

DISTRIBUTION AND TAXONOMY OF THE SMALL POCKET
GOPHERS OF NORTHWESTERN OREGON

by

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A perusal of scientific works invariably proves the presence of a schism between the writing and the writer. Only rarely and briefly does one glimpse the warmth of the personality beneath impersonal reporting of observations, inductions, interpretations, theorizations and testings that are embodied in the scientific method. In the pre-faces and acknowledgments, however, one sees revealed a different person, a man humbly examining himself in retrospect. And well this is so; one who once proves a sensitivity to his debts to others seldom permits audacity and brashness to enter his scientific writing. But how, in a few sentences, does one acknowledge this debt, even by an expression of gratitude, to all that have made the investigation possible and fruitful?

One cannot name the united members of our nation who have provided the educational facilities and often even the funds for one willing to strive therein. One cannot ignore the parade of teachers and professors who for 21 years have continually offered more than the student was able or willing to grasp. One cannot recount the friends and companions who have supplemented the educational system with their conversations and discussions which gradually became integrated into this which we call comprehension. One cannot express the inner feelings brought to mind by a major professor who with dexterity gravitated about himself a heterogeneous group of graduate students and instilled into them a deep sense of easy comradery and intellectual curiosity. Certainly a father who has devoted much of his lifetime in a quiet unassuming search for knowledge of birds and

mammals, a father who surrounded his sons with his interest and facilities without dictating the direction of their search for an education, deserves more than a mere passing mention. What does one say of a wife that not only puts up with the peculiarities of a life with a biologist but also was to be found patiently cleaning odoriferous skulls with meticulous care?

Frankly I feel incapable of adequately expressing my sincere gratitude to this entire host of unnamed persons. Perhaps I may rather contrive an indirect repayment through the still younger generations of students by being one small contributor to these who, like ourselves, are charged with the preservation and improvement of our culture.

TABLE OF CONTENTS

Introduction	1
Variation in cranial characters, statistical analyses	7
Objectives and methods	7
Analysis of lineal measurements	18
Analysis of proportions	36
Variation in cranial characters, non-statistical analysis	51
Variation in body dimensions	64
Variation in coat color	74
Molt	89
Coat color and phylogeny	92
Distribution and differentiation	98
Systematic accounts	112
<u>Thomomys monticola mazama</u>	113
<u>Thomomys monticola oregonus</u>	118
<u>Thomomys monticola pumilus</u>	124
<u>Thomomys monticola niger</u>	130
<u>Thomomys monticola hesperus</u>	136
<u>Thomomys monticola mutabilus</u>	142
Plates 1 to 24	149
Bibliography	197

DISTRIBUTION AND TAXONOMY OF THE SMALL POCKET GOPHERS
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INTRODUCTION

Pocket gophers, a group of rodents peculiar to North and Middle America, belong to the family Geomyidae. Members of the genus Thomomys are abundant over almost the entire western half of the United States, southwestern Canada, and much of Mexico. Within this extensive range the factors of low motility and geographic discontinuity of habitat have subdivided this genus of fossorial rodents into numerous species, and these have been further differentiated into even more numerous subspecies by the forces of organic evolution. Five species are currently recognized as ranging within the boundaries of the state of Oregon: (1) Thomomys bulbivorus is the large camas pocket gopher of the Willamette Valley; (2) Thomomys townsendii, another large gopher, has two subspecies which inhabits the southeastern corner of the state; (3) Thomomys bottae, with two subspecies, extends into southwestern Oregon from the region of greater abundance in California; (4) Thomomys talpoides, with several subspecies, ranges through most of Oregon east of the Cascade Mountains, and (5) Thomomys monticola whose subspecies extend westward from the Oregon Cascades, and adjacent mountains, to the Pacific Coast. This investigation is concerned with the distribution and taxonomic inter-relationships between the races of the last species as they occur in northwestern Oregon.

Four recognized forms of monticola gophers are to be found in this region of the state, these are: Thomomys m. mazama ranging

throughout the Cascades; Thomomys m. oregonus inhabiting the Willamette and certain adjacent valleys; Thomomys m. niger found along the central Oregon coast; and Thomomys m. hesperus occupying valleys and ridges of the northcentral Oregon coast. During the course of the investigation two additional undescribed forms were found to be present. Tentatively bearing the names assigned here until properly established under the rules of zoological nomenclature, they are: Thomomys m. pumilus found in the vicinity of Scappoose, Columbia County, and Thomomys m. mutabilis discovered in the Nehalem Valley, Clatsop County.

While examining the distribution and life history of the unique black pocket gopher, Thomomys m. niger, in 1948 and 1949 the paucity of available information became distressingly apparent. A few months of concentrated field work resulted in an extension of the range northward to the Yachats River and into the Alsea drainage system, more than doubling the residual range published in the most recent literature, Bailey's 1936 Mammals and life zones of Oregon, after deletion of that area south of the Siuslaw River erroneously included due to mislocation of the type locality, Seaton (27, pp.25-27). Procurement of a fresh and rather long series of specimens opened the possibility of making a more adequate taxonomic comparison with other forms to be found in adjacent regions. The investigation was expanded, therefore, to include the other members of the species in that area from the Cascade Mountains westward to the Pacific Coast and from the Umpqua River northward to the Columbia River.

Historically, recognition of the forms with which we are

concerned followed shortly the original description of monticola by Allen in 1893. Merriam described as full species mazama in 1897 (17, p.214), niger and hesperus in 1901, and at the same time placed the fourth form, oregonus, as a subspecies of Thomomys douglasii (18, pp.115-117). The pioneer period was culminated in Bailey's monographic Revision of the pocket gophers of the genus Thomomys in 1915. He placed mazama as a subspecies of monticola and added some new distributional records to modifications of the earlier descriptions (2, pp.121-131). The years since have produced only light sporadic collecting of specimens, mainly by private collectors in the region. In 1936 when Bailey's Mammals and life zones of Oregon was published it contained some additional information on distribution and habits along with abbreviated systematic accounts.

Elsewhere in the range of Thomomys adequate collections outlined the general distributional patterns and with the growing concepts of the newer systematics effected considerable taxonomic revaluation and realignment of species and subspecies. Goldman, recognizing the specific distinction of the monticola gophers from the related and more widespread talpoides group, in 1943 placed the forms oregonus, niger and hesperus as subspecies of monticola (12, pp.146-147). His conclusions, although undoubtedly based upon personal examination of examples from each form, were not supported by any record of critical analysis of the populations.

While the systematic interrelationships have gradually emerged, the distribution of each form remained poorly defined and the de-

scriptions, especially of cranial features, were often inadequate to assist in the ready determination of affinities of new specimens collected. As it progressed, therefore, certain aims became solidified for the conduct of a study which could at least partially rectify the situation. These were:

- (1) To find out what forms of gophers occur in northwestern Oregon (excluding the camas pocket gopher Thomomys bulbivorous).
- (2) To ascertain the geographic range of each.
- (3) To determine and catalog the variation in each form.
- (4) To compile descriptions by means of which accurate identifications and comparisons are possible.
- (5) To provide brief information on habits and habitats as gleaned in the pursuit of the above.

The initial phase, primarily a field problem, was conducted from 1948 to 1953. The search for gophers was first concentrated in locales recorded in published accounts, then extended peripherally until ultimately much of the accessible areas of the region had received at least a cursorial examination. Undoubtedly many colonies were not discovered by the technique employed, that of driving slowly along, scrutinizing cleared areas wherever vegetation was short enough to reveal telltale mounds on either side of the road, with occasional examination of certain promising areas on foot. In spite of the crudeness of the method, necessitated by the total area demanding attention, its effectiveness is reflected in the overall

success in finding new extensions of range for each form. Specimens procured by use of the standard Macabee gopher trap were prepared in the field. Thus a more or less randomized sample, a series of adequate length to show geographical, sexual and age variation, was obtained throughout the range of each form along with a first hand acquaintanceship with the particular habits of the animal and the habitats occupied. My own efforts were supplimented by those of my father, Alex Walker, who not only placed the skins from his private collection at my disposal but also engaged in active field collecting when opportunity allowed, making a contribution of some 130 specimens. A total of approximately 480 specimens of Thomomys monticola from the area under consideration were ultimately obtained for examination.

The second or laboratory phase involved determination and cataloging of variation. Standard cranial measurements taken on cleaned skulls were recorded and from these a random sample formed a basis for statistical analyses. Eight factorial analyses were conducted on certain lineal cranial measurements and seven more were made on selected ratios between lineal measurements. Other cranial features, such as the configuration of certain bones which do not lend themselves readily to statistical treatment, were typed into various classes and the trends within and between subspecies populations recorded. Variation in body size, as indicated by measurements recorded on the label by the collector, were also subjected to statistical analyses. Variation in coat color and coat

pattern were examined both macroscopically and microscopically.

In the final phase the findings of both field and laboratory were synthesized into the subspecies accounts wherein conscious effort has been made to compile descriptions and comparisons of maximum usefulness. These accounts seek to reflect the geographical and historical as well as the morphological dimensions of the subspecies.

VARIATIONS IN CRANIAL CHARACTERS, STATISTICAL ANALYSES

OBJECTIVES AND METHODS. The objective of statistical analysis in a taxonomic study is twofold. First, it attempts to determine meristically the relationships between populations in contrast to the less strict, and even erroneous, personal impressions that constantly threaten the nonstatistical approach. A nonstatistical analysis yields only a purely descriptive report of facts observed in the available sample with little information as to the reliability of extrapolating the presented figures to include the entire population from which the sample was drawn. On the other hand, statistical analysis makes possible the induction of features of an infinite total population from the sample with a degree of reliability chosen by the investigator. Secondly, unsuspected but distinctly worth while character evaluations and interpretations may emerge from the masses of raw data treated with careful statistical applications. The improvement of statistical techniques and availability of electric calculating machines are reflected in the increasing use of this type of analysis in taxonomy as well as in other phases of animal biology. Its proven value seems self-evident.

The raw data consist of cranial measurements taken to the nearest one-tenth of a millimeter with vernier calipers. All are standard measurements used in the taxonomy of the genus Thomomys; several are defined and illustrated in Hall (14, pp.672-685). In the present work each is explained with the statistical analysis of

lineal dimensions and illustrated in Plate 5. It is not meant to be inferred that the analyzed measurements are the only ones of taxonomic worth. In the selection of the examined characters consideration was given the lineal dimensions of various portions of the skull. Thus, measurements of length include an overall dimension, basilar length, lengths of such unrelated parts as the alveolar length of the upper molariform teeth the palatilar length on the ventral surface of the skull and the nasal length on the dorsal surface. Vertical construction is sampled by the height of the brain case. The width of various parts is indicated by zygomatic breadth, breadth at the mastoids and the least interorbital constriction.

Not readily apparent in the lineal comparisons alone, the possibility that the populations vary in some proportions is checked by selected ratios. For example, examination of the lineal data may indicate that subspecies A is larger than subspecies B for characters x and y. By means of the ratios we may find that $A \frac{x}{y}$ is equal to, or is significantly larger or smaller, than $B \frac{x}{y}$. This information is well worth the additional computations.

The method of statistical analysis used is a 2X6 factorial experiment with equal numbers of observations. This type of analysis of variance allows the effects of two factors to be studied simultaneously. In addition the interaction from these two factors may be discerned. The two factors here studied are sex, with two replications, and subspecies, with six replications. Each of the six subspecies is represented in a column by twenty-four observations, twelve for males and twelve for females. There are, therefore,

seventy-two observations for each sex.

The mean squares for variation due to subspecies, sex, interaction and error are computed. These quantities are used in each factorial experiment to test three hypotheses; (1) there is no interaction between sex and subspecies, (2) the population means for the sexes are equal, and (3) the population means for each of the subspecies are equal. There is a critical region for each of these hypotheses, if the calculated F-value falls within this region the hypothesis is rejected as false and the term "significant" is used. If, on the other hand, the calculated F-value does not fall in the critical region the hypothesis is accepted as true and is so indicated by the term "not significant". If a hypothesis is rejected one or more alternatives must be considered as true.

The level of significance used throughout the experiments is 1%, that is, the probability of rejecting the correct hypothesis is one in one hundred.

