fundamental number ( $NF = 60$ ). All goats, both domestic (*Capra hircus*) and wild (*C. ibex*, *C. falconeri*) have  $2n = 60$ , and karyotypes comprised entirely of acrocentric autosomes, a pattern consistent with the primitive bovid chromosome complement proposed by WURSTER and BENIRSCHKE<sup>7</sup>. *Ammotragus lervia* has a karyotype similar to  $2n = 58$  *Ovis*<sup>8</sup>. Within *Ovis*, diploid numbers vary; the karyotypes observed in *O. vignei* ( $2n = 58$ ), *O. ammon* ( $2n = 56$ ), and in *O.*

*musimon*, *O. orientalis*, *O. canadensis* and *O. dalli* ( $2n = 54$ ) were postulated to be derived from a series of centric fusions resulting in 1, 2, or 3 pairs of biarmed autosomes<sup>9</sup>.

A Giemsa-banding technique<sup>10</sup> was first utilized by us to evaluate chromosomal homologies of the biarmed autosomes of wild sheep<sup>11</sup>. More recently, these G-band

<sup>1</sup> G. G. SIMPSON, Bull. Am. Mus. Nat. Hist., 1945, 85.

<sup>2</sup> J. R. ELLERMAN and T. C. S. MORRISON-SCOTT, Checklist of Palearctic and Indian Mammals 1758 to 1946 (Brit. Mus. Nat. Hist., London 1951).

<sup>3</sup> V. GEIST, Mountain Sheep. A Study in Behavior and Evolution (University of Chicago Press, Chicago 1971).

<sup>4</sup> E. THENIUS and H. HOFER, Stammesgeschichte der Säugetiere (Springer Verlag, Berlin 1960).

<sup>5</sup> B. KURTÉN, Pleistocene Mammals of Europe (Aldine, Chicago 1968).

<sup>6</sup> S. PAYNE, The Prehistoric Society 2, 368 (1968).

<sup>7</sup> D. H. WURSTER and K. BENIRSCHKE, Chromosoma 25, 152 (1968).

<sup>8</sup> H. HECK, D. WURSTER and K. BENIRSCHKE, Z. Säugetierk. 33, 172 (1968).

<sup>9</sup> C. F. NADLER, K. V. KOROBITSINA, R. S. HOFFMANN and N. N. VORONTSOV, Z. Säugetierk. 38, 109 (1973).

<sup>10</sup> M. SEABRIGHT, Chromosoma 36, 204 (1972).

<sup>11</sup> C. F. NADLER, R. S. HOFFMANN and A. WOOLF, Experientia 29, 117 (1973).

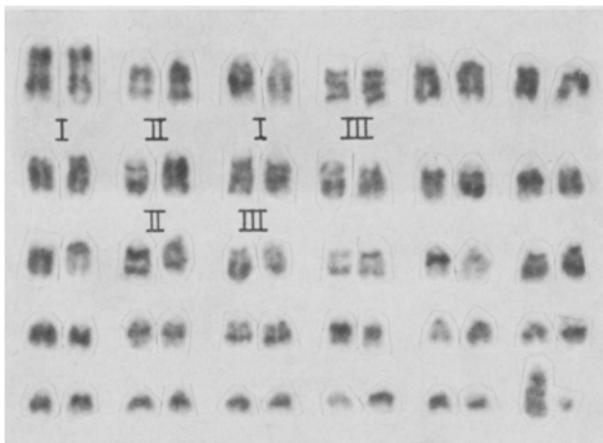


Fig. 1. Karyotype of a male *Capra aegagrus* ( $2n = 60$ ) from Iran. Chromosomes presumed homologous to biarmed pairs I, II, and III of  $2n = 54$  sheep are designated by corresponding Roman numerals.

