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The Somatic Chromosomes of Some
North American Marmots (Sciuridae),
with Remarks on the Relationships of
Marmota browerii Hall and Gilmore

Robert L. Rausch*

Virginia R. Rausch[†]

*Arctic Health Research Center, rausch@u.washington.edu

[†]Arctic Health Research Center

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THE SOMATIC CHROMOSOMES OF SOME
NORTH AMERICAN MARMOTS (SCIURIDAE),
WITH REMARKS ON THE RELATIONSHIPS
OF *MARMOTA BROWERI* HALL AND GILMORE

by

R. L. RAUSCH and V. R. RAUSCH

Les auteurs définissent les caryotypes de deux espèces néarctiques de marmottes, *Marmota olympus* ($2n=40$) et *M. vancouverensis* ($2n=42$), et donnent des précisions sur les caryotypes de *M. flaviventris*, *M. monax ochracea* et *M. marmota*. Les six espèces de *Marmota* ($NF=66$) d'Amérique du Nord forment un groupe distinct des espèces d'Asie centrale ($NF=70$) dont le caryotype est connu. Les données caryologiques et les preuves zoogéographiques basées sur la répartition de deux espèces néarctiques de cestodes spécifiques de l'hôte démontrent que *M. broweri*, dans l'Alaska septentrional, est une relictte du pré-Würm. Elle semble avoir plus d'affinités avec le groupe nord américain de *caligata* qu'avec *M. camtschatica* du nord de la Sibérie. La présence sur *M. broweri* de la puce asiatique, *Oropsylla silantiewi*, n'est pas expliquée. Quelques caractéristiques écologiques et éthologiques de *M. broweri* sont décrites brièvement et comparées avec celles d'autres espèces. Les groupes familiaux de *M. broweri* hibernent dans un même terrier dont l'entrée est bouchée ; la copulation a lieu avant que les animaux sortent de leur abri hivernal, à la mi-mai ; ils se servent de leurs glandes faciales pour marquer leur territoire.

Recent contributions toward an understanding of the evolution and relationships of sciurids of the genus *Marmota* include those of Hoffmann and Nadler (1968), who provided a karyotype of *Marmota flaviventris* (Audubon and Bachman) and who based a revised concept of speciation within the genus on chromosomal characteristics and other taxonomic criteria ; of Vorontsov *et al.* (1969), who determined karyotypes of 3 Asian species and discussed comparative karyology of palaearctic and nearctic marmots as well as the possible isolating mechanisms involved in the speciation of Asian marmots ; and of Fernandez-Donoso *et al.* (1969), who determined the karyotype of *M. marmota* L. The chromosomes of 2 North American and 4 Asian species have not been described.

It is the purpose of this paper to define some chromosomal characteristics of the 2 North American species, *M. olympus* (Merriam) and *M. vancouverensis* Swarth, and to report both additional observations on the chromosomes of other species and information

about biological attributes of the north Alaskan *M. broweri* Hall and Gilmore.

MATERIALS AND METHODS

Somatic cells were studied from marmots of 5 species :

M. flaviventris (1 ♀), Kamloops, British Columbia, June, 1964 ; *M. marmota* (1 ♂, 1 ♀), born in the Zoologisches Garten, Basel, received November, 1965 ; *M. monax ochracea* Swarth (1 ♂), central Alaska (lat. 64°18' N., long. 146°20' W.), June, 1969 ; *M. monax preblorum* Howell (1 ♀), New Hampshire, June, 1967 ; *M. olympus* (1 ♂), Deer Park, Clallam County (Olympic Peninsula), Washington, August, 1965 ; *M. vancouverensis* (1 ♀), Mt. Washington, Vancouver Island, August, 1965.

Bone marrow for the cytological preparations was obtained from the sternum and ribs. The procedures were the same as outlined earlier (Rausch and Rausch, 1965). No attempt was made to obtain additional specimens of *M. vancouverensis*, which is considered to be an endangered species. Permission to collect additional specimens of *M. olympus* in the Olympic National Park was not granted. The arrangement of chromosomal pairs in the karyotypes is according to a subjective interpretation.

Some of the characteristics of *M. broweri* have been determined through studies carried on intermittently (by R. L. Rausch and F. H. Fay) for several years in the Brooks Range and through observation of a colony of captive animals for 6 years.

DESCRIPTION OF KARYOTYPES

M. olympus (Fig. 1).

The diploid number of chromosomes is 40, as reported earlier (Rausch and Rausch, 1965). The following autosomal pairs are present : 4 metacentric, of which one has a clearly median centromere ; 3 submetacentric ; 5 subtelocentric ; 7 acrocentric. The assumed X-chromosome is submetacentric ; the Y-chromosome appears to be subtelocentric.

M. vancouverensis (Fig. 2).

Diploid number : 42, made up of 3 pairs of metacentric, 4 submetacentric, 5 subtelocentric, and 9 acrocentric. The X-chromosomes probably are a submetacentric pair.

M. monax ochracea (Fig. 3).

The karyotype of *M. monax* was described by Couser *et al.* (1963) from animals collected in the northeastern United States. The karyotype presented here was determined from a specimen obtained near the northwestern limit of the range of the species.

and agrees with that reported by Couser *et al.* In our material, the Y-chromosome appears to be subtelocentric. We also compared the chromosomes of a single female from New Hampshire, which is of the same subspecies studied by Couser *et al.*

M. flaviventris (Fig. 4).

The diploid number of 42 chromosomes, determined from a female marmot from British Columbia (Rausch and Rausch, 1965), was confirmed by Hoffmann and Nadler (1968), who described the karyotype of a male from Colorado. The karyotype of the female contains 4 pairs of metacentric (including what we consider to be the X-chromosome, in agreement with Hoffmann and Nadler), 3 submetacentric, 5 subtelocentric, 9 acrocentric.