The hypothesis that there is no interaction between sex and subspecies implies that significant differences between the sexes does not affect the significant differences between the subspecies, in other words, the two factors are independent. If the calculated F-value obtained by division of the interaction mean square by the error mean square is greater than 3.17, with 5 and 132 degrees of freedom, it is termed significant and the hypothesis is rejected in favor of the alternative that the two factors are not independent. Interaction significance requires a somewhat modified procedure in

completing the analysis. The mean squares for sex and subspecies are tested by the interaction mean square rather than the error mean square. Examination of sex means by subspecies is conducted as outlined below when sex is shown significant but if the subspecies F-value is significant the means must be analyzed by sex. Therefore the subspecies means of the males are ranked and examined for significance by Tukey's method separately from the ranked means of the females.

Table 1. ANALYSIS OF VARIANCE

Variation Due To:	d.f.	Mean Square	F	Critical Region
Subspecies	5	A	$\frac{A}{E'}$	greater than 3.17
Sex	1	B	$\frac{B}{E'}$	greater than 6.85
Interaction	5	AB	$\frac{AB}{E}$	greater than 3.17
Error	132	E		
Pooled	137	E'		

If interaction is shown to be not significant the basic hypothesis that the factors are independent is accepted and the interaction mean square and error mean squares are pooled and used to test the significance of subspecies and sex with increased degrees of freedom. Where the two factors are independent the factorial analysis accomplishes a considerable saving in time and material, in fact two single factor experiments would require twice the total number of observations in order to equal the precision obtained

by the factorial experiment (7, p.125).

In dividing the sex mean square by the pooled mean square the critical region for the hypothesis that the population means for the sexes are equal is any value greater than 6.85, with 1 and 137 degrees of freedom. If the calculated F-value is significant the hypothesis is rejected and either the mean for the males is larger or is smaller than the mean for the females. Examination of the totals for males and females will readily indicate which of the two alternatives is acceptable. However, we may wish to know in which, if not in all, of the subspecies the sexes differ significantly. Consequentially the data is broken down into a set of six analyses, one for each subspecies, and each an analysis of variance designated as a single classification (sex) with equal number of observations (twelve in each of the two sexes). An F-value is obtained by division of the newly computed sex mean square and error mean square. With 1 and 22 degrees of freedom any value greater than 7.95 falls in the critical region, hence is significant. For that particular subspecies sexual dimorphism is present; examination of sex totals for that subspecies will indicate whether males or females average the larger.

The hypothesis that the population means of the subspecies are all equal is tested, in the absence of significant interaction, by division of the subspecies mean square by the pooled mean square. With 5 and 137 degrees of freedom the critical region includes any F-value greater than 3.17 at the 1% significance level. Rejection

of the hypothesis necessitates acceptance of the alternative that not all of the population means are equal but does not indicate which of the subspecies differ from each other, this requires further testing.

The method here used, Tukey's method (26, pp.99-114), involves computation of the least significant difference, designated LSD, by the formula:

$$LSD = t_{\alpha} \sqrt{\frac{2s^2}{N}}$$

where t_{α} is tabulated 1% value of student's t-distribution, with the number of degrees of freedom of the s^2 . The s^2 is the pooled mean square in the analysis of variance table and N the number of observations in each sample. Including the constant quantities from the following set of analyses the formula may be rewritten:

$$LSD = 2.62 \sqrt{\frac{2s^2}{24}}$$

The subspecies means are ranked according to size. If the gap between any two adjacent sample means is larger than the LSD we may conclude the respective population means on each side are different. If, in any group of three or more means, the difference between the extreme means exceeds LSD the test of the extreme mean is applied using the statistic given by Nair (20 pp. 118-144):

$$v = \frac{|\bar{x} - \bar{\bar{x}}|}{\sqrt{\frac{s^2}{N}}}$$

where \bar{x} is the extreme, smallest or largest, of the group treatment means and $\bar{\bar{x}}$ is the mean of the group treatment means. The hypothesis

that the extreme mean is drawn from the same population as the other means of the group is rejected at the 1% point if the v-value is larger than 2.97 providing there are six means in the group, 2.85 for five means, 2.68 for four means, or 2.43 for three means. The process is repeated until no further means are separated. The means separated from one side form a subgroup, if there are three or more means in any subgroup they are subjected to the same process.

Separation by LSD is indicated by the symbol # after the difference between the ranked subspecies means in the tables presented with each experiment. Differentiation by the test of the extreme mean is designated by *.

So far the statistical inference has been confined to a question of whether or not specified population means, as represented by the respective sample means, are equal. A second approach, the estimation of confidence intervals, increases the usefulness of the data. The actual mean of the infinite total population, a quantity unavailable unless every single specimen is collected and analyzed, a truly unlikely situation, probably does not exactly equal the sample mean, in fact it seldom will! However, an interval may be calculated, enclosed by the confidence limits, that will include the total population mean with a chosen degree of reliability which is called the confidence coefficient. The practicality of this estimation becomes apparent when one wishes to compare the mean of a new and undetermined sample with a previously existing investigation. Comparison of sample means, even where sample size is relatively small, to previous comprehensive estimations of several

characters will generally facilitate tentative assignment to taxonomic category.

The confidence interval with a confidence coefficient of .99 is determined as the sample mean (\bar{x}) plus and minus the quantity

$$t_{.01} \frac{s}{\sqrt{N}}$$

where $t_{.01}$ is the 1% value of student's t-distribution with the degrees of freedom of the error mean square, s is the square root of the error or pooled mean square and N the number of observations. Using the quantities common to the following experiments this may be rewritten:

$$\bar{x} \pm 2.62 \sqrt{\frac{\text{error (pooled) mean square}}{N}}$$

and simplified:

$$\bar{x} \pm .53469 \sqrt{\text{error (pooled) mean square}}$$

The assumptions upon which analysis of variance is based are:

- (1) the samples are random samples drawn from normal populations,
- (2) the variances of the populations are equal, and (3) the treatment and environmental effects are additive. Since we cannot prove that all of these qualifications are completely satisfied they must remain as assumptions; however, a slight departure from the assumptions will not cause serious error in the tests. The collection of observations based on specimens obtained throughout the geographic range and at various times of the year may or may not be a random sample. Where the series of specimens available exceeded sample size the twelve used as a sample were determined by use of a random number table. Non-normality does not affect the F-test seriously but tends to increase

the rejection of the true hypothesis a little more frequently than the significance level used. The homogeneity of variance of the populations was checked in two cases with Bartlett's method which in itself assumes random samples drawn from normal populations whose means may or may not be equal. The hypothesis that the subspecies population variances are equal in the cases of zygomatic breadth, Table 2, and basilar/mastoid ratio, Table 3, is acceptable. The principle affect of nonadditivity is some loss of information.

Since the techniques of statistical methodology are even now undergoing a rapid evolution it is deemed advisable to include, in the data presented with each experiment, the sum of squares obtained in preliminary steps of the analysis of variance. This provides, without the inclusion of bulky raw data, information for future tests that may be designed on analysis of variance. The necessity of assembling a new series of observations, a lengthy time consuming process, is eliminated should such application of different tests be desirable at a future date.

Table 2

BARTLETT'S TEST: ZYGOMATIC BREADTH

	ss	d.f.	1/d.f.	s ²	log s ²	(d.f.)log s ²
mutabilus	11301.67	24	.041666	470.90	2.67296	
oregonus	11147.46	24	.041666	464.48	2.66697	
niger	10523.10	24	.041666	438.46	2.64193	
hesperus	10012.95	24	.041666	417.21	2.62035	
mazama	9805.59	24	.041666	408.57	2.61126	
pumilus	9557.37	24	.041666	398.22	2.60012	
Sum		A	.249996		15.81359	C 379.52616
Pooled	62348.14	144	B .006944	432.97	2.63646	D 379.65024
Difference		A-B	.243052			D-C .12408

$$\chi^2 = \frac{2.3026 (D-C)}{1 + \frac{A-B}{3(k-1)}}$$

$$\frac{2.3026 (.12408)}{1 + \frac{.243052}{15}}$$

$$\frac{.28571}{1.016203} = 0.2811 \text{ with 5 d.f. Not significant.}$$

Critical region: $\chi^2 > 15.09$

Table 3

BARTLETT'S TEST: BASILAR/MASTOID

	ss	d.f.	1/d.f.	s ²	log s ²	(d.f.)log s ²
mazama	80.8811	24	.041666	3.3700	0.52763	
niger	80.8456	24	.041666	3.3686	0.52744	
hesperus	77.7422	24	.041666	3.2393	0.51045	
mutabilus	75.2627	24	.041666	3.1359	0.49636	
pumilus	74.9614	24	.041666	3.1234	0.49463	
oregonus	69.7409	24	.041666	2.9059	0.46328	
Sum			A .249996		3.01979	C 72.47496
Pooled	459.4339	144	B .006944	3.1905	0.50385	D 72.55440
Difference			A-B .243052			D-C .07944

$$\chi^2 = \frac{2.3026 (D-C)}{1 + \frac{A-B}{3(k-1)}}$$

$$\frac{2.3026 (.07944)}{1 + \frac{.243052}{15}}$$

$$\frac{.18292}{1.01620} = 0.1800 \text{ with 5 d.f. Not significant}$$

Critical region: $\chi^2 > 15.09$

ANALYSIS OF LINEAL MEASUREMENTS. The analysis of dimensions of various well defined cranial areas is designed to reveal the amount of variation within and, especially, between the populations as induced from a sample. Eight features are so examined independently. The data are presented as are the findings with no attempt at interpretation. They are integrated below in the subspecies accounts.

1. BASILAR LENGTH

A. Data.

	T O T A L S			SUM OF SQUARES	
	Male	Female	M & F	Male	Female
mutabilis	386.5	374.5	761.0	12461.91	11694.51
niger	378.5	371.9	750.4	11970.29	11550.97
oregonus	373.1	364.5	737.6	11621.87	11099.51
mazama	377.5	359.9	737.4	11882.13	10796.57
hesperus	371.5	362.8	734.3	11526.19	10975.30
pumilus	358.8	341.4	700.2	10738.86	9719.32
Total	2245.9	2175.0	4420.9		

B. Analysis of variance.

Variation Due To:	d.f.	Mean Square	F	Remarks
Subspecies	5	17.65	12.75	Significant
Sex	1	34.91	25.23	Significant
Interaction	5	.93	.66	Not significant
Error	132	1.40		
Pooled	137	1.38		

C. Analysis of sex.

	Error Mean Square	Sex Mean Square	F	Remarks
mutabilis	.93	6.04	6.49	Not significant
niger	2.59	1.81	.70	Not significant
oregonus	2.25	3.08	1.37	Not significant
mazama	.42	12.91	30.74	Significant
hesperus	1.45	3.15	2.17	Not significant
pumilus	.78	12.61	16.17	Significant

D. Analysis of subspecies.

	Mean	Difference	Confidence Minimum	Limit Maximum
mutabilus	31.7083		31.0795	32.3371
niger	31.2667	.4415*	30.6379	31.8955
oregonus	30.7333	.5334	30.1045	31.3621
mazana	30.7250	.0073	30.0962	31.3538
hesperus	30.5958	.1292	29.9670	31.2246
pumilus	29.1750	1.4208	28.5462	29.8038

Basilar length is the distance from the anteriormost mid-ventral border of the foramen magnum to the posteriormost margins of the alveoli of the upper incisors, see Plate 5 .

Data accumulated from the original observations are summarized in section A above, and subjected to the analysis of variance, the pertinent portion of which is presented in section B. Of the three F-tests both subspecies and sex exhibit significant values while interaction is not significant.

Sexual dimorphism is present. The sex totals indicate the males average slightly longer in basilar length than the females, but to determine exactly which subspecies display significant dimorphism an individual F-test between the sexes of each subspecies is necessary. The results of these tests are shown in section C. It is seen that the males are significantly longer than the females, on the level of the population means, only in mazana and pumilus.

In the analysis of variance the subspecies F-value is significant, therefore the alternative hypothesis that differences do occur between the subspecies populations must be accepted. However, it is pertinent to ascertain just where among the six populations this difference

lies. In section D, analysis of subspecies, essential information for further testing and the results are presented in tabular form.