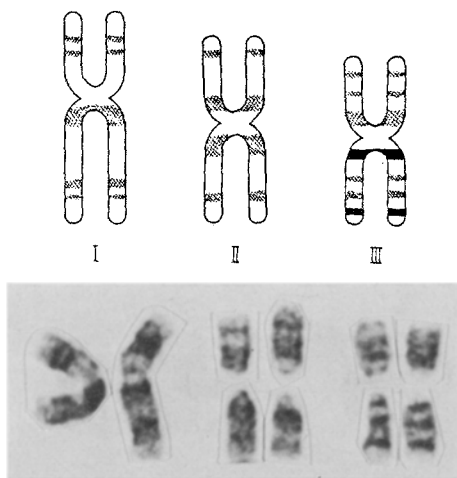


Fig. 2. Schematic representation of G-bands of the 3 biarmed autosomes from  $2n = 54$  Old and New World wild sheep (from NADLER et al.<sup>11</sup>) compared with homologous chromosome arms from *Ammotragus*.

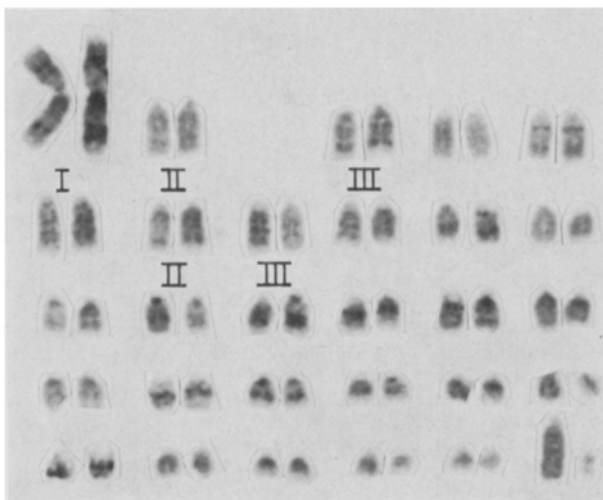


Fig. 3. Karyotype of a male *Ammotragus lervia* ( $2n = 58$ ). Roman numerals designate biarmed pair I and the acrocentrics presumed homologous to biarmed pairs II and III of  $2n = 54$  *Ovis*.

homologies have been extended to include all chromosomes of domestic goats and sheep (*O. aries*,  $2n = 54$ ); each of the 23 acrocentric autosomal pairs of the sheep was matched by an identical goat autosome, and the arms of the 3 biarmed autosomal pairs of sheep were identical with the remaining 6 acrocentrics of the goat<sup>12</sup>. These G-band homologies, together with meiotic pairings and G-band patterns in  $F_1$  and  $F_2$  hybrid sheep (*O. musimon*  $\times$  *O. canadensis*)<sup>11</sup>, confirm the Robertsonian relationship postulated among sheep, and suggest that  $2n = 58$  is the ancestral karyotype in *Ovis*.

The present report describes the G-band patterns of the wild goat, *Capra aegagrus*, *Ammotragus lervia*, and *Ovis vignei*; compares these patterns with those of domestic goat and sheep; and evaluates pathways of chromosomal evolution among these caprines.

**Materials and methods.** The following specimens were studied: 1. *Ammotragus lervia* Pallas, 1 male from unknown locality obtained from the Highland Park Zoo, Pittsburgh, Pennsylvania; 2. *Ovis vignei* Blyth, 1 male from northeastern Iran ( $37^\circ 20' N$ ;  $56^\circ 07' E$ ); 3. *Capra aegagrus* Erxleben, 1 male from northeastern Iran ( $37^\circ 20' N$ ;  $56^\circ 07' E$ ).

Chromosomes were analyzed from skin biopsies grown in tissue culture by Dr. T. C. Hsu, M. D. Anderson Hospital, Houston, Texas. G-band preparations were made by the trypsin-Giemsa staining method of SEABRIGHT<sup>10</sup>.

