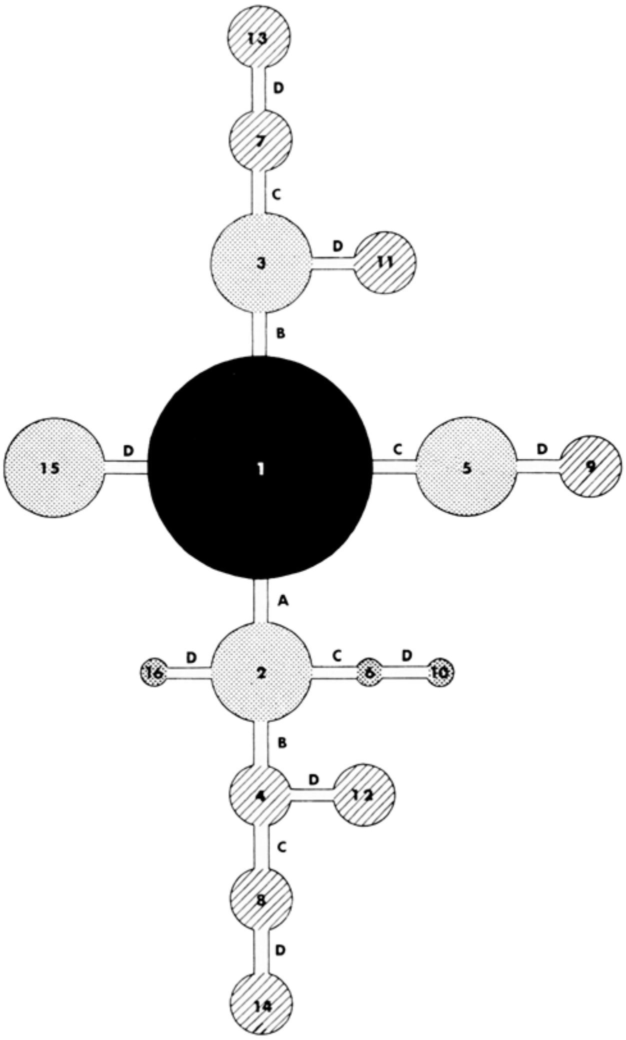

Fig. 5. A schematic model of the cell divisions that result in the 16 cells of a tsetse-fly egg-chamber and its ring-canals. The numerical numbering follows that in Figure 4; the alphabetical numbering indicates A, first cell division; B, second division; C, third division; and D, fourth division. The sizes of the cells in the diagram give an (exaggerated) indication of the size differences between the various cells of the egg-chamber towards the end of the yolk-deposition stage.

to each other, and each ring-canal is simply a short tube projecting into the 2 adjacent cells (Figures 2 and 3).

There are in all 15 such ring-canals in each egg-chamber. Two cells (including the oocyte) have 4 ring-canals, 2 cells have 3, 4 cells have 2, and 8 cells have 1 ring-canal each (Figure 4). Taking into consideration this very precise location of ring-canals, and the suggestion that ring-canals are a result of arrested cytokinesis[5,7], a model has been constructed to indicate the manner in which the cells comprising the egg-chamber may have been derived by mitosis (Figure 5). It is clear then that the 16 cells arise from the division of all the 8 third-generation cells.

It is not certain what the function of the ring-canals is in insect egg-chambers. There is some suggestive evidence that cytoplasmic contents flow through this canal: (1) cytoplasmic contents apparently stain similarly on either side of a ring-canal[8]; (2) large or distinctive cytoplasmic organelles are often seen within the canal[7,9]; and (c) radioautographic studies of the incorporation of injected tritiated uridine demonstrates that the labelled RNA appears in the cytoplasm adjacent to a ring-canal before it is noted in the cytoplasm of the adjoining cell[10]. However, the intercommunication through ring-canals and the manner in which this is regulated has still to be unequivocally demonstrated[11].

Zusammenfassung. In der Ovariole der Tsetsefliege werden 15 Trophozyten und eine Oozyte festgestellt, die in wohlgeordneter Weise durch 15 Ringbildungen miteinander verbunden sind. Eine Anordnung, welche die Rekonstruktion der vorausgegangenen Mitosen dieser 16 Zellen möglich macht.