The initial step in Tukey's method involves calculation of the LSD.

$$\text{LSD} = .8898 = 2.62 \sqrt{\frac{2(1.3839)}{24}}$$

Reference to the column of differences between the subspecies means reveals the gap between hesperus and pumilus, 1.4208, exceeds LSD. The mean of the population of pumilus is separable from all other subspecies population means by a lesser basilar length. The difference between the extreme remaining means, mutabilus and hesperus, being greater than LSD the test of the extreme mean is applied with the following hypotheses and results.

(1) mutabilus equals niger, oregonus, mazama and hesperus.

$$v = \frac{.7025}{.2402} = 2.92. \text{ Critical value } 2.85. \text{ Significant.}$$

(2) niger equals oregonus, mazama and hesperus.

$$v = \frac{.4365}{.2402} = 1.82. \text{ Critical value } 2.68. \text{ Not significant.}$$

As pumilus differs from all other subspecies by a lesser basilar length, as indicated by the LSD test, so the test of the extreme mean shows the mean of the mutabilus population to differ significantly from all other subspecies population means by a greater basilar length.

Confidence limits for the subspecies population means are computed as: Sample mean \pm .6288 ($.53469 \sqrt{1.3839}$). Again reference to section D may be made; examination of recorded minimum and maximum confidence limits indicates the population mean of pumilus will

not fall within the interval of any other subspecies population mean. From the practical standpoint the confidence intervals produce a working basis for comparison of new, unknown, sample means. A basal mean lying in the interval of pumilus probably represents a population not separable, for that single character at least, from the pumilus population but at the same time distinct from the other subspecies. By the same reasoning a mean of say 31.2, while excluding the probability of affinity with the pumilus population, could not be assigned to one of the remaining populations of hesperus, mazama, oregonus, niger or mutabilis with any degree of certainty.

2. ZYGOMATIC BREADTH

A. Data.

	T O T A L S			SUM OF SQUARES	
	Male	Female	M & F	Male	Female
<u>mutabilis</u>	263.7	256.8	520.5	5798.37	5503.30
<u>oregonus</u>	260.0	256.6	516.6	5642.60	5504.86
<u>niger</u>	253.5	248.5	502.0	5366.07	5157.03
<u>hesperus</u>	248.7	241.0	489.7	5170.53	4842.42
<u>mazama</u>	248.0	236.7	484.7	5132.78	4672.81
<u>pumilus</u>	245.7	232.8	478.5	5035.83	4521.54
Total	1519.6	1472.4	2992.0		

B. Analysis of variance.

Variation Due To:	d.f.	Mean Square	F	Remarks
Subspecies	5	12.4298	16.47	Significant
Sex	1	15.4711	20.50	Significant
Interaction	5	.5521	.72	Not significant
Error	132	.7625		
Pooled	137	.7548		

C. Analysis of sex.

	Error Mean Square	Sex Mean Square	F	Remarks
mutabilus	.515	1.99	3.86	Not significant
oregonus	1.230	.48	.39	Not significant
niger	.995	1.04	1.04	Not significant
hesperus	.844	2.47	2.93	Not significant
mazama	.516	5.32	10.31	Significant
pumilus	.470	6.94	14.77	Significant

D. Analysis of subspecies.

	Mean	Difference	Confidence Minimum	Limit Maximum
mutabilus	21.6875		21.2151	22.1599
oregonus	21.5250	.1625	21.0526	21.9974
niger	20.9167	.6083*	20.4443	21.3891
hesperus	20.4042	.5125*	19.9318	20.8766
mazama	20.1958	.2084	19.7234	20.6682
pumilus	19.9375	.2583	19.4651	20.4099

The measurement of zygomatic breadth is taken as the greatest distance across the zygomatic arches perpendicular to the long axis of the skull.

In the analysis of variance it will be noted sex is significant; the alternative hypothesis that sexual dimorphism is present is accepted. The totals of each sex indicates the males, as a whole, have broader zygomatic arches than the females. However, as revealed by the individual F-tests between the sexes of each subspecies in section C, the males are significantly broader only in the populations of mazama and pumilus.

To trace the source of the significance for subspecies appearing in the analysis of variance Tukey's method is employed.

LSD is computed:

$$\text{LSD} = .6571 = 2.62 \sqrt{\frac{2(.7548)}{24}}$$

Examination of the differences between ranked means in section D indicates no possible separation by use of LSD. Tests of the extreme mean obtains the following results:

- (1) mutabilus equals oregonus, niger, hesperus, mazama and pumilus.

$$v = \frac{.9097}{.1773} = 5.13. \quad \text{Critical value } 2.97. \quad \text{Significant.}$$

- (2) oregonus equals niger, hesperus, mazama and pumilus.

$$v = \frac{.5532}{.1773} = 5.24. \quad \text{Critical value } 2.85. \quad \text{Significant.}$$

- (3) niger equals hesperus, mazama and pumilus.

$$v = \frac{.5532}{.1773} = 2.68. \quad \text{Critical value } 2.68. \quad \text{Significant.}$$

- (4) pumilus equals hesperus and mazama.

$$v = \frac{.2417}{.1773} = 1.36. \quad \text{Critical value } 2.43. \quad \text{Not significant.}$$

- (5) niger equals mutabilus and oregonus.

$$v = \frac{.4597}{.1773} = 2.59. \quad \text{Critical value } 2.43. \quad \text{Significant.}$$

The population means of mutabilus and oregonus are separable from all others by greater zygomatic breadth. Niger is separable from mutabilus and oregonus by lesser zygomatic breadth and is further separable from hesperus, mazama and pumilus by greater breadth.

Confidence limits for the subspecies population means are computed as: Sample mean \pm .4724 (.53469 $\sqrt{.7548}$). The confidence intervals show the following separation between subspecies:

- (1) pumilus, mazama, and hesperus do not overlap oregonus or mutabilus, and (2) pumilus does not overlap niger.

3. MASTOID BREADTH.

A. Data.

	T O T A L S			SUM OF SQUARES	
	Male	Female	M & F	Male	Female
oregonus	218.7	214.3	433.0	3989.59	3833.03
mutabilus	216.8	212.8	429.6	3919.24	3775.70
hesperus	204.9	203.0	407.9	3506.43	3436.64
niger	203.5	203.0	406.5	3456.93	3437.28
mazama	205.1	196.9	402.0	3508.67	3232.31
pumilus	203.0	193.3	396.3	3435.66	3116.93
Total	1252.0	1223.3	2475.3		

B. Analysis of variance.

Variation Due To:	d.f.	Mean Square	F	Remarks
Subspecies	5	9.5209	28.54	Significant
Sex	1	5.7205	17.15	Significant
Interaction	5	.5272	1.62	Not significant
Error	132	.3263		
Pooled	137	.3336		

C. Analysis of sex.

	Error Mean Square	Sex Mean Square	F	Remarks
oregonus	.444	.806	1.82	Not significant
mutabilus	.201	.667	3.32	Not significant
hesperus	.469	.151	.32	Not significant
niger	.414	.010	.00	Not significant
mazama	.213	2.802	13.15	Significant
pumilus	.217	3.920	18.06	Significant

D. Analysis of subspecies.

	Mean	Difference	Confidence Limit	
			Minimum	Maximum
oregonus	18.0417		17.7329	18.3505
mutabilus	17.9000	.1417	17.5912	18.2088
hesperus	16.9958	.9042#	16.6870	17.3046
niger	16.9375	.0583	16.6287	17.2463
mazama	16.7500	.1875	16.4412	17.0588
pumilus	16.5125	.2375	16.2037	16.8213

The mastoid breadth is measured as the greatest distance across the mastoid bones perpendicular to the long axis of the skull.

The presence of significance in both sex and subspecies means is determined by the analysis of variance, interaction is not significant. Since sex is significant the alternate hypothesis that sexual dimorphism is present must be accepted. The subspecies totals by sex indicate the males are broader across the mastoids than the females, but it will be noted this difference is not constant among the subspecies. The individual F-tests in section C demonstrate significance only in the populations of mazama and pumilus. The sample means for the males and females of mazama, 17.09 and 16.41 respectively, differ by .7 mm. and the means of pumilus, 16.92 for the males and 16.11 for the females differ by .8 mm.

The difference between the adjacent subspecies means of mutabilus and hesperus, .9042, is greater than LSD which is computed:

$$\text{LSD} = .4368 = 2.62 \sqrt{\frac{2(.3336)}{24}}$$

Because the difference between the extremes of the remaining group means exceeds LSD the test of the extreme mean is applied.

(1) pumilus equals hesperus, niger and mazama.

$$v = \frac{.2864}{.1180} = 2.43. \quad \text{Critical value } 2.68. \quad \text{Not significant.}$$

From the foregoing tests it is concluded that the population means for mastoid breadth of oregonus and mutabilus, by their larger values, are separable from those of hesperus, niger, mazama and pumilus.

Confidence limits for the subspecies population means are computed as: Sample mean \pm .3088 (.53469 $\sqrt{.3336}$). There is no overlap between the confidence intervals of oregonus and mutabilus on one hand and hesperus, niger, mazama and pumilus on the other.

4. HEIGHT OF BRAIN CASE.

A. Data.

	T O T A L S			S U M O F S Q U A R E S	
	Male	Female	M & F	Male	Female
<u>oregonus</u>	139.7	136.3	276.0	1627.37	1550.03
<u>mutabilus</u>	134.0	133.9	267.9	1496.86	1495.37
<u>pumilus</u>	134.1	133.0	267.1	1499.49	1475.26
<u>hesperus</u>	133.8	132.7	266.5	1494.06	1468.21
<u>niger</u>	134.2	130.6	264.8	1505.74	1421.76
<u>mazama</u>	131.3	131.2	262.5	1437.29	1435.64
Total	807.1	797.7	1604.8		

B. Analysis of variance.

Variation Due To:	d.f.	Mean Square	F	Remarks
Subspecies	5	.88393	6.94	Significant
Sex	1	.61360	4.82	Not significant
Interaction	5	.10194	.79	Not significant
Error	132	.12835		
Pooled	137	.12738		

C. Analysis of subspecies.

	Mean	Difference	Confidence Minimum	Limit Maximum
<u>oregonus</u>	11.5000		11.3092	11.6908
<u>mutabilis</u>	11.1625	.3375#	10.9717	11.3533
<u>pumilus</u>	11.1292	.0333	10.9384	11.3200
<u>hesperus</u>	11.1042	.0250	10.9134	11.2950
<u>niger</u>	11.0333	.0709	10.8425	11.2241
<u>mazama</u>	10.9375	.0958	10.7467	11.1283

The height of the brain case is a vertical measurement taken perpendicular to the long axis of the skull from the points of maximum ventral inflation of the auditory bullae to the roof of the skull at the anterior point of the interparietal.

No significant sexual dimorphism or interaction is present.

Subspecies significance is contributed by the gap between oregonus and mutabilis which exceeds the LSD, hence oregonus is separable by a higher brain case from all other subspecies.

$$LSD = .2328 = 2.62 \sqrt{\frac{2(.12738)}{24}}$$

The difference between the extremes of the remaining subspecies means does not exceed the LSD terminating the process.

Confidence limits calculated to include the subspecies population mean are computed as: Sample mean \pm .1908 (.53469 $\sqrt{.12738}$). The confidence interval of oregonus does not overlap the intervals of hesperus, niger or mazama.