**Results.** *Capra aegagrus* displayed  $2n = 60$  and a karyotype comprised of 29 pairs of acrocentric autosomes, an acrocentric *X* and minute biarmed *Y* chromosome (Figure 1). Clearly recognizable by their G-bands were the 6 acrocentric chromosomes comparable to and presumably homologous with the 3 biarmed chromosomes of  $2n = 54$  wild sheep (pairs I, II, III; Figure 2)<sup>11</sup> and of domestic sheep (pairs 1/3, 2/8, 4/9; EVANS et al.<sup>12</sup>). *A. lervia* and *O. vignei* had a  $2n = 58$  and identical karyotypes containing 1 pair of biarmed and 27 pairs of acrocentric autosomes, a large acrocentric *X* and minute biarmed *Y* chromosome (Figures 3 and 4). G-band patterns of the biarmed chromosomes were identical in both species and were indistinguishable from the pattern described previously for the largest biarmed autosomal pair (pair I) of *Ovis musimon*, *O. orientalis*, *O. canadensis*, and *O. musimon*  $\times$  *O. canadensis*  $F_1$  and  $F_2$  hybrids (Figure 2)<sup>11</sup>. Among the acrocentric chromosomes of *A. lervia* were pairs with patterns resembling those seen in biarmed pairs II and III of  $2n = 54$  wild (Figure 2)<sup>11</sup> and domestic sheep<sup>12</sup>. G-band patterns of the acrocentric autosomes from *O. vignei* are not sufficiently clear to allow identification of their biarmed homologues (pair II, III). Patterns of the acrocentric autosomes and *X* chromosomes resemble those described by EVANS et al.<sup>12</sup> in domestic sheep and goats.

**Discussion.** Giemsa-banding techniques provide direct evidence for structural homologies between chromosomes in different species of caprines. The largest pair of biarmed chromosomes in *Ovis aries*, *O. musimon*, *O. orientalis* and *O. canadensis* is structurally homologous, not only among these species, but also with the single biarmed chromosome pair of *O. vignei* and with the single biarmed pair of *Ammotragus*. Finally, arms of the biarmed autosomes can be identified with acrocentric autosomes in the karyotype of *Capra*. These homologies support the contention that the  $2n = 60$ ,  $FN = 60$  karyotype still found in *Capra* is ancestral<sup>7</sup>, and that the  $2n = 58$ ,  $FN = 60$  karyotype of

<sup>12</sup> H. J. EVANS, R. A. BUCKLAND and A. T. SUMMER, *Chromosoma* 42, 383 (1973).

*Ammotragus* is derived from the ancestral caprine form by one centric fusion. Furthermore, the identity between *Ammotragus* and *Ovis vignei* karyotypes supports GEIST's<sup>3</sup> view that an *Ammotragus*-like form was directly ancestral to *Ovis*. Finally, the chromosomal homologies in the series of 1 to 3 biarmed autosomal pairs in *Ovis* lend further strength to the argument that *Ovis vignei* ( $2n = 58$ ) is descended from the ancestral *Ovis* population, and that  $2n = 54$  *Ovis* are the most recently evolved of wild sheep<sup>9,11</sup>.

The fossil record indicates that *Ovis* and *Capra* have been separated for more than a million years<sup>4,5</sup>. During that time, their chromosomes exhibited structural stability, evolutionary change consisting merely of whole-arm rearrangements. Morphological<sup>2</sup> and behavioral<sup>3</sup> differences between sheep and goats are thus due to the accumulation of gene differences. The cytogenetic evidence suggests there are two main lineages among surviving caprines. Starting from a hypothetical rupicaprine-type ancestor with a primitive  $2n = 60$ ,  $FN = 60$  karyotype, one lineage evolved through an intermediate,

aoudad-like form to the true sheep, with reductions in diploid number. In the true goat (*Capra*) lineage, morphological differentiation proceeded while the karyotype remained conservative; in contrast, the thar (*Hemitragus*) has remained morphologically close to the hypothetical rupicaprine ancestor<sup>3</sup> while its chromosome number has been reduced ( $2n = 48$ )<sup>7</sup>. The 5th member of the tribe Caprini, the bharal (*Pseudois nayaur*) has a reduced chromosome number ( $2n = 54$ )<sup>13</sup> but morphologically exhibits convergence toward true sheep<sup>2,3</sup>. G-bands in *Hemitragus* and *Pseudois* must be studied to confirm their chromosomal relationship to other caprines and it will be of interest to determine whether the biarmed chromosomes of *Pseudois* are homologous to those of  $2n = 54$  *Ovis*. If so, it would support the concept of convergent evolution at the chromosomal level<sup>9</sup>.

**ВЫВОДЫ.** Хромосомы и Г-полосы диких баранов, Африканских гривистых баранов, и безоаровых козлов изучали. *Capra aegagrus* из Ирана показало  $2n = 60$ , и кариотип содержит 29 пары акроцентрических аутосом. Шесть из этих аутосомов одинаковый с трёх пар двуплечных аутосом у диких баранов и домашних овец ( $2n = 54$ ). *Ammotragus levia* и *Ovis vignei* ( $2n = 58$ ) имели кариотипы и Г-полосы пар двуплечных аутосом неразличимый.