M. marmota (Fig. 5).

Our findings in 2 specimens of *M. marmota* agree closely with those reported by Fernandez-Donoso *et al.* (1969). The diploid number is 38, and autosomes in the karyotype include 4 metacentric, 5 submetacentric, 5 subtelocentric, and 4 acrocentric pairs. Two pairs (1 questionably) classed as acrocentric by Fernandez-Donoso *et al.* appear to us to be subtelocentric. The X-chromosome we also identified as a medium-sized submetacentric and the Y-chromosome as subtelocentric.

COMPARISON OF KARYOTYPES

The karyotypes of 10 species of *Marmota* have been described, and the diploid number of another was reported by Vorontsov *et al.* (1969). Some characteristics of the chromosomes of marmots are summarized in Figure 6.

NORTH AMERICAN SPECIES

In karyotype, *M. caligata* (Eschscholtz) and *M. flaviventris*, as noted by Hoffmann and Nadler (1968), differ in the form of the X-chromosome, which is submetacentric in *M. caligata* and metacentric in *M. flaviventris*. The karyotype of *M. vancouverensis* may be most similar to *M. caligata* (the Y-chromosome of *M. vancouverensis* is unknown). The karyotype of *M. olympus* suggests an affinity with these 3 species. It differs in having an additional pair of metacentric autosomes, but with a corresponding, perhaps, lack of 2 pairs of acrocentric autosomes. The chromosome identified as X is submetacentric, like that of *M. caligata*. *M. olympus*

was placed in the *caligata*-group on morphological grounds by Howell (1915).

M. monax and *M. broweri* have distinctive chromosomal characteristics that separate them from members of the *caligata*-group as well as from one another. Both have a reduced number of autosomes.

The fundamental number (NF — number of major chromosomal arms; Matthey, 1945 *et seqq.*) of the 6 species of North American marmots is 66. Hoffmann and Nadler (1968) determined the number of major autosomal arms to be 62 for *M. broweri*, *M. caligata*, *M. flaviventris*, and *M. monax*. *M. olympus* and *M. vancouverensis* also have 62 major autosomal arms.

EURASIAN SPECIES

Besides *M. marmota* and *M. himalayana* (Hodgson), 6 species [*M. baibacina* (Brandt), *M. bobak* (Müller), *M. camtschatica* (Pallas), *M. caudata* (Jacquemont), *M. menzbieri* (Kashkarov), and *M. sibirica* (Radde)] were recognized by Bobrinskii *et al.* (1944), Ognev (1947), Vinogradov and Gromov (1952), and Gromov *et al.* (1965). Bibikov (1967) accepted only 6 Eurasian species as valid, considering *M. baibacina* and *M. sibirica* to be subspecies of *M. bobak*.

Vorontsov *et al.* (1969) determined that *M. baibacina*, *M. caudata*, *M. menzbieri*, and *M. sibirica* each has a diploid number of 38 chromosomes. They concluded that the karyotypes of *M. baibacina* and *M. caudata* are indistinguishable, and that the karyotype of *M. menzbieri* closely resembled that of the latter 2, but their material was considered inadequate to confirm that it is identical. Nonetheless, other taxonomic criteria seem to indicate that these members of the « *bobak*-group » represent distinct species (Galkina, 1962). As pointed out by Hsu and Mead (1969), all taxonomic characters, of which the karyotype is only one, must be considered in attempts to distinguish species.

The karyotype presented here of *M. marmota* ($2n = 38$) differs from those of the middle Asian marmots in having 1 less pair of submetacentric autosomes and 1 more pair of acrocentric autosomes.

Vorontsov *et al.* (1969) determined that the NF of *M. baibacina*, *M. caudata*, *M. menzbieri*, and *M. sibirica* is 70. For *M. marmota*, Fernandez-Donoso *et al.* (1969) suggested that the number of major autosomal arms is 60, but pointed out that their pair No. 18 may

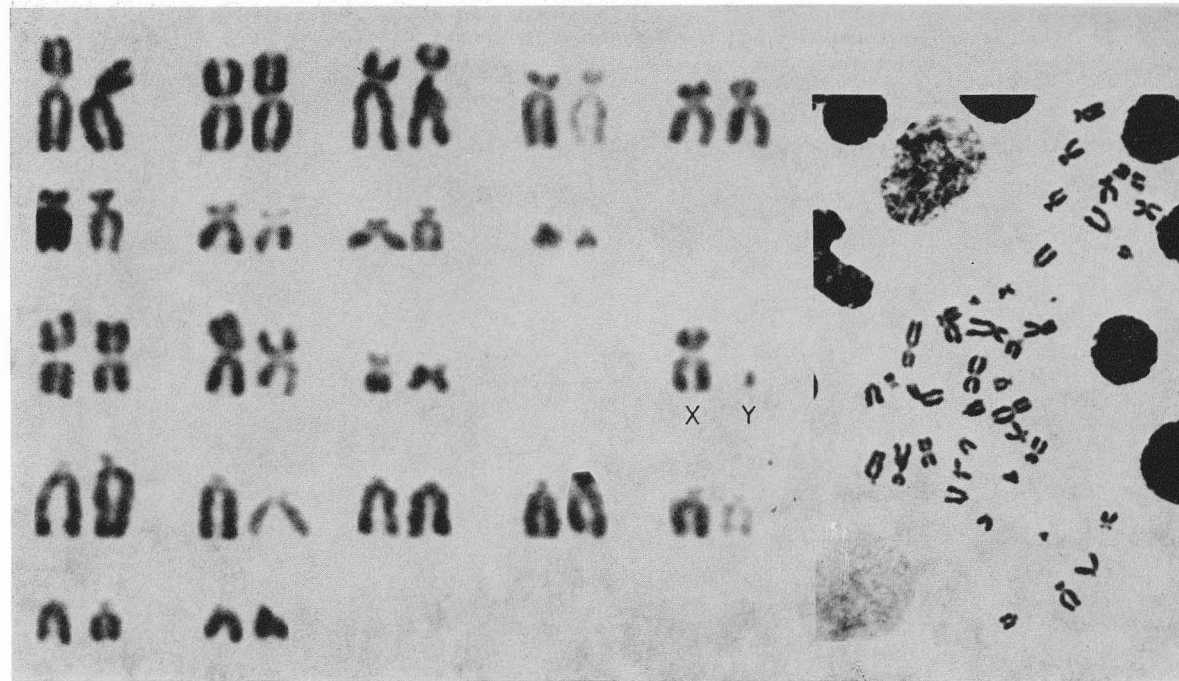


Fig. 1. — Karyotype of male *M. olympus*. In this and following figures, the chromosomes were arranged from those shown in insets.