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COGITATIONES

Chromosomes and Systematics of some North American Species of the Genus *Marmota* (Rodentia: Sciuridae)

The North American members of the genus *Marmota*, the marmots, were last revised by A. H. Howell[1]. He recognized 3 groups of species: the woodchuck, *M. monax* (Linnaeus); the yellow-bellied marmot, *M. flaviventris* (Audubon and Bachman); and the hoary marmot group, consisting of the hoary marmot, *M. caligata* (Eschscholtz), the Olympic marmot, *M. olympus* (Merriam), and the Vancouver Island marmot, *M. vancouverensis* Swarth. Subsequently, a new form was described[2] from the Brooks Range of northern Alaska as a race of the hoary marmot, *M. c. broweri* Hall and Gilmore. Ellerman[3] retained these latter forms in the *caligata* group, and added the black-capped marmot, *M. camtschatica* (Pallas), of eastern Siberia to it. He then went further[4] submerging the entire *caligata* group within the *M. marmota* group, which as he

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understood it, also included the Alpine marmot, *M. marmota* (Linnaeus), and the Central Asian gray marmot, *M. baibacina* (Kastschenko), and Menzbier's marmot, *M. menzbieri* (Kashkarov). RAUSCH[5], following this lead, arranged all of the North American forms of the *caligata* group as races of *M. marmota*, although some authorities[6] still retained *M. caligata*, *M. olympus*, and *M. vancouverensis* as distinct species. The different karyotypes suggested, as did other evidence, that *M. broweri* was specifically distinct from *M. caligata*, and that *M. olympus* and *M. vancouverensis* might not be as closely related to *M. caligata* as formerly supposed.

Chromosomes have previously been studied from specimens of *M. monax preblorum* Howell, 2*n*38, by COUSER et al.[7], and from *Marmota c. caligata* (Eschscholtz), 2*n*42, *M. c. broweri* Hall and Gilmore, 2*n*36, *M. olympus* (Merriam), 2*n*40, and *M. flaviventris avara* (Bangs), 2*n*42, by RAUSCH and RAUSCH[8]. Karyotypes have not been reported from *M. flaviventris* and *M. olympus* and there are no published descriptions of chromosomes from Palearctic *Marmota*. Finally, except for the discussion pertaining to the taxonomic status of *M. broweri* and *M. caligata*[8], there has been no correlation of chromosome characters with other lines of taxonomic evidence.

The purposes of this report are to describe the karyotype of *M. flaviventris*, to confirm the diploid number of *M. caligata* by examination of a specimen from an unstudied part of its geographic range and to correlate the chromosomes of North American Marmots with a revised systematic concept of the genus *Marmota*[9].

Materials and methods. Chromosomes were analyzed from the bone marrow of a male *M. flaviventris luteola* Howell collected at Isabell Glacier Cirque, Boulder Co., Colorado and from the testis of a male *Marmota caligata nivaria* (Howell) collected at Logan Pass, Glacier National Park, Montana.

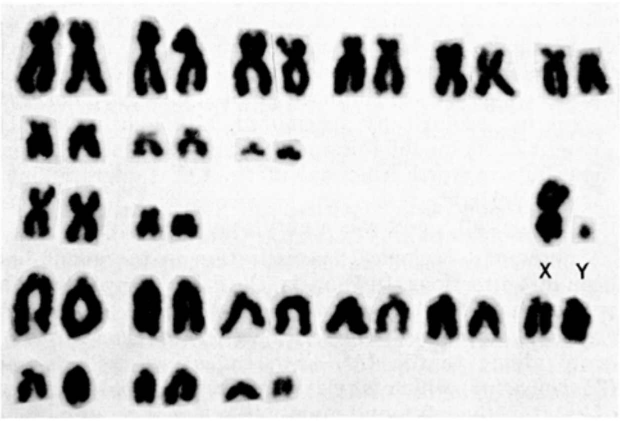
A colchicine-hypotonic-citrate-cell-suspension technique was used to examine the mitotic chromosomes[10]; testis tubules were placed in 1% Na citrate for 1 h, fixed in MCP, hydrolyzed for 14 min in 1 *N* HCl at 60 °C, Feulgen stained, and squashed.