5. PALATILAR LENGTH

A. Data.

	T O T A L S			S U M O F S Q U A R E S	
	Male	Female	M & F	Male	Female
mutabilus	231.0	222.8	453.8	4455.50	4140.36
oregonus	222.7	218.0	440.7	4139.61	3969.64
niger	220.3	215.5	435.8	4053.83	3883.13
hesperus	220.8	213.3	434.1	4073.74	3794.87
mazama	217.5	208.8	426.3	3945.77	3635.44
pumilus	208.1	196.3	404.4	3614.49	3214.07
Total	1320.4	1274.7	2595.1		

B. Analysis of variance

Variation Due To:	d.f.	Mean Square	F	Remarks
Subspecies	5	11.3536	19.08	Significant
Sex	1	14.5034	24.38	Significant
Interaction	5	.2956	.48	Not significant
Error	132	.6063		
Pooled	137	.5950		

C. Analysis of sex.

	Error Mean Square	Sex Mean Square	F	Remarks
mutabilus	.566	2.801	4.95	Not significant
oregonus	.726	.920	1.27	Not significant
niger	1.027	.967	.94	Not significant
hesperus	.658	2.343	3.56	Not significant
mazama	.268	3.153	11.76	Significant
pumilus	.392	5.802	14.80	Significant

D. Analysis of subspecies.

	Mean	Difference	Confidence Limit	
			Minimum	Maximum
mutabilus	18.9083		18.4958	19.3208
oregonus	18.3625	.5458*	17.9500	18.7750
niger	18.1583	.2042	17.7458	18.5708
hesperus	18.0875	.0708	17.6750	18.5000
mazama	17.7625	.3250	17.3500	18.1750
pumilus	16.8500	.9125#	16.4375	17.2625

The measurement of palatilar length is taken as the distance between the anteriormost point on the posterior border of the palate to a line connecting the posteriormost margins of the alveoli of the upper incisors.

Upon reference to the sex totals by subspecies in section A it will be noted the males display a somewhat greater palatilar length than the females. However, dimorphism attains the level of significance, as determined by individual F-tests in Section C, only in the populations of mazama and pumilus. The sample means for mazama are 18.12 for the males and 17.40 for the females, a difference of about .7 mm. For pumilus the means are respectively 17.34 and 16.36 with a difference of nearly 1 mm.

The first process of Tukey's method, tracing the location of the significance discerned in the analysis of variance for subspecies means, is calculation of LSD.

$$LSD = .5832 = 2.62 \sqrt{\frac{2(.5950)}{24}}$$

The difference between pumilus and mazama being .9125, exceeding the LSD, pumilus is separable from all other subspecies by the shorter palatilar length. Since the difference between the extremes of the remaining subspecies means is greater than LSD the test of the extreme mean is used to test the hypotheses and obtain the results following:

- (1) mutabilis equals oregonus, niger, hesperus and mazama.

$$v = \frac{.6525}{.1474} = 4.14. \quad \text{Critical value } 2.85. \quad \text{Significant.}$$

(2) mazama equals oregonus, niger and hesperus.

$$v = \frac{.3302}{.1574} = 2.10. \text{ Critical value } 2.68. \text{ Not significant.}$$

In addition to finding pumilus differing from all other subspecies by a shorter palatilar length, mutabilus is also found to be separable from all other subspecies by greater length.

The computed confidence limits designed to include the true subspecies population means are: Sample mean \pm .4125 (.53469 $\sqrt{.5950}$). The confidence intervals show separation between the following subspecies: (1) pumilus does not overlap any other subspecies, and (2) mutabilus does not overlap pumilus, oregonus or niger.

6. ALVEOLAR LENGTH.

A. Data.

	T O T A L S			SUM OF SQUARES	
	Male	Female	M & F	Male	Female
mutabilus	104.1	104.4	208.5	903.27	909.04
niger	101.7	101.2	202.9	863.69	854.66
oregonus	100.5	101.1	201.6	843.05	854.25
hesperus	100.7	99.2	199.9	846.65	821.72
mazama	97.2	96.1	193.3	788.54	770.55
pumilus	95.0	93.5	188.5	752.96	728.99
Total	599.2	595.5	1194.7		

B. Analysis of variance.

Variation Due To:	d.f.	Mean Square	F	Remarks
Subspecies	5	2.1307	19.78	Significant
Sex	1	.0951	.88	Not significant
Interaction	5	.0344	.31	Not significant
Error	132	.1105		
Pooled	137	.1077		

C. Analysis of subspecies.

	Mean	Difference	Confidence Limit	
			Minimum	Maximum
<u>mutabilis</u>	8.6875		8.5120	8.8630
<u>niger</u>	8.4542	.2333*	8.2787	8.6297
<u>oregonus</u>	8.4000	.0542	8.2245	8.5755
<u>hesperus</u>	8.3292	.0708	8.1537	8.5047
<u>mazama</u>	8.0542	.2750#	7.8787	8.2297
<u>pumilus</u>	7.8542	.2000	7.6787	8.0297

The alveolar length of the maxillary tooth row is taken on the skull from the anteriormost point to the posteriormost point of the alveoli of the molariform teeth.

Neither interaction or sexual dimorphism is significant in the analysis of variance but subspecies F-value is significant. The initial step in locating the differences among the subspecies is computation of LSD.

$$\text{LSD} = .2482 = 2.62 \sqrt{\frac{2(.1077)}{24}}$$

The LSD, .2482, is exceeded by the gap between the means of hesperus and mazama, .2750. Tests of the extreme mean indicates further separation.

(1) mutabilis equals niger, oregonus and hesperus.

$$v = \frac{.21980}{.06699} = 3.28. \text{ Critical value } 2.68. \text{ Significant.}$$

(2) hesperus equals niger and oregonus.

$$v = \frac{.06530}{.06699} = .97. \text{ Critical value } 2.43. \text{ Not significant.}$$

The results of the two tests, LSD and test of the extreme mean, may be summarized: (1) mutabilis is separable from all others by a greater alveolar length, and (2) mazama and pumilus are separable from

mutabilus, niger, oregonus and hesperus, but not from each other, by less alveolar length.

Confidence limits are computed as: Sample mean \pm .1755 (.53469 $\sqrt{.1077}$). The confidence interval of pumilus does not overlap the intervals of hesperus, oregonus, niger or mutabilus while the interval of mazama does not overlap that of mutabilus.

7. LENGTH OF NASALS.

A. Data.

	T O T A L S			S U M O F S Q U A R E S	
	Male	Female	M & F	Male	Female
mutabilus	171.3	166.3	337.6	2449.67	2308.73
hesperus	167.3	161.0	328.3	2339.85	2165.00
mazama	166.4	160.4	326.8	2312.00	2152.58
oregonus	160.6	160.5	321.1	2159.58	2153.17
niger	157.8	158.0	315.8	2087.94	2096.36
pumilus	160.1	151.3	311.4	2137.89	1909.45
Total	983.5	957.5	1941.0		

B. Analysis of variance.

Variation Due To:	d.f.	Mean Square	F	Remarks
Subspecies	5	3.7017	5.90	Significant
Sex	1	4.6944	7.48	Significant
Interaction	5	.5459	.87	Not significant
Error	132	.6305		
Pooled	137	.6274		

C. Analysis of sex.

	Error Mean Square	Sex Mean Square	F	Remarks
mutabilus	.384	1.041	2.71	Not significant
hesperus	.560	1.654	2.95	Not significant
mazama	.598	1.500	2.51	Not significant
oregonus	.759	.001	.00	Not significant
niger	1.313	.001	.00	Not significant
pumilus	.168	3.227	19.21	Significant

D. Analysis of subspecies.

	Mean	Difference	Confidence Limit Minimum	Maximum
<u>mutabilis</u>	14.0667		13.6432	14.4902
<u>hesperus</u>	13.6792	.3875*	13.2557	14.1027
<u>mazama</u>	13.6167	.0625	13.1932	14.0402
<u>oregonus</u>	13.3792	.2375	12.9557	13.8027
<u>niger</u>	13.1583	.2209	12.7348	13.5818
<u>pumilus</u>	12.9750	.1833	12.5515	13.3985

The length of the nasals is taken along the mid-dorsal suture of the skull from the anteriormost point of the nasal bones, excluding any cartilage, to a line perpendicular to the long axis determined by the posteriormost projection of either nasal bone.

The analysis of variance in section B indicates the presence of significance in both sex and subspecies but not in interaction. As determined by the individual F-tests, computed on the sexes of each subspecies in section C, only pumilus shows significant sexual dimorphism in length of the nasal bones, the males averaging approximately .8 mm. longer than the females in the sample. The means are 13.4 and 12.6 respectively.

Comparison with existing gaps between ranked subspecies means in section D reveals no possible separation by LSD.

$$\text{LSD} = .5989 = 2.62 \sqrt{\frac{2(.6274)}{24}}$$

The test of the extreme mean offers the following results:

- (1) mutabilis equals hesperus, mazama, oregonus, niger and pumilus.

$$v = \frac{.5875}{.1617} = 3.63. \text{ Critical value } 2.97. \text{ Significant.}$$

- (2) pumilus equals hesperus, mazama, oregonus and niger.

$v = \frac{.3867}{.1617} = 2.39$. Critical value 2.85. Not significant.

Mutabilus is separated from all other subspecies by greater length of the nasals.

The confidence limits calculated to include the subspecies population mean are computed as: Sample mean $\pm .4235$ ($.53469 - \sqrt{.6274}$).

No overlap occurs between the confidence interval of mutabilus, the subspecies exhibiting the greatest nasal length, and those of either pumilus or niger, the two subspecies with the least nasal length.

8. INTERORBITAL CONSTRICTION.

A. Data.

	T O T A L S			S U M O F S Q U A R E S	
	Male	Female	M & F	Male	Female
pumilus	81.9	80.9	162.8	559.09	545.73
mutabilus	80.0	78.2	158.2	533.44	509.76
oregonus	79.0	78.7	157.7	520.42	517.15
mazama	77.4	77.3	154.7	500.04	498.39
niger	77.1	77.2	154.3	495.99	497.38
hesperus	75.7	75.4	151.1	477.73	474.32
Total	471.1	467.7	938.8		

B. Analysis of variance.

Variation Due To:	d.f.	Mean Square	F	Remarks
Subspecies	5	.67710	16.81	Significant
Sex	1	.08030	1.99	Not significant
Interaction	5	.02094	.51	Not significant
Error	132	.04102		
Pooled	137	.04029		

C. Analysis of subspecies.

	Mean	Difference	Confidence Limit	
			Minimum	Maximum
<u>pumilus</u>	6.7833		6.7833	6.8906
<u>mutabilis</u>	6.5917	.1916 [#]	6.4844	6.6990
<u>oregonus</u>	6.5708	.0209	6.4635	6.6781
<u>mazama</u>	6.4458	.1250	6.3385	6.5531
<u>niger</u>	6.4292	.0166	6.3219	6.5365
<u>hesperus</u>	6.2958	.1334*	6.1885	6.4031

Measurement of the interorbital constriction is taken as the least horizontal distance across the dorsal surface of the skull between the orbits.

In so far as the measurement of interorbital constriction is concerned both interaction and sexual dimorphism are absent. However, significant differences are shown to occur within the subspecies. The gap between the adjacent means of pumilus and mutabilis, .1916, exceeds the LSD which is computed:

$$\text{LSD} = .1518 = 2.62 \sqrt{\frac{2(.04029)}{24}}$$

Tests of the extreme mean are made among the remaining subspecies means.

- (1) Hesperus equals mutabilis, oregonus, mazama and niger.

$$v = \frac{.17090}{.04097} = 4.17. \text{ Critical value } 2.85. \text{ Significant.}$$

- (2) mutabilis equals oregonus, mazama and niger.

$$v = \frac{.08230}{.04097} = 2.01. \text{ Critical value } 2.68. \text{ Not significant.}$$

Pumilus is distinct in having a greater interorbital breadth than any other subspecies and hesperus is separable from all others by the lesser interorbital breadth.

Confidence limits for the subspecies population means are computed as: Sample mean \pm .1073 ($.53469 \sqrt{.04029}$). From the tabulated minimum and maximum confidence limits in section C it will be noted that: (1) the interval of hesperus does not overlap those of oregonus, mutabilis, or pumilus, and (2) pumilus does not overlap hesperus, niger or mazama.

ANALYSES OF PROPORTIONS. The ratios here selected are designed to reveal the relative proportions along which the skull is constructed. Although significant differences occur in the lineal dimensions this does not determine whether or not any two measurements combine in identical proportions in all of the subspecies, such comparison is the purpose of the following set of analyses. By the same reasoning, the presence of significant variation in proportional ratios does not indicate the contribution of either or both components and frequent reference will necessarily be made to the lineal analyses for interpretive information. It should be noted that in each case the larger measurement is divided by the smaller, resulting in a figure greater than 1.