MAMMALIA, 1971

PL. V

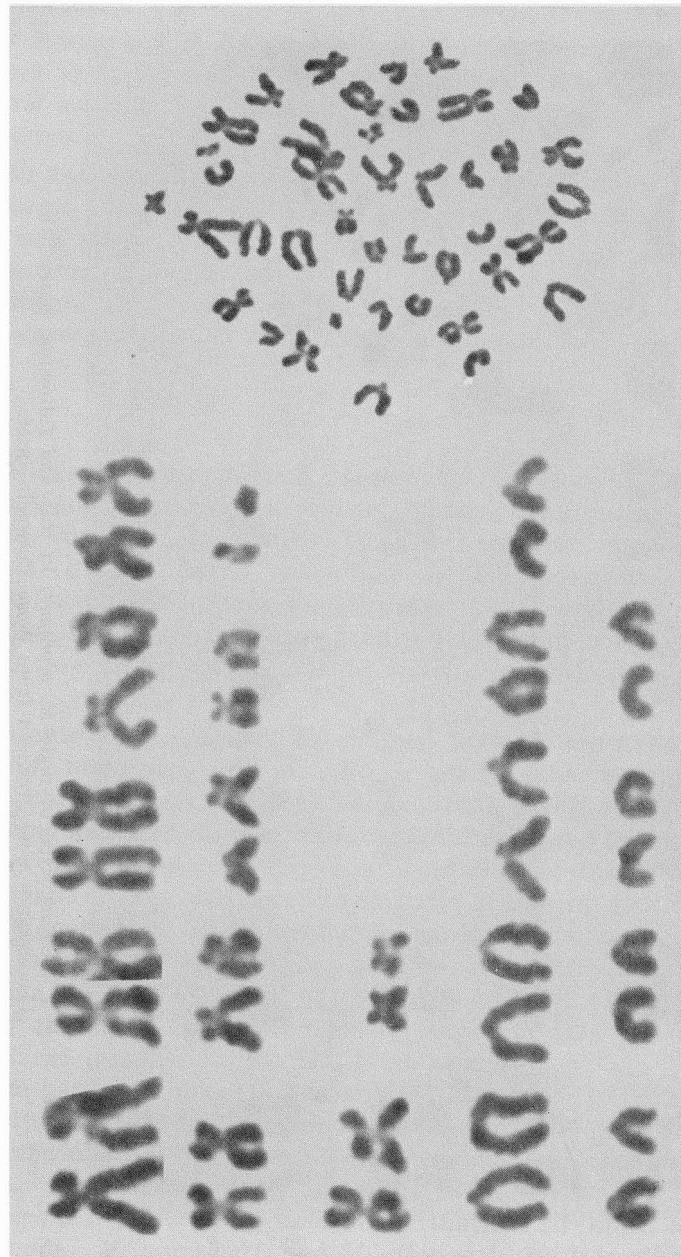


Fig. 2. --- Karyotype of female *M. vancouverensis*. The X-chromosomes may be the sixth pair of the first group.

MAMMALIA, 1971

PL. VI

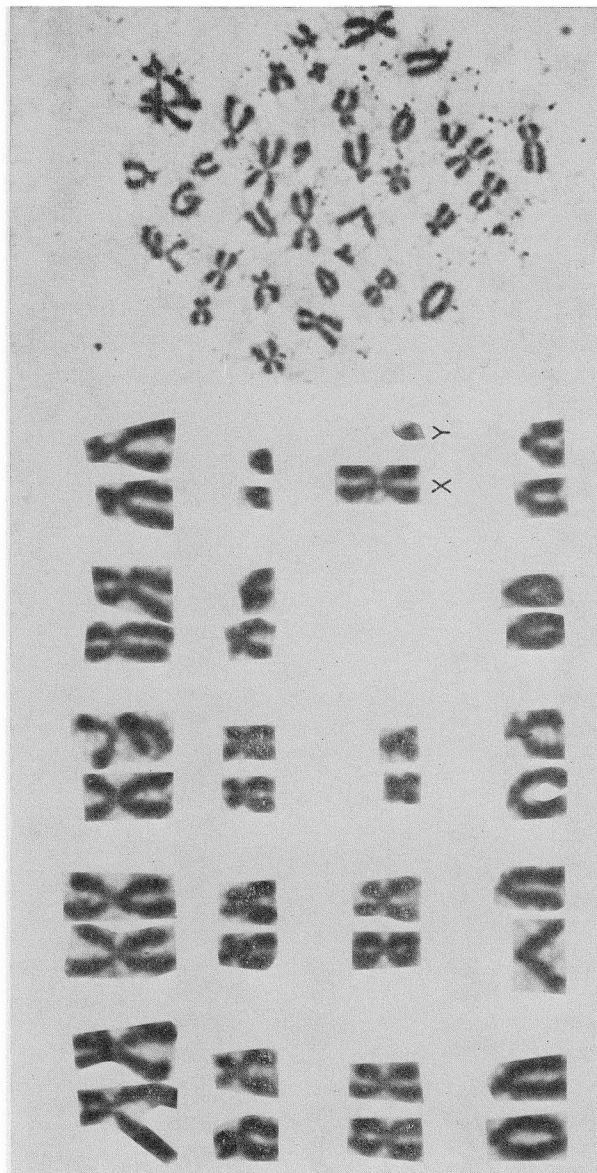


Fig. 3. — Karyotype of male *M. monax ochracea*, from the northwestern limits of the range of the species.