Results. The diploid chromosome number of the Coloradan *M. flaviventris luteola* is 42, which agrees with the number reported for *M. f. avara* from British Columbia[8]. The karyotype (Figure) contains 22 metacentrics and submetacentrics, 18 acrocentrics, a metacentric *X* and minute *Y* chromosome. Comparison of this karyotype with that of *M. caligata*[8] indicates their autosomes are indistinguishable; *flaviventris* and *caligata* differ only in *X* chromosome morphology, *caligata* having a submetacentric *X* chromosome.

The testis preparations of *M. caligata nivaria* from Montana at the southern extreme of the species' range display 20 autosomal bivalents and a sex bivalent, thus confirming the 2*n* of 42 from Alaskan *M. c. caligata*, from the northern extreme[8].

The Table summarizes the known chromosome characters of *Marmota*. The data suggest that *M. flaviventris* and *M. caligata* with 2*n*42 and indistinguishable autosomes comprise a group of closely-related species; they may also share a relationship with *M. olympus*, 2*n*40, and perhaps *M. vancouverensis* whose chromosomes have not been analyzed. In contrast, *M. monax* and *M. broweri* have successively lower diploid numbers and appear less closely related cytologically to the *flaviventris-caligata* group.

Discussion. Although the various species of *Marmota* exhibit different diploid numbers, they all share the same FN (number of autosome arms) which suggests the different karyotypes are interrelated by a series of Robertsonian centric fusions or fissions. It is impossible conclusively to differentiate fusion from fission cytologically in mammals but fusion is traditionally considered the more plausible mechanism of karyotype evolution; this problem is discussed elsewhere with presentation of indirect evidence for centric fission or dis-



Karyotype of a male *Marmota flaviventris luteola*. × 2000.

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Chromosome characteristics of some North American Marmots

	Autosomes			Sex chromosomes			
Species	2*n*	M & S	A	*X*	*Y*	FN	References
M. caligata	42	22	18	S	minute	62	RAUSCH and RAUSCH[8]
M. flaviventris	42	22	18	M	minute	62	RAUSCH and RAUSCH[8] and present paper
M. olympus	40	–	–	–	–	–	RAUSCH and RAUSCH[8]
M. monax	38	26	10	M	A (small)	62	COUSER et al.[7]
M. broweri	36	28	6	M	minute	62	RAUSCH and RAUSCH[8]

M, metacentric; S, submetacentric; A, acrocentric; FN, fundamental No. of autosomal arms (metacentrics contain 2 arms and acrocentrics contain 1 arm).

sociation of chromosomes in evolution of the prarie dog (*Cynomys*) karyotype[11].

If fusion of acrocentrics to produce metacentrics had occurred during evolution of marmot species, then *M. flaviventris* and *M. caligata* could be regarded as cytologically more ancestral than *M. monax* and *M. broweri*. Conversely, if dissociation or fission of metacentrics with resultant production of acrocentrics were operative *M. broweri* and *M. monax* could be considered the more primitive species. Correlation of the chromosome data with other lines of evidence is required to clarify the question concerning directions of evolution within *Marmota*. Using gross morphological, ecological, and zoogeographic information, an integrated evolutionary hypothesis with several alternatives can be proposed.

The genus *Marmota* appeared in the early Pliocene in North America, perhaps evolving from large, terrestrial ground squirrel-like forms (*Protospermophilus*)[12]. In late Pliocene, *Marmota* was present in eastern Eurasia[13,14], and reached western Eurasia in the Pleistocene[15]. The fossil record thus clearly indicates that the marmots arose in North America, and subsequently migrated across the Bering land connection into Eurasia in the Pliocene, contrary to the suggestion of MOORE[16]. The least specialized, ecologically, of the North American marmots is *M. monax*, which lives in a variety of habitats[17–20] throughout its range, the largest in the genus. Moreover, *M. marmota* of the Alps and Carpathians morphologically most resembles *M. monax*, as HOWELL himself pointed out[1]; *M. marmota* also is not ecologically specialized, although commonly thought of as an inhabitant of the alpine zone[21]. Thus, the primitive North American marmot that migrated into Eurasia probably resembled *M. monax* and *M. marmota* morphologically, and was a eurytopic species.