1. BASILAR LENGTH/MASTOID BREADTH.

A. Data.

	T O T A L S			S U M O F S Q U A R E S	
	Male	Female	M & F	Male	Female
mazama	22.103	21.936	44.039	40.7577	40.1234
niger	22.321	21.701	44.022	41.5695	39.2761
hesperus	21.321	21.453	43.175	39.3611	38.3811
mutabilis	21.398	21.088	42.486	38.1894	37.0733
pumilus	21.209	21.200	42.409	37.4987	37.4627
oregonus	20.473	20.413	40.886	34.9688	34.7721
Total	129.226	127.791	257.017		

B. Analysis of variance

Variation Due To:	d.f.	Mean Square	F	Remarks
Subspecies	5	.05897	20.69	Significant
Sex	1	.01430	5.02	Not significant
Interaction	5	.00201	.70	Not significant
Error	132	.00288		
Pooled	137	.00285		

C. Analysis of subspecies.

	Mean	Difference	Confidence Limit Minimum	Maximum
mazama	1.83496	.00071	1.80642	1.86350
niger	1.83425	.03529	1.80571	1.86279
hesperus	1.79896	.02871*	1.77042	1.82750
mutabilus	1.77025	.00321	1.74171	1.79879
pumilus	1.76704	.06346#	1.73850	1.79558
oregonus	1.70358		1.67504	1.73212

The basilar/mastoid ratio reveals the relationship between the dimensions of overall length and width of the cranium. Reference to section B of the above table indicates that, of the three F-tests, subspecies, sex and interaction, only subspecies is significant. To ascertain the location of this significance application of both LSD and test of the extreme mean is necessary.

$$LSD = .04037 = 2.62 \sqrt{\frac{2(.00285)}{24}}$$

The gap between pumilus and oregonus, .06346, exceeds the LSD.

(1) pumilus equals mazama, niger, hesperus and mutabilus.

$$v = \frac{.03405}{.0109} = 3.12. \text{ Critical value } 2.85. \text{ Significant.}$$

(2) mutabilus equals mazama, niger and hesperus.

$$v = \frac{.03935}{.0109} = 3.61. \text{ Critical value } 2.68. \text{ Significant}$$

(3) hesperus equals mazama and niger.

$$v = \frac{.02376}{.0109} = 2.18. \text{ Critical value } 2.43. \text{ Not significant.}$$

Oregonus displays a low value and is distinguished thereby from all other subspecies. Mutabilus and pumilus, while possessing larger values than oregonus, have significantly smaller ratios than mazama, niger or hesperus.

Reviewing the lineal components we find that there is separation between the subspecies by basilar length, and oregonus and mutabilus are separable from hesperus, niger, mazama and pumilus by mastoid breadth. The extreme mastoid breadth of oregonus is responsible for the significantly smaller ratio. Revelation of unsuspected data comes when pumilus groups with mutabilus, although pumilus has the smallest mean for both basilar length and mastoid breadth. The ratio approximates that of mutabilus which has the largest basilar mean and, with oregonus, is in the group of largest mastoid means.

Confidence limits for the subspecies population means are calculated as: Sample mean \pm .02854 ($.53469 \sqrt{.00285}$). Examination of the confidence intervals in section C indicates: (1) oregonus does not overlap any other subspecies, and (2) pumilus and mutabilus, while distinct from oregonus, do not overlap niger or mazama.

2. BASILAR LENGTH/HEIGHT OF BRAIN CASE

A. Data.

	T O T A L S			SUM OF SQUARES	
	Male	Female	M & F	Male	Female
mutabilus	34.622	33.583	68.205	100.0193	94.0786
niger	33.914	34.178	68.092	96.1801	97.5691
mazama	34.501	32.945	67.446	99.3230	90.5569
hesperus	33.348	32.826	66.174	92.7760	89.9056
oregonus	32.052	32.347	64.399	85.7534	87.4246
pumilus	32.117	30.811	62.928	86.0415	79.1356
Total	200.554	196.690	397.244		

B. Analysis of variance.

Variation Due To:	d.f	Mean Square	F	Remarks
Subspecies	5	.19252	14.30	Significant
Sex	1	.10370	7.70	Significant
Interaction	5	.02622	2.02	Not significant
Error	132	.01298		
Pooled	137	.01346		

C. Analysis of sex.

	Error Mean Square	Sex Mean Square	F	Remarks
mutabilus	.01013	.04498	4.44	Not significant
niger	.02536	.00291	.01	Not significant
mazama	.01086	.10088	9.29	Significant
hesperus	.00964	.01136	1.18	Not significant
oregonus	.01696	.00363	.02	Not significant
pumilus	.00495	.07106	14.36	Significant

D. Analysis of subspecies.

	Mean	Difference	Confidence Limit Minimum	Maximum
mutabilus	2.84187	.00471	2.77979	2.90395
niger	2.83716	.02691	2.77508	2.89924
mazama	2.81025	.05300	2.74817	2.87233
hesperus	2.75725	.07396*	2.69517	2.81933
oregonus	2.68329	.06129	2.62121	2.74537
pumilus	2.62200		2.55992	2.68408

The basilar/height of brain case ratio indicates the relationship between the dimensions of length and height in the construction of the cranium.

The sex mean square yields a significant F-value when divided by the pooled mean square, therefore the hypothesis that sexual dimorphism is present is accepted. Quite apparent from the tabulated subspecies totals by sex in section A, this dimorphism is not constant among the six populations, in fact, individual F-tests in section D indicate only mazama and pumilus exhibit significant differences in ratios. In both cases the males display a greater ratio value than the females, that is, the males have a longer basilar length relative to the height of the brain case. This is substantiated by the findings in the lineal analyses.

That all subspecies do not come from the same population in regards to this particular ratio is demonstrated by the significant subspecies F-value. As the initial step in determining which subspecies are separable the LSD is computed.

$$LSD = .08777 = 2.62 \sqrt{\frac{2(.10347)}{24}}$$

LSD is not exceeded by any gap between the ranked means. Since the

difference between the largest and smallest mean is greater than the LSD the test of the extreme mean is applied.

- (1) pumilus equals mutabilus, niger, mazama, hesperus and oregonus.

$$v = \frac{.13654}{.02369} = 5.76. \text{ Critical value } 2.97. \text{ Significant.}$$

- (2) oregonus equals mutabilus, niger, mazama and hesperus.

$$v = \frac{.10256}{.02369} = 4.33. \text{ Critical value } 2.85. \text{ Significant.}$$

- (3) hesperus equals mutabilus, niger and mazama.

$$v = \frac{.05438}{.02369} = 2.31. \text{ Critical value } 2.68. \text{ Not significant.}$$

By test of the extreme mean pumilus and oregonus are separable from mutabilus, niger, mazama and hesperus by the greater proportion of brain case height to basilar length.

It will be recalled from preceding analyses that, while pumilus is separable by the shorter basilar length, oregonus is distinct with the largest mean for height of the brain case.

Confidence limits are computed: Sample mean $\pm .06208$ (.53469 $\sqrt{.01347}$). Comparison of the confidence intervals indicates: (1) pumilus does not overlap hesperus, mazama, niger or mutabilus, and (2) oregonus does not overlap mazama, niger or mutabilus.

3. MASTOID BREADTH/HEIGHT OF BRAIN CASE.

A. Data.

	T O T A L S			SUM OF SQUARES	
	Male	Female	M & F	Male	Female
mutabilus	19.416	19.177	38.593	31.4330	30.6912
oregonus	18.786	18.829	37.615	29.4230	29.5871
mazama	18.763	18.133	36.896	29.3771	27.4236
hesperus	18.433	18.443	36.876	28.3536	28.3754
niger	18.214	18.606	36.820	27.7176	28.8763
pumilus	18.173	17.442	35.615	27.5358	25.3674
Total	111.785	110.630	222.415		

B. Analysis of variance.

Variation Due To:	d.f.	Mean Square	F	Remarks
Subspecies	5	.040532	13.27	Significant
Sex	1	.009260	3.03	Not significant
Interaction	5	.007682	2.67	Not significant
Error	132	.002878		
Pooled	137	.003054		

C. Analysis of subspecies.

	Mean	Difference	Confidence Limit	
			Minimum	Maximum
mutabilus	1.60804	.04075*	1.57849	1.63759
oregonus	1.56729	.02996	1.53774	1.59684
mazama	1.53733	.00083	1.50778	1.56688
hesperus	1.53650	.00233	1.50695	1.56605
niger	1.53417	.05021#	1.50462	1.56372
pumilus	1.48396		1.45441	1.51351

As the basilar/mastoid ratio examines proportionally the dimensions of width and length and the basilar/height of brain case the dimensions of height and length, so the mastoid/height of brain case correspondingly analyzes construction in the third plane, height and width.

In this ratio sexual dimorphism and interaction are absent.

Only the subspecies F-value is significant. Both LSD and test of the extreme mean provide indication of the exact location of that significance between the subspecies.

$$\text{LSD} = .04179 = 2.62 \sqrt{\frac{2(.003054)}{24}}$$

LSD is exceeded by the gap between the means of pumilus and niger, .05021. The difference between the largest remaining mean, mutabilus, and the smallest, niger, exceeds LSD.

(1) mutabilus equals oregonus, mazama, hesperus and niger.

$$v = \frac{.05137}{.01128} = 4.55. \text{ Critical value } 2.85. \text{ Significant.}$$

(2) oregonus equals mazama, hesperus and niger.

$$v = \frac{.02247}{.01128} = 2.08. \text{ Critical value } 2.68. \text{ Not significant.}$$

These results may be summarized: (1) pumilus is distinct from all other subspecies by a lesser ratio value, and (2) mutabilus is separable from all others by a greater ratio value.

If reference is made to the lineal analyses of mastoid breadth and height of brain case it will be noted the small ratio of pumilus results from a narrow mastoid measurement and a moderately high brain case. Similarly the large ratio of mutabilus is a reflection of a broad mastoid and a moderate brain case height.

Calculation of the confidence limits for the subspecies means yields: Sample mean \pm .02955 (.53469 $\sqrt{.003054}$). Examination of the minimums and maximums tabulated above reveals: (1) the confidence interval for the mean of pumilus does not overlap those of oregonus or mutabilus, and (2) the interval for the mean of mutabilus, while not

overlapping that of pumilus, is distinct from the intervals of niger, hesperus and mazama.

4. BASILAR LENGTH/PALATILAR LENGTH.

A. Data.

	T O T A L S			SUM OF SQUARES	
	Male	Female	M & F	Male	Female
pumilus	20.703	20.877	41.580	35.7277	36.3298
mazama	20.837	20.629	41.466	36.1897	35.4773
niger	20.616	20.646	41.262	35.4274	35.5448
hesperus	20.194	20.415	40.609	33.9878	34.7364
mutabilus	20.091	20.172	40.263	33.6571	33.9131
oregonus	20.102	20.064	40.166	33.6816	33.5582
Total	122.543	122.803	245.346		

B. Analysis of variance.

Variation Due To:	d.f.	Mean Square	F	Remarks
Subspecies	5	.016188	16.93	Significant
Sex	1	.000470	.49	Not significant
Interaction	5	.001000	1.05	Not significant
Error	132	.000955		
Pooled	137	.000956		

C. Analysis of subspecies.

	Mean	Difference	Confidence Limit	
			Minimum	Maximum
pumilus	1.73252		1.71599	1.74905
mazama	1.72775	.00477	1.71122	1.74428
niger	1.71925	.00850	1.70272	1.73578
hesperus	1.69204	.02721#	1.67551	1.70857
mutabilus	1.67762	.01442	1.66109	1.69415
oregonus	1.67358	.00404	1.65705	1.69011

In the three preceding experiments significant differences are displayed among the subspecies in major dimensions along the three

planes of length, width and height. This, and the following experiments, inquire into the possibility that similar differences do exist in two measurements on the same plane. Basilar length is an indication of overall cranial length of which palatilar length is approximately the anterior two-thirds.

The only significant separation, as indicated by the F-values in section B, lies within the subspecies means. To ascertain the location of this separation LSD is computed.

$$\text{LSD} = .02339 = 2.62 \sqrt{\frac{2(.000956)}{24}}$$

LSD is exceeded by .02721, the difference between the means of niger and hesperus, thus forming two groups of three means each, the group of larger means, including pumilus, mazama and niger, being separable from the group of smaller means, hesperus, mutabilis and oregonus.