MAMMALIA, 1971

PL. VII

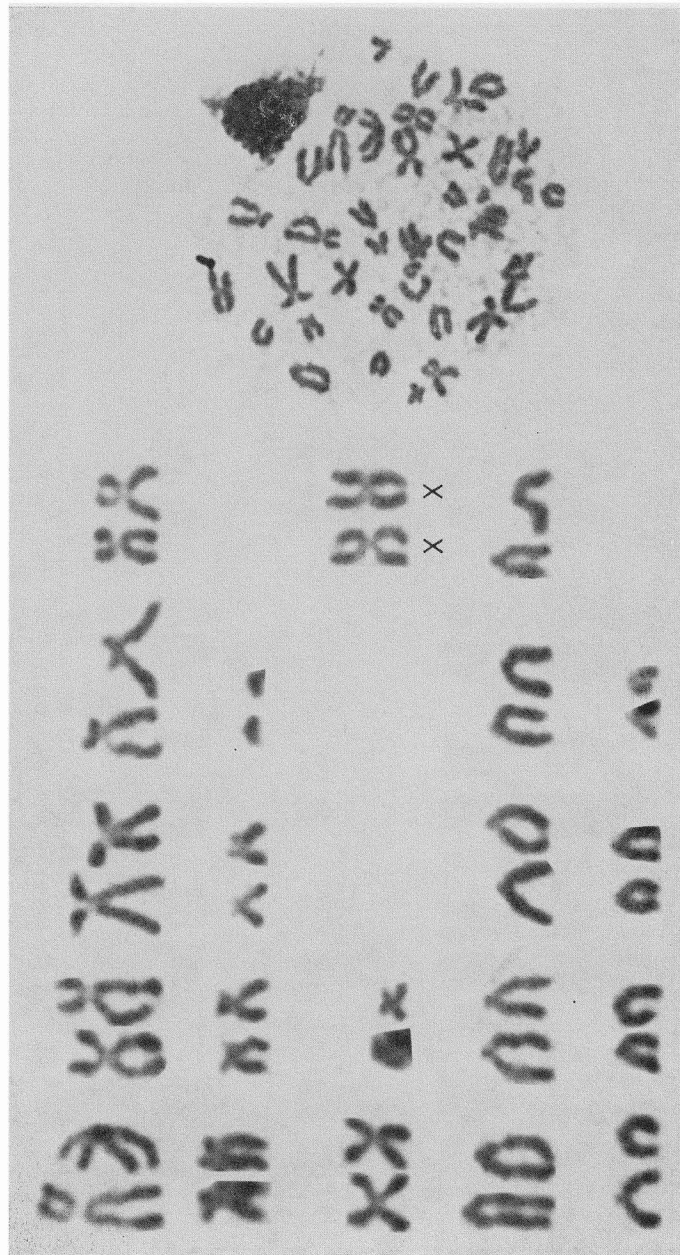


Fig. 4. — Karyotype of female *M. flaviventris*.

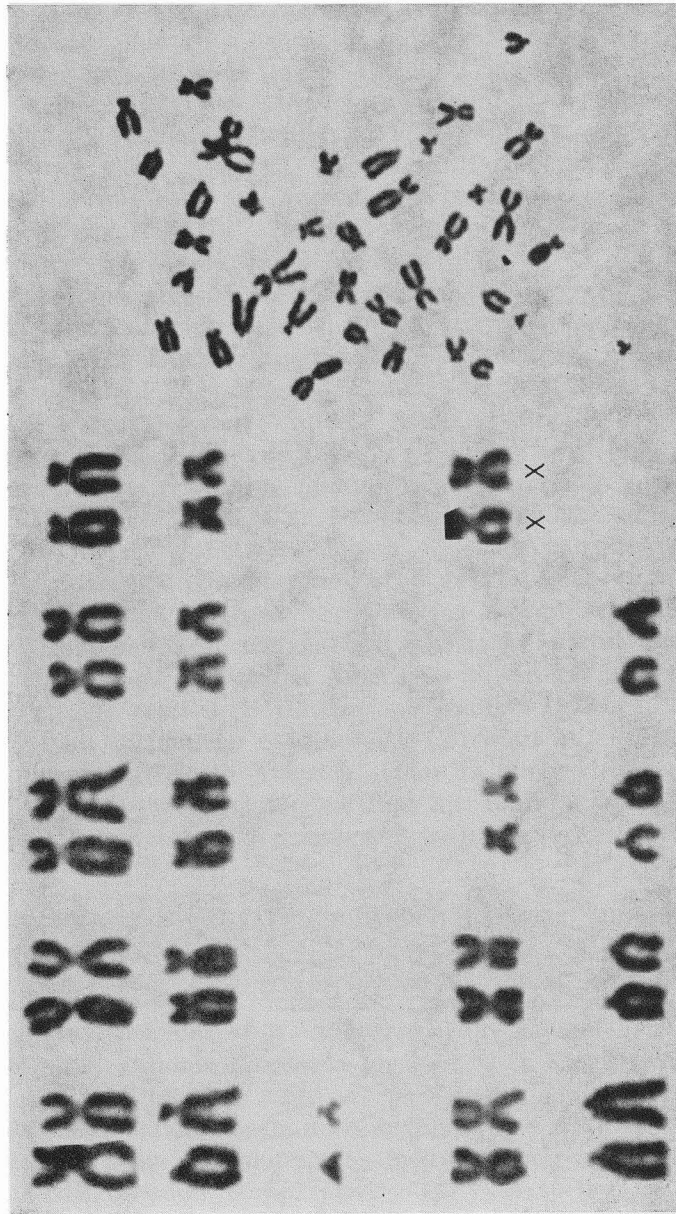


Fig. 5. — Karyotype of female *M. marmota*.