Subsequent ecological specialization in the genus has been in 2 directions. In Eurasia, the *bobac* group[9] includes species that have become adapted to colonial life in open grassland (*M. bobac, M. siberica, M. himalayana* in part), or to alpine tundra (*M. camtschatica*), as well as one (*M. baibacina*) which is relatively unspecialized in choice of habitat, though found mainly in rocky or mountainous country[13]. In North America, the open grassland niche has been pre-empted by prairie dogs (*Cynomys*), but *M. caligata* is adapted to alpine habitats[17,20]. The relict species, *M. olympus* and *M. vancouverensis*, with very small ranges, are generally thought of as alpine marmots also[17,22], but in fact appear adapted to an even narrower ecological niche, whose habitat component is within the high subalpine to alpine zones of the belt of very high precipitation along the Pacific Coast[9,23]. Like *M. baibacina* in Central Asia, *M. flaviventris* occupies a variety of habitats within mountains and 'badlands'[24]. Finally, the alpine *M. broweri* of northern Alaska is morphologically and ecologically very similar to *M. camtschatica* of eastern Siberia, and clearly represents a late Pleistocene (Wurm-Wisconsin) remigration into North America[9].

The primitive marmot of the Pliocene, according to the above analysis, probably had 38 diploid chromosomes. Subsequent Pleistocene evolution of *Marmota* in Eurasia then led to the more specialized marmots of the *bobac* group with 2*n*36, by centric fusion; *M. broweri* represents the recent penetration of this principally Old World group of marmots into North America. Elsewhere in North America during the early Pleistocene, the marmots became separated into eastern and western populations. The eastern group remained unspecialized, and evolved into *M. monax*, retaining 2*n*38, but the western group became more adapted to mountainous terrain, and by centric fission, 2*n* became 40. This chromosome number is retained in the relict species *M. olympus* (and perhaps *M. vancouverensis*), which as a result of environmental pressures of the later Pleistocene, became very much restricted in range and habitat. Finally, late Pleistocene evolution of this western group led, by further centric fission, to *M. caligata* and *M. flaviventris*, 2*n*42. *M. caligata* became a highly specialized alpine marmot of the northern and north-central Rocky Mountains, Cascades, and Coast Ranges; *M. flaviventris*, while remaining a specialized rock-dwelling marmot, did not become so narrowly restricted in other aspects of its habitat requirements.

Alternatively, the primitive Pliocene marmot may have had 2*n*40, and *M. monax*, while remaining close to its original morphology and ecology, may have evolved 2*n*38 by centric fusion, and *M. caligata* and *M. flaviventris* evolved 2*n*42 by centric fission, *M. olympus* retaining the primitive number. In Eurasia, the *M. bobac* group would have evolved 2*n*36 by centric fusion, as in the first alternative, but from a diploid number of 40, rather than 38. In either case, the morphological, ecological, and zoogeographic evidence indicates that both fission and fusion are involved in the evolution of the genus *Marmota*.

The alternatives to this hypothesis may be tested by determining the karyotypes of the remaining species of marmots, especially the Old World forms. *Marmota marmota* should have 2*n*38 (Alt. 1) or 40 (Alt. 2). *Marmota vancouverensis* should be 2*n*40. The hypothesis does not include the Central Asian *M. menzbieri* or *M. caudata*, but determination of their karyotypes should permit their integration into this evolutionary scheme[25].

Zusammenfassung. Die Zahl der diploiden Chromosomen von *Marmota caligata* und *M. flaviventris* ist 42 in Bevölkerungen der nördlichen und südlichen Verbreitungsgebiete beider Spezies. Ein Vergleich zwischen den bisher veröffentlichten Informationen über *Marmota*-Chromosomen mit Angaben über ihre Morphologie, Ekologie, Zoogeographie legt nahe, dass die ursprüngliche Chromosomenzahl 2*n* 38–40 war.

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