Examination of subspecies means for basilar and palatilar lengths reveals, in general, a slight increase in basilar length is accompanied by a more rapid increase in palatilar length. However, mazama, with its shorter palatilar length, appears to be an exception to the general trend.

Confidence limits, with a confidence coefficient of .99, are computed as: Sample mean \pm .01653 (.53469 $\sqrt{.000956}$). The confidence intervals of oregonus and mutabilis do not overlap those of niger, mazama and pumilus, while that of hesperus is distinct from those of mazama and pumilus.

5. LENGTH OF NASALS/ALVEOLAR LENGTH.

A. Data.

	T O T A L S			SUM OF SQUARES	
	Male	Female	M & F	Male	Female
mazama	20.573	20.035	40.608	35.3951	33.5578
pumilus	20.291	19.423	39.714	34.4059	31.4619
hesperus	19.951	19.506	39.457	33.2642	31.8160
mutabilus	19.749	19.124	38.873	32.5612	30.5347
oregonus	19.195	18.803	37.998	30.8580	29.5184
niger	18.784	18.700	37.484	29.5637	29.3555
Total	118.543	115.591	234.134		

B. Analysis of variance.

Variation Due To:	d.f.	Mean Square	F	Remarks
Subspecies	5	.055164	5.95	Significant
Sex	1	.060520	6.52	Not significant
Interaction	5	.002830	.30	Not significant
Error	132	.009517		
Pooled	137	.009273		

C. Analysis of subspecies.

	Mean	Difference	Confidence Limit	
			Minimum	Maximum
mazama	1.69200		1.64195	1.74205
pumilus	1.60470	.03725*	1.60470	1.70480
hesperus	1.64404	.01071	1.59399	1.69409
mutabilus	1.61970	.02434	1.56965	1.66975
oregonus	1.58325	.03645	1.53320	1.63330
niger	1.56183	.02142	1.51178	1.61188

This experiment, as the preceding one, deals with two measures of length, the nasal length taken on the dorsal surface of the skull and the alveolar length of the upper molariform tooth row on the ventral surface.

It will be noted in section B that only subspecies shows a significant F-value, sexual dimorphism and interaction is lacking. Since all subspecies means do not belong to the same population, Tukey's method determines the significant separations.

$$LSD = .07284 = 2.62 \sqrt{\frac{2(.009273)}{24}}$$

LSD is greater than any gap between adjacent ranked means, however, the difference between the largest and smallest means exceeds LSD indicating use of the test of the extreme mean.

(1) mazama equals pumilus, hesperus, mutabilus, oregonus and niger.

$$v = \frac{.06609}{.01965} = 3.36. \text{ Critical value } 2.97. \text{ Significant.}$$

(2) niger equals pumilus, hesperus, mutabilus and oregonus.

$$v = \frac{.05088}{.01965} = 2.59. \text{ Critical value } 2.85. \text{ Not significant.}$$

Mazama is separable from all other subspecies by a larger nasal/alveolar value, that is, relative to the nasal length the alveoli are shorter. That mazama is distinct from all subspecies but pumilus by a shorter alveolar length was obtained in the lineal analysis.

Confidence limits for the subspecies population means are computed as: Sample mean \pm .05005 (.53469 $\sqrt{.009273}$). There is no overlap between the confidence intervals of pumilus with those of niger or oregonus.

6. ZYGOMATIC BREADTH/MASTOID BREADTH.

A. Data.

	T O T A L S			S U M O F S Q U A R E S	
	Male	Female	M & F	Male	Female
niger	14.951	14.686	29.637	18.6396	17.9902
mutabilus	14.600	14.478	29.078	17.7734	17.4777
pumilus	14.522	14.453	28.975	17.5801	17.4117
mazama	14.515	14.426	28.941	17.5829	17.3543
hesperus	14.535	14.249	28.784	17.6259	16.9281
oregonus	14.265	14.336	28.601	16.9684	17.1441
Total	87.388	86.628	174.016		

B. Analysis of variance.

Variation Due To:	d.f.	Mean Square	F	Remarks
Subspecies	5	.005182	4.50	Significant
Sex	1	.004010	3.48	Not significant
Interaction	5	.000736	.63	Not significant
Error	132	.001168		
Pooled	137	.001152		

C. Analysis of subspecies.

	Mean	Difference	Confidence Limit	
			Minimum	Maximum
niger	1.23487		1.21671	1.25303
mutabilus	1.21158	.02329*	1.19342	1.22974
pumilus	1.20731	.00427	1.18915	1.22547
mazama	1.20587	.00144	1.18771	1.22403
hesperus	1.19933	.00654	1.18167	1.21799
oregonus	1.19171	.00762	1.17355	1.20987

There is a significant difference in the mean ratios for the subspecies but not for sex or interaction. The initial step in determining location of the significance between the populations by Tukey's method entails calculation of LSD.

$$LSD = .02569 = 2.62 \sqrt{\frac{2(.001152)}{24}}$$

No gap between adjacent ranked means is as large as LSD but since the difference between the largest and smallest mean ratios, niger and oregonus, exceeds LSD the test of the extreme mean is applied.

(1) niger equals mutabilus, pumilus, mazama, hesperus and oregonus.

$$v = \frac{.02643}{.00693} = 3.81. \text{ Critical value } 2.97. \text{ Significant.}$$

(2) oregonus equals mutabilus, pumilus, mazama and hesperus.

$$v = \frac{.01145}{.00693} = 1.65. \text{ Critical value } 2.85. \text{ Not significant.}$$

It would seem that the zygoma, arching free from the main skull case,

would be less conservative in variation than those bones of the brain case limited in extent on all sides by adjacent members. However, the supposition is not supported by the facts of this experiment. Except for niger the proportion of the zygomatic breadth attained by the mastoid is statistically uniform in spite of quite some variation in the sample means for each character when considered independently. In niger a moderate zygomatic breadth combines with a small mastoid breadth to give a significantly larger ratio value.

Confidence limits for the subspecies populations, based upon the mean ratios, are computed: Sample mean $\pm .01816 (.53469 - \sqrt{.001152})$. The only means for which chance of overlap is not greater than 1% are those of niger and oregonus.

7. MAXIMUM BREADTH/MINIMUM BREADTH OF NASALS.

A. Data.

	T O T A L S			S U M O F S Q U A R E S	
	Male	Female	M & F	Male	Female
oregonus	27.22	25.18	52.40	64.2306	54.8696
niger	22.52	24.02	46.54	43.2220	48.8806
hesperus	22.88	22.50	45.38	44.5366	42.5048
mutabilus	23.32	20.56	43.88	42.5048	45.7684
mazama	21.72	21.00	42.72	40.0354	39.4650
pumilus	21.54	19.80	41.34	39.0090	32.9387
Total	139.20	133.06	272.26		

B. Analysis of variance.

Variation Due To:	d.f.	Mean Square	F	Remarks
Subspecies	5	.63561	6.74	Significant
Sex	1	.26180	2.77	Not significant
Interaction	5	.09530	1.01	Not significant
Error	132	.09434		
Pooled	137	.09437		

C. Analysis of subspecies.

	Mean	Difference	Confidence Limit	
			Minimum	Maximum
oregonus	2.18333		2.01907	2.34759
niger	1.93916	.24417 [#]	1.77490	2.10342
hesperus	1.89083	.04833	1.72657	2.05509
mutabilus	1.82833	.06250	1.66407	1.99259
mazama	1.78000	.04833	1.61574	1.94426
pumilus	1.72250	.05750	1.55824	1.88676

The maximum breadth is taken distally across the paired nasal bones perpendicular to the long axis at the point of greatest dialation. The minimum breadth is taken in a similar fashion across the proximal portion of the bones.

Only the F-value for subspecies is significant. LSD is computed as .23234.

$$LSD = .23234 = 2.62 \sqrt{\frac{2(.09437)}{24}}$$

The gap between oregonus and niger, .24417, exceeds the LSD. The difference between the largest and smallest remaining mean ratios is less than LSD so the process terminates. Oregonus is distinct from all other subspecies by a higher mean ratio. Examination of the raw data reveals this is largely due to a smaller minimum breadth.

The confidence limits including the subspecies population means are computed as: Sample mean \pm .16426 ($.53469 \sqrt{.09437}$). Examination of the tabulated confidence intervals indicates that of oregonus does not overlap those of mutabilus, mazama and pumilus.

VARIATION IN CRANIAL CHARACTERS, NON-STATISTICAL ANALYSES

Having completed the statistical analysis of cranial features of the six subspecies we turn now to non-statistical handling. The statistical experiments have revealed general architectural dimensions of the structure and relationships between some of these dimensions. The non-statistical characters are chosen to show, by a critical scrutiny, the detailed plan of shape and configuration of some variable cranial bones or their parts. Like an architect's blue print these cranial plans fall short of fully describing the complete structure, yet nevertheless they serve their purpose well as a practical means to an end, that of understanding subspecific relationships through similarities and dissimilarities.

It is not to be denied that data based upon assignment of a feature to one of two or more categories could be analyzed statistically, especially by one of the Chi-square tests. However, the variability, the inherent errors of assignment of intermediates, the personal bias, in general the crudities of the observational method would negate the labor involved in calculating an analysis. In fact the results might give a misleading and unfounded impression of non-existent accuracy. It is better, then, to present merely the gross observations of raw data with generalizations couched in guarded language.

1. INTERPARIETAL.

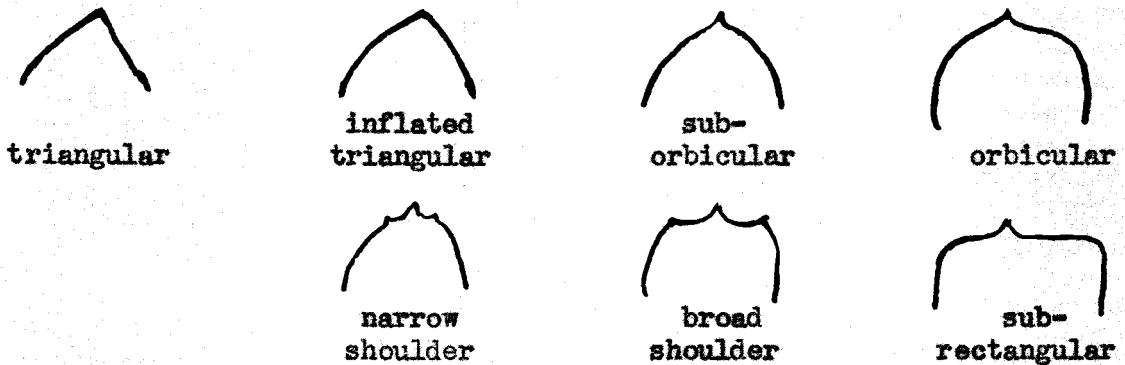
The interparietal has proven of importance in furnishing

specific characters in the genus Thomomys. Because of its individual variability it is of lesser importance in the classification of the closely related subspecies. Distinct in early life, it becomes smaller and the margins obscure in the older specimens as the outer borders are resorbed by pressure from the invading parietals. For the purpose of comparative analysis among the subspecies various aspects of size and configuration will be considered independently.

The larger gopher of the species, mutabilis, undoubtedly exhibits a slightly broader interparietal expanse but the individual variability, coupled with the difficulty of accurately determining exact measurements, forces abandonment of statistical handling of this structure. A brief investigation into the ratio of interparietal width to length for twelve males of each of the six subspecies revealed no significance. As a general indication of proportion, however, the length appears to equal approximately 75% of the width. On the other hand, features of configuration have been used repeatedly in previous descriptions of the subspecies and even a cursorial examination of a series of skulls indicates the merits of describing the trends present.

The anterolateral border, separating the parietal and interparietal, may roughly follow even curves with variation in inflation anteriorly from triangular to inflated triangular to suborbicular and finally to orbicular. The smooth flow of the line may be interrupted by a forwardly directed angularity, thus forming a narrow shouldered condition from an inflated triangle, a broad shoulder from

the suborbicular condition or a quadrilateral or a subrectangular form from the orbicular state.