Species	Metacentric (Median & Median Region)	Submetacentric	Subtelocentric	Acrocentric (Terminal Region)	X Y	2n NF
<i>caligata</i>					X ₁	42 66
<i>vancouverensis</i>						42 66
<i>flaviventris</i>					X ₁	42 66
<i>olympus</i>					X ₁	40 66
<i>monax</i>					X ₁	38 66
<i>broweri</i>					X ₁	36 66
<i>marmota</i>					X ₁	38 ⁶⁴ ₆₆ 68
<i>baibacina</i>					X ₁	38 70
<i>caudata</i>					X ₁	38 70
<i>menzbieri</i>					X ₁	38 70

MAMMALIA, 1971

Pl. IX

Fig. 6. — Comparison of known karyotypes of *Marmota* spp. based upon work of the authors and upon the publication of Vorontsov *et al.* (1969). The four chromosomal sets displayed were arranged by inspection.

not be acrocentric, as classified. We suggest an NF (following Matthey, 1945) of 68 for *M. marmota*, with only 4 pairs of acrocentric autosomes, and with 64 major autosomal arms. On the other hand, if the combination $2n = 38, 28 \text{ V}$ [6th pair of the submeta-subtelocentric group (see Fig. 5) acrocentric] or $2n = 38, 26 \text{ V}$ [according to Fernandez-Donoso *et al.* (1969)] is valid, then the NF is either 66 or 64. The species of *Marmota* for which the fundamental numbers are known thus comprise 3 groups : 1) 6 in North America, $\text{NF} = 66$; 2) 4 in middle Asia, $\text{NF} = 70$; 3) the European *M. marmota*, $\text{NF} = 64-68$.

M. baibacina and *M. sibirica* are sometimes grouped in relationship with *M. bobak*, from which Bibikov (1967) considers them to be only subspecifically distinct. *M. bobak* may be expected also to have a diploid chromosomal number of 38 and an NF of 70. Two of the most distinctive middle Asian species, *M. caudata* and *M. menzbieri*, are karyotypically very similar to members of the *bobak*-group. The remaining middle Asian species, *M. himalayana*, may also be found to have an NF of 70. Ellerman and Morrison-Scott (1951), basing their conclusion on other morphological criteria, considered *M. himalayana* to be a subspecies of *M. bobak*. The karyotype has not been described for *M. camtschatica*, which is widely distributed in northeastern Siberia in habitat ecologically similar to that of the North American *M. broweri*, to which it may be closely related (Hoffmann and Nadler, 1968).

Hoffmann and Nadler considered *M. broweri* to be a late Pleistocene invader of North America. There is fairly strong evidence, also, to support the opposite view that this marmot is a pre-Würm relict which had a common ancestor with the *caligata*-group.

COMPARATIVE CHARACTERISTICS OF *M. BROWERI*

DENNING HABITS

Individual colonies of *M. broweri* occupy several dens in summer, but the animals hibernate together in a single winter den, which for each colony is relatively permanent, some in the central Brooks Range having been used regularly for at least 20 years. The winter dens are characteristically on exposed ridges that become free of snow comparatively early in spring. In autumn, after the animals enter for hibernation, the entrance to the den is plugged for a short distance from the surface with a mixture of soil, small stones, fragments of vegetation, and feces ; the animals emerge in spring, during the first 2 weeks of May, only after the

obstruction has thawed sufficiently to permit its removal. Since hibernation begins in early September, the marmots are active for about 4 months of the year.

Colonies of *M. camtschatica* also have a single winter den, similarly situated in relation to topography, in which the animals hibernate together (Kapitonov, 1960 *a*). Other Eurasian marmots known to hibernate in groups include *M. marmota*, *M. caudata*, and members of the *bobak*-group (Schocher, 1946 ; Bibikov, 1967, p. 68). Among the North American species, *M. monax* seems to hibernate singly (Grizzell, 1955 ; de Vos and Gillespie, 1960) ; whether or not this is the case with members of the *caligata*-group evidently has not been determined.

The winter den of *M. broweri* has apparently a single burrow to the surface, plugged at the entrance, the remainder leading to the nest unobstructed. In the winter den of *M. camtschatica*, several burrows lead to the surface. All but the last of the openings are plugged from the outside, beginning at ground level ; in the last, the plug usually extends from 30 to 60 cm inward (Kapitonov, 1960 *b* ; Bibikov, 1967, p. 67). Besides *M. broweri* and *M. camtschatica*, marmots of other species also fill in their burrows in autumn, but usually at greater depths, e. g., *M. marmota* (Schocher, 1946) and, as first observed by Radde (1862, p. 163), *M. bobak*. The arrangement of the plugs differs among the dens of members of the *bobak*-group (Bibikov, 1967, p. 67). In North America, *M. monax* plugs the burrows leading to the nest (Grizzell, 1955). Evidently nothing is known about the structure of winter dens of members of the *caligata*-group.

MARKING OF TERRITORY

M. broweri marks its territory by means of a secretion produced by face-glands, by rubbing the sides of the face on rocks around the den and along regularly used trails (R. L. Rausch and F. H. Fay, unpublished data). Such marking by *M. marmota* has been described in detail by Koenig (1957), but evidently has not been reported for any other species of *Marmota*. Bibikov (1967, p. 107) stated that the presence of face-glands in Asian marmots suggests that they similarly mark their territories, but that such behavior has been little investigated.

The face-glands of *M. marmota* were first reported by Tiedemann (1816) and were described in greater detail by Schaffer (1940, p. 281). Such glands are present in all North American species of

Marmota (R. L. Rausch and J. G. Bridgens, unpublished data). They are clearly functional in *M. caligata*; the limited material from the other members of the *caligata*-group was obtained late in the summer, when the glands were quiescent. In *M. monax*, also, circumstantial evidence indicates that the glands are used for marking territory. The glands were enlarged and prominent, containing a considerable amount of aromatic fluid, in a large male *M. monax* collected by one of us (RLR) in central Ohio on 28 June 1968. The hair of the face was worn away bilaterally over the glandular areas, and the presence of embedded soil among the glands indicated that the animal had been rubbing the sides of his face on hard surfaces.

The glands of similar structure, present bilaterally in the lower lips of the North American marmots, may also be involved in the marking of territory. The anal glands seem to be used only under conditions of stress and have no relationship to territoriality. These findings will be discussed in detail elsewhere.