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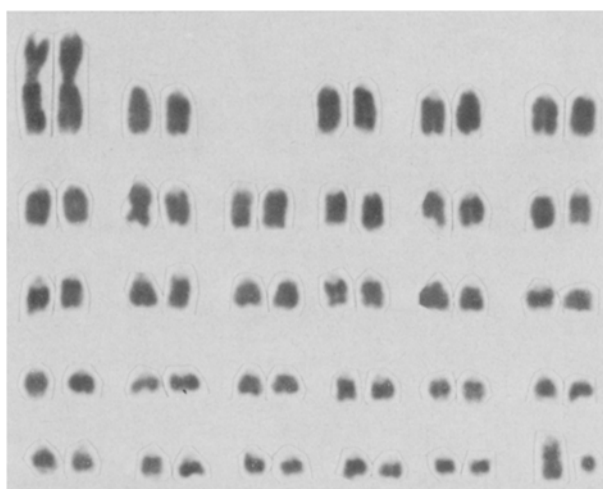


Fig. 4. Karyotype of a male *Ovis vignei* ( $2n = 58$ ). The biarmed autosomes conform to the pattern of pair I.

<sup>13</sup> W. L. HARD, Mammal. Chromos. Newsl. 10, 228 (1969).

<sup>14</sup> Supported by National Science Foundation Grants No. GB 32114X and 29131X, the Sprague Foundation, and a grant from the Trustees of the Rachelwood Wildlife Research Preserve. We thank Dr. T. C. Hsu for valuable suggestions, Mr. ARTHUR POPHAM for obtaining the specimens from Iran, and the Highland Park Zoo, Pittsburgh, Pennsylvania, for permission to biopsy their specimen.

## Effects of Abscissic Acid on Photosynthesis of Protoplasts from *Petunia hybrida*

Protoplasts from plants are suitable experimental objects for investigations in which substances are taken up by cells, since chemicals can reach the cell surface directly. Therefore, it is convenient to use them for experiments concerned with effects of phytohormones on metabolism. So far, some work on the application of auxins<sup>1-3</sup> has been described, and recently we have made some investigations on the influence of zeatin on photosynthesis and respiration of isolated mesophyll protoplasts from *Petunia* (KULL and HOFFMANN, in preparation).

Application of abscissic acid (ABA) leads to a decrease of photosynthetic rate in treated leaves, very likely due to stomatal closure caused by the phytohormone<sup>4-6</sup>. Some observations<sup>7</sup> suggest that mesophyll photosynthesis is not affected directly. Recently it was found that in illuminated and unilluminated dark grown *Avena* seedlings and in etio-chloroplasts of the same species, ABA reduced the levels of ribulosediphosphate carboxylase

activity<sup>8</sup>. We studied the effect of ABA on the photosynthesis of mesophyll protoplasts from *Petunia*. The influence of ABA on the respiration of these isolated protoplasts was briefly investigated in connection with our work on zeatin.

<sup>1</sup> D. W. GREGORY and E. C. COCKING, J. exp. Bot. 17, 68 (1966).

<sup>2</sup> J. B. POWER and E. C. COCKING, J. exp. Bot. 27, 64 (1970).

<sup>3</sup> M. H. BAYER, Plant Physiol. 57, 898 (1973).

<sup>4</sup> C. J. MITTELHEUSER and R. F. M. VAN STEVENINCK, Nature, Lond. 227, 281 (1969); Planta 97, 83 (1971).

<sup>5</sup> W. R. CUMMINS, H. KENDE and K. RASCHKE, Planta 99, 347 (1971).

<sup>6</sup> J. POSKUTA, R. ANTOSZEWSKI and M. FALTYNOWICZ, Photosynthetica 6, 370 (1972).

<sup>7</sup> R. J. JONES and T. A. MANSFIELD, Physiologia plant. 26, 321 (1972).

<sup>8</sup> F. A. M. WELLBURN, A. R. WELLBURN, J. L. STODDART and K. J. TREHARNE, Planta 171, 337 (1973).