Examination of 325 skulls including various numbers of males and females for each of the six subspecies yields the following data: triangular 1; inflated triangular 32; narrow shoulder 60; suborbicular 78; broad shoulder 120; orbicular 23; and rectangular 11. While error is inherent in assigning particular intermediates as to type it is apparent the suborbicular type, especially when coupled with interruptive angularity of the broad-shoulder type, includes the majority of the interparietals. Expected numbers by sex were calculated for each subspecies from the overall distribution of types. Hesperus and niger show approximately the same ratios as the six subspecies taken collectively, mutabilis displays considerable angularity and inflation, oregonus while retaining angularity produces less inflation. On the other hand mazama, most frequently suborbicular, is inflated but not angular and pumilus tends to be less inflated as well as not angular.

The posterior border, where the interparietal abuts against the supraoccipital, is distinct in younger individuals but is frequently

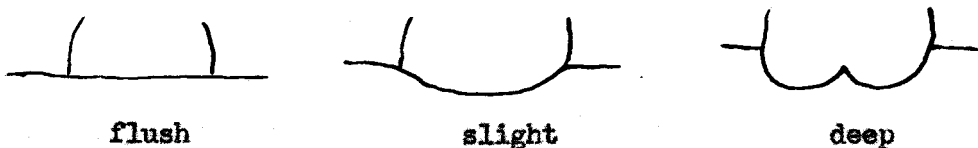
somewhat obliterated in older adults by fusion with the supraoccipital and formation of the lamboidal ridge. For convenience the shape of this border may be expressed as one of four general types: (1) truncate, in which the posterior border is squared at right angles to the long axis of the skull, (2) convex, the border sweeping in a smooth curve, the posteriormost extension occurring at the midline, (3) cordate, a notched condition with the center a V between lateral smoothly rounded curves in an inverted heart-base, and (4) angular, a concave notch between lateral angular projections.



Returning to the examination of the 325 skulls, the distribution of types is truncate 93, convex 106, cordate 48, and angular 78. Deviation is found in some of the subspecies; oregonus displays a remarkably high incidence of truncate borders with only a scattering of other types, pumilus shows equal amounts of truncate and convex borders but notching is virtually absent. The remaining subspecies approximate the general distribution except for variation within the notched condition which is about equally divided between cordate and angular in hesperus and mazama but largely angular in mutabilis and niger.

Finally, the degree of encroachment of the interparietal into the supraoccipital will be considered. This is best indicated by location of the junction of parietal-occipital suture with the border

of the interparietal. The condition of each skull may be typed as: (1) flush, the parietal-occipital suture being directly continuous with the posterior border of the interparietal, (2) slight, the parietal-occipital suture being smoothly confluent with the posterior border of the interparietal which arches posteriorward medially from the junction, or (3) deep, where the junction occurs more on the lateral border of the interparietal which extends markedly posteriorly into the supraoccipital.



This character is not entirely independent of the shape of the posterior border. Usually, but not always, the truncate border will also be flush and the notched condition coupled with either slight or deep extension.

The distribution of types for the six subspecies taken collectively is flush 118, slight 156, and deep 51. In mazama the types of 70 of 77 skulls were about equally divided between slight and deep with only 7 being flush. Of the remaining subspecies only hesperus with 4 in 68 and niger with 9 in 70 exhibit any deep extensions. The flush condition is more marked in oregonus and pumilus than in the remaining subspecies. In these cases many typed slight were just that, extremely slight with either truncate or convex borders.

2. NASAL.

The paired nasal bones, held firmly between the ascending arms

of the premaxillaries, form the roof of the nasal cavity with the narrower posterior proximal end securely ankylosed with the frontals and the free broader distal end, in life, supporting the cartilaginous extension and nose pad. These soft parts are removed in preparing the skull for observation. A glance at any series of skulls immediately proves the futility of ascribing a single shape or size to any particular subspecies. While not as satisfying, perhaps, a quantitative indication of trends within the typed variations is far more realistic.

The characteristic features of size of the nasals have already been analyzed. To review briefly; mutabilus is separable as a population from the other five subspecies by greater length of the nasals and oregonus, because of its lesser minimum breadth across the proximal portion, displays a significantly larger maximum/minimum ratio mean.

The proximal border may be a point lateral to the midline formed by each nasal bone. This point, depending upon the angle, can be spoken of as sharply emarginate or broadly emarginate. In other cases the posterior extension of the nasals may be abbreviated into either a rounded or a truncated condition.



sharply
emarginate



broadly
emarginate



rounded



truncated

Of 325 skulls the posterior border of the nasals of 176 were sharply emarginate, 88 broadly emarginate, 35 rounded, and 26 truncated. In all but one subspecies the ratio stands about two sharply emarginate to one broadly emarginate with a smattering of rounded and truncated in each series. In mutabilus, however, approximately a half of the specimens exhibited either the rounded or truncated condition.

The increase in breadth from behind forward may be gradual, giving straight lateral borders to the cuneate nasals, or it may be abrupt resulting from an uneven flaring. Where flaring occurs it is always distal, as if the nasals were suddenly freed from the constraining premaxillaries. To realize the prevalence of the variable spatulate condition it is only necessary to note that 257 specimens showed lateral inflation distally while the borders of 68 were straight or very nearly so. Again mutabilus does not conform with the other subspecies, 28 of 45 specimens display cuneate nasals with straight edges.

In dorsal aspect the nasal bones do not present an even surface, the proximal two-thirds may be involved in formation of an elliptical depression with a rather abrupt distal transformation into a domed elevation. The variations from this condition are numerous and difficult to typify, nullifying their usefulness as taxonomic characteristics.

3. PREMAXILLA.

The paired bones of the premaxilla constitute the greater part

of the rostrum; inferiorly they just enclose the palatine foramen with a tongue on each side, laterally they sweep forward then back in an arc from the ventral to dorsal surface where they separate the nasals from the maxillary root of the zygoma and articulate posteriorly with the frontal. The extension of the premaxilla beyond the posteriormost point of the nasals is estimated to the nearest one-tenth millimeter beneath a dissecting microscope. Since this extension varies from 0 to almost 2 millimeters three categories may be arbitrarily formed: (1) short, 0 to .5 mm., (2) medium, .6 to 1.2 mm., and (3) long, 1.3 mm. and over. The tally on 325 skulls lumped from six subspecies is 54 short, 187 medium, and 84 long. The majority of the extensions will be classified as medium in all six subspecies but certain trends should be noted. Better than one-third of the premaxillary extensions of nazana are short. In hesperus, oregonus and pumilus the extensions not medium are about equally divided between short and long while in mutabilis and niger they are all medium or long, 36 medium and 34 long being recorded for the latter subspecies.

In all but one subspecies the premaxillary narrows to a sharply emarginate termination. Due to the narrow proximal nasals of oregonus it is comparatively broad, the posterior portion most frequently rounded or broadly emarginate.

4. FRONTAL.

On the dorsal surface of the skull the frontal articulates posteriorly with the parietal and squamosal, laterally with the

alisphenoid, orbitosphenoid and lacrimal and anteriorly with the maxilla, premaxilla and nasals. In all six subspecies, it should be noted, the anterolateral wings extend forward between the premaxilla and maxillary root of the zygoma to a point constantly anterior to the proximal border of the nasals.

5. ZYGOMATIC ARCH.

The zygoma consists of a small bone, the jugal, supported anteriorly by the zygomatic arm of the maxillary and by the zygomatic arm of the squamosal behind. The curve of the arch spreads outward and downward from the squamosal insertion only to sweep upwards and forward for most of its length, then inward to the maxillary insertion, the dorsal surface coming level with the top of the skull.

The expanse, measured as the zygomatic breadth, has already been statistically analyzed. Mutabilus and oregonus exhibit the greatest mean breadth, niger is intermediate and the three remaining populations, hesperus, mazama and pumilus, display narrower arches. With a moderate zygomatic breadth, coupled to a comparatively narrow mastoid breadth, a significantly larger mean ratio is indicated for niger.

The base of the maxillary arm stands at an angle varying between about 60 and 80 degrees from the longitudinal axis of the skull. A template of plastic material was improvised for the determination of this angle for the males. For all subspecies, except oregonus, the skulls were assigned three classes, 60 degrees containing 35 skulls, 65 degrees with 55 and 70 degrees with 23 skulls. The distribution revealed by oregonus is 60 degrees, none; 65 degrees, 6; 70 degrees,

3; 75 degrees, 4; and 80 degrees, 3. Clearly, of the six subspecies, the maxillary root of the zygomatic arch more closely approaches a right angle in the males of oregonus.

Laterally the horizontal outline of the arch presents two features, the point of maximum breadth and the shape of the outside border. If the skull is broadest at the maxillary arm, the arch is seen to be divergent anteriorly. The zygomata are parallel if the greatest breadth occurs at the jugal or is shared equally by the jugal and the ends of the maxillary and squamosal arms. The zygomatic arches are said to be divergent posteriorly if the point of greatest breadth lies along the squamosal arm. The examined populations reveal a nearly equal division between the posteriorly divergent and parallel conditions except for hesperus where one-fourth of the zygomatic arches are seen to be divergent anteriorly with 60 percent classed as parallel. Independent of divergence the outer border may be convex or more or less straight in outline. Occasionally the jugal bows inward presenting a concavity or has an angular protuberance which must be overlooked in assigning classes. While the exact tallies differ somewhat among the subspecies the arches of 328 skulls were about half straight bordered and half convex bordered with no important discernable trend away from this ratio.

That juveniles exhibit convex-bordered, posteriorly divergent arches is worthy of mention.

Following the horizontal outline posteriorly over the squamosal arm a notch is noted just anterior to the external auditory meatus in

about one-third of the specimens. A definite, deep notch is recorded even less frequently. Although occurring in other populations the deep notch becomes a trend in oregonus where 9 of 43 skulls show the condition, and mazama where it occurs in 9 of 77 skulls. The squamosal shelf is narrow posteriorly in pumilus then abruptly, but smoothly and without a notch, flares outward to the horizontal arm.

6. PTERYGOID.

The pterygoids, forming the lateral walls of the posterior nares, are more or less quadrangular vertical plates firmly attached to the vertical plates of the palatine anteriorly, ankylosed with the basisphenoid dorsally, and developing the hamular process curving posteriad to articulate with the tympanic bulla. The inferior face of the pterygoids is enlarged and flattened in an obliquely rotating manner becoming horizontal anteriorly where it is continuous with the palatine to form the sides of the postpalatal notch the apex of which is well imbedded in the palatine. Several features of configuration are of taxonomic value, first the shape of the notch between the palato-pterygoid plates.

The style of notching varies from an acute V to a broad U. In the entire sample of 45 mutabilis and 69 niger the U condition is in evidence. The remaining subspecies display both types as well as intermediates. Hesperus tends to the rounded type with 36 U-shaped and 26 V-shaped notches recorded. The examined specimens of mazama and oregonus, while showing both types, tend to concentrate in the area of V-shape. The extreme in this direction is reached with

pumilus wherein, except for three narrowly U-shaped examples, all spaces were V-shaped in 22 skulls.

The two wings of the palato-pterygoid plates, including the hamular process of the pterygoid, may be either parallel or divergent posteriorly. The divergent condition is typical except for an occasional parallel case in all but one subspecies. In niger, however, 32 of 69 skulls displayed pterygoids parallel, or very nearly so.

Examined in lateral view the pterygoids gently arch downward from the palatine, then posteriorly swing upward again towards the audital bullae. For the purpose of convenience this arch can be typed as low or high. The low type is frequently interrupted by a longitudinal flattening extending as much as two-thirds the length of the pterygoid. A low to moderate arch is characteristic of mazama, niger, hesperus and mutabilus with a low incidence of high arches, only 11 in 250 skulls. The high arch is typical of oregonus, occurring 34 times in 42 skulls. Pumilus appears to be intermediate but tending more to the lower arch with but 7 of 22 being high.

The inferior face of the pterygoid is transversely broad and heavily constructed in niger, moderately so in mutabilus, and generally light and fragile in the remaining subspecies.