BREEDING

In *M. broweri*, breeding evidently takes place before the animals are able to leave the winter den. On 6 and 7 May 1965, R. L. Rausch and F. H. Fay removed the frozen plug, 43 cm long, from a winter den in the Ukukkminilagat Valley, west of Chandler Lake, central Brooks Range. A trap set in the burrow captured an adult female early on 9 May. The uterus contained 4 early-stage embryos, which produced enlargements about 10 mm in diameter in the uterine horns. Breeding probably had occurred in late April. The stomach and intestine of this animal were empty and much contracted, indicating that it had not consumed food since becoming active.

M. camtschatica also breeds in the winter den, and the young are born 1 to 2 weeks after the adult marmots emerge in spring (Kapitonov, 1960 a). The middle Asian marmots apparently breed in the den (Bibikov, 1967, p. 132). *M. marmota* breeds after emergence (Müller-Using, 1957; Zelenka, 1965), as do *M. monax* and *M. flaviventris* (Grizzell, 1955; de Vos and Gillespie, 1960; Snyder and Christian, 1960; Nee, 1969). Observations on the breeding of other members of the *caligata*-group have not been reported.

M. camtschatica probably becomes sexually mature at an age of 3 years (Kapitonov, 1963). Observations on captive animals that had hibernated annually indicate that this is true also for *M. broweri*.

PARASITES

Mapping the occurrence of well known, highly host-specific parasites of marmots may provide zoogeographic indications of the distributional history of these mammals. Records of parasites from marmots, with particular reference to *M. marmota*, have been summarized by Hörning (1969).

Endoparasites (Cestoda).

Several species of cestodes of the family Anoplocephalidae are host-specific parasites of marmots, which become infected by ingesting, while feeding, the free-living mites that evidently serve as the intermediate host of these cestodes. Cestodes of 2 species are known only from North American marmots. *Diandrya composita* Darrah, 1930, described from *M. flaviventris*, has been recorded from all North American marmots except *M. monax* (R. L. Rausch, unpublished data). In Alaska, it is common in both *M. caligata* [49 (72 %) infected of 68 animals] and *M. broweri* [13 (42 %) infected of 31]. *D. composita* occurs commonly in *M. caligata* in the Yukon Territory, Canada (Ogilvie Mountains, at lat. 64°33' N., long. 138°15' W.); farther south, we found it in a specimen of *M. caligata* from Mt. Rainier, Washington, in 5 of 8 *M. olympus*, and in the single specimen of *M. vancouverensis* examined. The second species, *Catenotaenia reggiae* Rausch, 1951, was found in 15 (48 %) of 31 *M. broweri* and in *M. caligata* from Mt. Rainier. Since cestodes are lost by the marmots during hibernation, rates of infection in both *M. caligata* and *M. broweri* would be much higher if animals collected in spring were excluded.

Cestodes of 2 additional anoplocephaline genera, *Ctenotaenia* Railliet, 1893, and *Paranoplocephala* Lühe, 1910, occur in Eurasian marmots. *C. marmotae* (Frölich, 1802) [syn. *Cittotaenia marmotae* (Frölich, 1802)] is a common parasite of *M. marmota* and has been recorded from members of the *bobak*-group. *C. asiatica* Tokobaev and Erkulov, 1966, was described from *M. caudata* in Kirgizia. [Since the description was based upon small, immature specimens (Tokobaev and Erkulov, 1966), the taxonomic status of this species is uncertain.] *Paranoplocephala transversaria* (Krabbe, 1879) has been reported from *M. marmota*, *M. caudata*, *M. menzbieri*, and from members of the *bobak*-group. *P. ryjikovi* Spasskii, 1950, was described from *M. baibacina* and *Marmota* sp. in middle Asia.

The diversity of the cestodes in Eurasian and North American marmots indicates that the respective species evolved with their hosts after the ancestral form of *Marmota* reached what is now Eurasia during the late Pliocene (Gromov *et al.*, 1965, p. 404).

Ectoparasites (Siphonaptera).

The species of fleas regarded by Holland (1963) as Amphiberinian derivatives included none adapted to marmots. The common fleas of the *caligata*-group belong to the nearctic genus *Thrassis* Jordan. *Oropsylla arctomys* (Baker), a nearctic species, is found on *M. monax* throughout its range. Numerous species of fleas have been recorded from Eurasian marmots (Hörning, 1969). Those considered by Ioff and Skalon (1954) to be specific parasites of Asian marmots are *Oropsylla silantiewi* Wagner, *Ceratophyllus lebedewi* Wagner, *C. menzbieri* Ioff, and *Rhadinopsylla ventricosa* Ioff and Tiflov. Of these, *O. silantiewi* occurs on *M. camtschatica* (Kapitonov, 1963). *M. marmota* does not appear to have a host-specific flea (Hörning, 1969).

The host-specific flea of *M. caligata* in Alaska is *Thrassis pristinus* Stark, which we have recorded only from animals collected on the Kenai Peninsula. There also, at Homer, we obtained on *M. caligata* a single specimen of *Dasyipsyllus stejnegeri* (Jordan), a rarely found parasite of birds (G. P. Holland, personal communication). One specimen of *M. monax* from central Alaska was infested by *Oropsylla arctomys*. Fleas are relatively uncommon on *M. broweri*, and the first was collected at Peters Lake in the eastern Brooks Range on 13 June 1963 by F. H. Fay and R. L. Rausch. These, identified by Dr. G. P. Holland, represented the first North American record of *Oropsylla silantiewi*. Subsequently, this flea has been collected in small numbers from *M. broweri* in the central Brooks Range (Chandler Lake and Ukukkminilagat Valley). The occurrence of *O. silantiewi* on *M. broweri* supports the hypothesis that this marmot is closely related to *M. camtschatica*, as suggested by Hoffmann and Nadler (1968).

DISCUSSION

Without the advantage of knowledge of the karyotypes of any of the Eurasian species, Hoffmann and Nadler (1968) based their interpretation of speciation in the genus *Marmota* upon the hypothesis that the primitive marmot of Pliocene time had 38 diploid chromosomes and probably resembled *M. monax* and *M. marmota*.

morphologically. Accordingly, *M. monax* would have retained the « primitive » number of chromosomes ; evolution in the *bobak*-group would have led by means of centric fusion to a diploid number of 36 ; and, as a result of centric fission, members of the *caligata*-group would have diploid numbers of 40 and 42 chromosomes. Alternatively, Hoffmann and Nadler suggested that the ancestral form had a diploid number of 40, in which case the primitive number would have been retained by *M. olympus*, and evolution of the other species would again have involved Robertsonian rearrangements. In either case, *M. broweri*, with a diploid number of 36, was considered to be a late Pleistocene invader from Eurasia. They did not take into account *M. menzbieri*, *M. caudata*, and *M. himalayana*.

Vorontsov *et al.* (1969), not having seen the paper by Hoffmann and Nadler (1968), considered the karyotype of *M. caligata* to be ancestral and that of *M. monax* to be significantly more specialized. Based upon the hypothesis that the prevalence of meta- and submetacentric chromosomes is an indication of karyotypic evolution, they considered *M. broweri* to be the most recently differentiated of the North American species of *Marmota*. They considered the karyotype of *M. monax* to be intermediate between those of *M. caligata* and *M. broweri*, and suggested that the possibility of the derivation of *M. broweri* from *M. monax* during post-glacial time could not be excluded.

Vorontsov *et al.* recognized certain similarities between the karyotype of *M. broweri* and those of *M. menzbieri*, *M. caudata*, and *M. baibacina* (predominance of meta- and submetacentric elements ; 3 pairs of acrocentric chromosomes), but also pointed out that the North American species lack the equivalent of their submetacentric pair VIII (Vorontsov *et al.*, 1969, fig. 11). Because of this, they expressed reservations about the assumption that *M. broweri* is closely related to any of the Eurasian species. (This pair is absent also in *M. olympus*, *M. vancouverensis*, and *M. flaviventris* ; see Fig. 6). They concluded that the essential diversity between the karyotypes of the North American and Eurasian marmots is indicative of their long separation, and that the similarity of the karyotypes of the middle Asian marmots is indicative of a relatively recent differentiation of these species. They further concluded that the diversity of the karyotypes of North American marmots is evidently correlated with the greater age of these species and (p. 332) « ...with the sympatric distribution of the majority of the species of nearctic marmots. » In the

latter conclusion, they were apparently misled by inaccuracies in maps showing the distribution of North American marmots and by the failure of such maps to take into account ecological segregation.

Maps in Hall and Kelson (1959) show contiguous ranges of *M. caligata* and *M. broweri*. This interpretation seems to have been based largely upon two marginal records for *M. caligata*, one on the Seward Peninsula [« ...in the hills back of Nome. » (Bailey and Hendee, 1926, p. 20)], and one at Fort Yukon (Allen, 1877, p. 925). After having worked for several years on the Seward Peninsula, where he made a survey of the indigenous mammals and their distribution, Mr. John J. Burns, Alaska Department of Fish and Game, has found no evidence of the occurrence of marmots in this region (personal communication). Bailey and Hendee evidently obtained no specimens and based their record on information provided orally by local residents. Allen's description of the marmot obtained at Fort Yukon clearly involved *M. broweri* and not *M. caligata* (« ...the hinder part of the back spotted with black and dark chestnut... the whole upper surface of head is black, mixed slightly with gray; the nose and edge of the chin are also black. »). Since there is no suitable habitat for marmots in the vicinity of Fort Yukon, and since there has long been an interchange between the Indians living in the vicinity of what is now Arctic Village and those at Fort Yukon, we believe that the specimen referred to by Allen was brought to Fort Yukon from the Brooks Range. *M. broweri* occurs commonly in the vicinity of Arctic Village (Rausch, 1953).

M. caligata is restricted to alpine habitat throughout most of its range in Alaska. On the lower Kenai Peninsula and along the coast south at least to the mouth of the Copper River it is found also at sea level. No other species of marmot occurs in that region. *M. monax* occupies relatively arid lowlands in east-central Alaska, where it is found in small numbers in predominantly loess soils along river valleys. Locally, along tributaries of the 40-Mile River in eastern Alaska, *M. caligata* occupies talus down to altitudes where *M. monax* occurs in the same valleys. However, the two species there also appear to be ecologically segregated.

The map published by Rausch (1953) requires modification in that the range of *M. broweri* extends farther to the west in the Brooks Range [Pruitt, 1966, p. 525 (designated *M. caligata*)]. The eastern distributional limits of *M. broweri* have not been accurately determined. This species may occur as far east as the

Richardson Mountains west of the Mackenzie River (Porsild, 1945). With the possible exception of this region, the ranges of *M. broweri* and *M. caligata* are disjunct.

From the evidence now available, we consider *M. broweri* to be probably a relict North American species which became established in the Brooks Range during pre-Würm time, rather than a late Pleistocene invader of middle Asian derivation or, as suggested by Rausch and Rausch (1965), a component of the late Pleistocene Amphiberingian fauna. Gromov *et al.* (1965, p. 404) believed that marmots were not involved in the faunal interchanges across the Amphiberingian region during late Pleistocene time, as was for example the long-tailed suslik, *Citellus parryi* (Richardson). Besides karyologic evidence for the distinctiveness of North American and Eurasian marmots (excluding *M. camtschatica*), the diverse cestode-faunas are indicative of a long period of separation of the two groups. In contrast, the same species of cestode occurs in the long-tailed suslik on both sides of Bering Strait (Rausch, 1954 ; Ovsukova, 1966).

The ecological and ethological characteristics shared by *M. broweri* with Eurasian species of *Marmota* other than *M. camtschatica* may also be found in members of the *caligata*-group. Marmots of all species probably mark their territories by means of the face-glands, but this behavior is perhaps most strongly expressed in *M. marmota* and *M. broweri*. Such behavior, so obvious in *M. broweri*, has not been observed in *M. camtschatica*. The ethological and ecological similarities between *M. broweri* and *M. camtschatica* appear to be no greater than those shared by each of these with other species of *Marmota*. The breeding of *M. broweri* and *M. camtschatica* before emergence from the winter den is probably an adaptation to the arctic environment and the consequent brevity of the annual period of activity. Among other species, only *M. sibirica* may inhabit regions of permanently frozen ground (Bibikov, 1967, p. 78).

The occurrence in the Amphiberingian region during pre-Würm time of a common ancestor of *M. broweri* and *M. camtschatica* could account for the presence of the palaearctic flea, *Oropsylla silantiewi*, on *M. broweri*. However, *M. broweri* and *M. camtschatica* would then be expected to share the same species of cestodes. No cestodes were found in 116 specimens of *M. camtschatica* examined by Kapitonov (1963), while the two species of cestodes occurring commonly in *M. broweri* are found also in members of the *caligata*-group. At least three alternative hypotheses might be

considered to account for the recognized parasite-host assemblages : 1) the nearctic species of cestodes may yet be found in *M. camtschatica*, although this seems improbable ; 2) such cestodes became established in *M. broweri* through post-glacial contact with *M. caligata* ; 3) *M. broweri* is a derivative of the *caligata*-group, and not closely related to *M. camtschatica*.

One species of cestode, *Diandrya composita*, found commonly in *M. broweri*, has been recorded from *M. caligata* in Alaska and the Yukon Territory as well as from all members of the *caligata*-group at lower latitudes ; a second, *Catenotaenia reggiae*, is also common in *M. broweri*, but elsewhere has been recorded only from *M. caligata* in the Cascade Mountains, far to the south. *M. caligata*, a post-glacial invader of Alaska, evidently has at present its most extensive post-glacial range at high latitudes ; its range and that of *M. broweri* appear not to be contiguous. Moreover, if the cestodes had been transferred from *M. caligata* to *M. broweri* during post-glacial time, transfer of the nearctic flea, *Thrassis pristinus*, typically found on *M. caligata*, presumably also would have occurred. To postulate a derivation of *M. broweri* from an ancestor of the *caligata*-group would explain the composition of its cestode-fauna.

Both the karyologic findings and the zoogeographic implications of the occurrence of the two species of cestodes indicate that the affinities of *M. broweri* are with the North American marmots, rather than with *M. camtschatica*. The determination on karyologic grounds that *M. camtschatica* is more closely related to the North American marmots than to those in middle Asia would not necessarily indicate a close relationship with *M. broweri*. *M. camtschatica* is perhaps the least divergent of the Eurasian species of *Marmota*, but nevertheless its precursor must have become established in what is now northeastern Siberia before the host-specific cestodes arose in an ancestral marmot of the *caligata*-group.

Our attempts to explain the presence of the Asian flea on *M. broweri* by means of a hypothesis that is compatible with the other, more cogent evidence for the affinities of this marmot have been unsuccessful. Unlike cestodes, ectoparasites such as fleas may be transferred to and transported by animals other than the usual host. In Tian'-Shan', Shvarts and Lavrentev (1961) found *O. silantiewi* to be common on marmots and recorded it also from the rodents *Microtus gregalis* (Pallas) and *Ellobius talpinus* (Pallas). Transfer of fleas from rodents to their predators has been frequently reported. A wolverine, *Gulo gulo* L., collected by Mr. J. E.

Hemming of this laboratory on the Kenai Peninsula, was infested by *Thrassis pristinus* and contained in its stomach the remains of a marmot, *M. caligata*. Fleas such as *O. silantiewi* might also be occasionally transported by birds. This flea was found once by Bibikov and Bibikova (1955) in their study of fleas associated with wheatears, *Oenanthe isabellina* (Temm.), and their nests in the mountains of central Asia, and conversely, two species of fleas from this bird were found on marmots. They concluded, however, that such birds have little importance in the dispersal of fleas specific for rodents. It is of interest that another species of wheatear, *Oenanthe oenanthe* (L.), which occupies the same habitat as *M. broweri* in the Brooks Range, migrates between northern Alaska and northeastern Siberia. The possibility that *O. silantiewi* was introduced incidentally into North America cannot be excluded at the present time.

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SUMMARY

Karyotypes are defined for 2 nearctic species of marmots, *Marmota olympus* ($2n = 40$) and *M. vancouverensis* ($2n = 42$), and supplemental information is included on the karyotypes of *M. flaviventris*, *M. monax ochracea*, and *M. marmota*. The 6 North American species of *Marmota* ($NF = 66$) comprise a distinct group as compared with the middle Asian species ($NF = 70$) for which the karyotypes are known. Karyologic findings and zoogeographic evidence based upon the distribution of 2 nearctic species of host-specific cestodes indicate that *M. broweri*, in northern Alaska, is a pre-Würm relict. Its affinities

appear to be with the North American *caligata*-group rather than with the northeastern Siberian *M. camtschatica*. The occurrence on *M. broweri* of the Asian flea, *Oropsylla silantiewi*, has not been explained. Some ecological and behavioral characteristics of *M. broweri* are briefly described and compared with those of other species. Family groups of *M. broweri* hibernate together in single winter dens that are plugged at the entrance ; copulation takes place before the animals emerge from the winter den, near mid-May ; face-glands are utilized in marking of territory.

Arctic Health Research Center,
Public Health Service, U. S. Department
of Health, Education, and Welfare,
College, Alaska 99701, U.S.A.

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ADDENDUM

In a report received after this paper had been submitted for publication on 1 May 1970, Liapunova and Vorontsov [Novye dannye o khromosomakh evraziiskikh surkov (*Marmota*, *Marmotinae*, *Sciuridae*, *Rodentia*), pp. 36-40 in Vorontsov, N. N. (ed.), *Mlekopitaiushchie (Evoliutsiia, Kariologiya, Sistematika, Faunistika)*, Novosibirsk, 1969] reported for *M. bobak bobak* $2n = 38$, NF (autosomes) = 66 ; *M. sibirica sibirica* $2n = 38$, NF (autosomes) = 66 ; *M. camtschatica camtschatica* $2n = 40$, NF (autosomes) = 62. They considered *M. camtschatica* to be of comparatively recent (?early Pleistocene) North American derivation.