7. BULLAE.

The tympano-periotic capsule is composed of three parts firmly ankylosed together, the invisible periotic proper, exposed only inside the cranial chamber, the anteroventral tympanic or audital bulla and the posteriodorsal mastoidal bulla. The capsule is securely

clasped in place by the paroccipital process of the exoccipital and the mastoid process of the squamosal. The mastoidal bulla varies in each population as to extent and from an almost flat lateral surface to a slightly inflated condition, however, no constant deviation of taxonomic value is observed. The tympanic bulla, on the other hand does display distinctive features.

The bulla is generally moderately inflated dorsoventrally and, when viewed from the rear, the lateral surface slopes flatly, or with very little convexity, from the point of maximum inflation to the mastoid process. The anterior outline may be roundly truncated, indicative of a shorter or more inflated region, or inclined anteromedially to the basisphenoid in a longer or less inflated bulla. Angularity is produced by an anterolateral protuberance articulating with the point of a spicule ascending from the external pterygoid plate of the palatine. Comparatively, the bulla of pumilus is more globular, that is, more inflated dorsoventrally with the ventrolateral outline more convex and the anterior region heavily inflated and with angularity reduced or wanting. Angularity is most pronounced in mazama coupled with a moderately inflated anterior region whereas hesperus and niger which are also moderately inflated are far less angular, although a weak angular condition frequently occurs. The anterior region of oregonus and mutabilus is generally well inflated with little, if any, angularity.

VARIATION IN BODY DIMENSIONS

Three standard dimensions, total length, tail length and length of hind foot, are habitually taken on any mammal before preparation of a scientific skin. These measurements, plus the ratio between total length and tail length, will now be statistically analyzed. The techniques employed remain the same as in the statistical treatment of cranial features explained above (pp.7-15).

1. TOTAL LENGTH.

A. Data.

	T O T A L S			S U M O F S Q U A R E S	
	Male	Female	M & F	Male	Female
mutabilis	2793	2656	5449	651051	588218
niger	2650	2572	5222	585830	552322
mazama	2669	2488	5157	593941	516310
hesperus	2598	2552	5150	563464	543440
oregonus	2488	2457	4946	517049	504003
pumilus	2362	2271	4633	465350	430181
Total	15561	14996	30557		

B. Analysis of variance.

Variation Due To:	d.f.	Mean Square	F	Remarks
Subspecies	5	3199.4	50.30	Significant
Sex	1	2217.0	34.85	Significant
Interaction	5	131.8	2.16	Not significant
Error	132	61.0		
Pooled	137	63.6		

C. Analysis of sex.

	Error Mean Square	Sex Mean Square	F	Remarks
mutabilis	61	782	12.82	Significant
niger	76	254	3.34	Not significant
mazama	35	1365	39.00	Significant
hesperus	78	88	1.13	Not significant
oregonus	78	43	.55	Not significant
pumilus	37	345	9.32	Significant

D. Analysis of subspecies.

	Mean	Difference	Confidence Limit	
			Minimum	Maximum
<i>mutabilis</i>	226.833		222.569	231.097
<i>niger</i>	217.583	9.250#	213.319	221.847
<i>mazama</i>	214.875	2.708	210.611	219.136
<i>hesperus</i>	214.583	.292	210.319	218.847
<i>oregonus</i>	206.083	7.500#	201.819	210.347
<i>pumilus</i>	193.042	13.041#	189.778	197.306

Total length is the measured distance from tip of nose to the end of the fleshy part of the tail when the mammal is laid out straight, but not stretched, upon its back.

The data accumulated from the original observations are presented in section A and inspected by analysis of variance in section B. The F-value for subspecies, 50.30, exceeds the critical value of 3.17, therefore is significant. Similarly the F-value for sex, 34.85, is greater than the critical value of 6.85. The F-test for interaction does not yield a value greater than the critical minimum of 3.17.

Sexual dimorphism is not constant, in fact the series of F-tests in section C reveals that only in *mutabilis*, *mazama* and *pumilus* are the male means for total length significantly larger than the female means.

In section D, analysis of subspecies, information essential to testing for location of significant distinction between the subspecies is presented. Following Tukey's method the LSD value is computed.

$$LSD = 6.031 = 2.62 \sqrt{\frac{2(63.6)}{24}}$$

Referring to the column of differences between means it will be noted three separations are possible by application of the LSD. mutabilus with a mean of 227 millimeters is significantly larger than the grouped means of niger with 217, mazama 215 and hesperus 214.

Oregonus is significantly shorter with a mean of 206 while pumilus is distinctly the smallest population with a sample mean of only 193.

Confidence limits for the subspecies population means are computed as: Sample mean \pm 4.264 (.53469 $\sqrt{63.6}$). Examination of the minimum and maximum confidence limits indicates the unknown true total population means, as estimated by the .01 confidence coefficient, are distinct as follows: (1) the mean of mutabilus does not overlap the mean of any other subspecies, (2) the mean of pumilus does not overlap the mean of any other subspecies, and (3) oregonus does not overlap the possible means of niger or mazama and probably not that of hesperus.

2. TAIL LENGTH.

A. Data.

	T O T A L S			SUM OF SQUARES	
	Male	Female	M & F	Male	Female
mutabilus	928	846	1774	72004	59722
hesperus	857	844	1701	61479	59680
mazama	352	787	1639	60614	51739
niger	787	780	1567	52025	50978
oregonus	775	723	1498	50229	43705
pumilus	687	665	1352	39515	36995
Total	4886	4645	9531		

B. Analysis of variance.

Variation Due To:	d.f.	Mean Square	F	Remarks
Subspecies	5	951.6	48.55	Significant
Sex	1	403.0	20.56	Significant
Interaction	5	39.0	2.06	Not significant
Error	132	18.9		
Pooled	137	19.6		

C. Analysis of sex.

	Error Mean Square	Sex Mean Square	F	Remarks
mutabilis	14.44	280.16	19.40	Significant
hesperus	26.98	7.08	.26	Not significant
mazama	11.22	176.04	15.70	Significant
niger	31.31	2.04	.06	Not significant
oregonus	14.60	112.66	7.72	Not significant
pumilus	14.87	20.16	1.36	Not significant

D. Analysis of subspecies.

	Mean	Difference	Confidence Limit Minimum	Confidence Limit Maximum
mutabilis	73.917	3.042*	71.549	76.285
hesperus	70.875	2.583	68.507	73.243
mazama	68.292	3.000*	65.924	70.660
niger	65.292	2.875	62.924	67.660
oregonus	62.417	6.084#	60.049	64.785
pumilus	56.333		53.965	58.965

Tail length is measured from the point where the caudal vertebrae may be flexed, adjacent to the sacrum, to the fleshy tip of the tail excluding hair.

The males exhibit longer tails than the females of each subspecies, however according to the F-tests in section C this difference approaches the critical value of 7.95 in oregonus and is definitely significant only in the population of mutabilis and mazama.

To determine the location of significance between the subspecies

population means LSD and test of the extreme mean are calculated following Tukey's directions.

$$\text{LSD} = 3.348 = 2.62 \sqrt{\frac{2(19.6)}{24}}$$

The difference between the smaller mean of pumilus and the adjacent mean of oregonus indicates the former is distinct from all larger subspecies by LSD. Tests of the extreme mean are:

- (1) mutabilus equals hesperus, mazama, niger and oregonus.

$$v = \frac{5.758}{.9037} = 6.37. \text{ Critical value } 2.85. \text{ Significant.}$$

- (2) oregonus equals hesperus, mazama and niger.

$$v = \frac{4.302}{.9037} = 4.76. \text{ Critical value } 2.65. \text{ Significant.}$$

- (3) niger equals hesperus and mazama.

$$v = \frac{2.861}{.9037} = 3.17. \text{ Critical value } 2.43. \text{ Significant.}$$

The above findings may be summarized. Four classes are formed in descending mean tail length, mutabilus being the largest, followed by hesperus and mazama grouped together, then niger and oregonus also grouped together, and finally the smallest pumilus.

Confidence limits designed to enclose the unknown actual population means are: Sample mean $\pm 2.368 (.54368 \sqrt{19.6})$. From the tabulated confidence limits in section D it will be noted: (1) the confidence interval of pumilus does not overlap any other interval, (2) there is no overlap between the interval of oregonus and the intervals of mazama, hesperus and mutabilus, (3) the interval of niger does not overlap those of hesperus or mutabilus, and (4) mazama does

not overlap the interval of mutabilus.

3. TOTAL LENGTH/TAIL LENGTH.

A. Data.

	T O T A L S			SUM OF SQUARES	
	Male	Female	M & F	Male	Female
pumilus	41.392	41.113	82.505	143.1680	141.3650
niger	40.729	39.698	80.427	139.4950	131.6806
oregonus	38.661	40.915	79.576	125.0933	140.2407
mazama	37.651	37.990	75.641	118.3271	120.4358
mutabilus	36.183	37.721	73.904	109.3020	118.7857
hesperus	36.532	36.406	72.938	111.8637	110.7402
Total	231.148	233.843	464.991		

B. Analysis of variance.

Variation Due To:	d.f.	Mean Square	F	Remarks
Subspecies	5	.62605	14.76	Significant
Sex	1	.05044	1.19	Not significant
Interaction	5	.06256	1.50	Not significant
Error	132	.04166		
Pooled	137	.04212		

C. Analysis of subspecies.

	Mean	Difference	Confidence Limit	
			Minimum	Maximum
pumilus	3.43771		3.32756	3.54786
niger	3.35113	.08658	3.24098	3.46128
oregonus	3.31567	.03545	3.20552	3.42582
mazama	3.15170	.16397#	3.04155	3.26185
mutabilus	3.07933	.07237	2.96918	3.18948
hesperus	3.03908	.04025	2.92893	3.14923

This experiment is to determine if significant differences exist in the relationship of tail length to total length between the examined populations. Sexual dimorphism and interaction are absent; subspecies F-value is significant, this significance is traced by computation of LSD and comparison to tabulated differences between adjacent subspecies means.

$$LSD = .15578 = 2.62 \sqrt{\frac{2(.04242)}{24}}$$

Two groups are formed by application of LSD; pumilus, niger and oregonus with larger ratio means are separable from mazama, mutabilis and hesperus with smaller means.

Concerning the results of the three experiments, this one plus total length and tail length, some interpretation appears timely. Four classes are separated by significance in both total length and tail length and, except for niger, the classes have the same composition in both experiments. The analysis of total length/tail length indicates further that the increase in lengths are interrelated. The populations with shorter total lengths display a lesser proportion of tail length, thus a higher ratio value. The populations with greater total length show the tail constitute a comparatively greater proportion of the total length.

Confidence limits are computed for the subspecies population means as: Sample mean \pm .11015 ($.53469 \sqrt{.04242}$). The true population means, as estimated from the sample by the confidence interval, do not occur in the same region: (1) for either mutabilis or hesperus when compared with pumilus, niger or oregonus, and (2) for pumilus and mazama.

4. HIND FOOT LENGTH.

A. Data.

	TOTALS			SUM OF SQUARES	
	Male	Female	M & F	Male	Female
mutabilus	360	348	708	10806	10094
niger	356	347	703	10568	10047
hesperus	345	327	682	9929	9469
mazama	351	328	679	10273	8974
oregonus	337	336	673	9475	9416
pumilus	318	312	630	8430	8118
Total	2067	2008	4075		

B. Analysis of variance.

Variation Due To:	d.f.	Mean Square	F	Remarks
Subspecies	5	32.1900	14.29	Significant
Sex	1	24.1700	10.73	Significant
Interaction	5	2.2520	3.47	Significant
Error	132	.6484		

C. Analysis of sex.

	Error Mean Square	Sex Mean Square	F	Remarks
mutabilus	.36	6.00	16.67	Significant
niger	.89	3.38	3.80	Not significant
hesperus	.69	2.65	3.84	Not significant
mazama	.68	22.04	32.41	Significant
oregonus	.86	.04	.05	Not significant
pumilus	.41	1.50	3.66	Not significant

D. Analysis of subspecies.

	MALES			FEMALES	
	Mean	Difference		Mean	Difference
mutabilus	30.0000	.3333	mutabilus	29.0000	.0833
niger	29.6667	.4167	niger	28.9167	.8334
mazama	29.2500	.5000	hesperus	28.0833	.0833
hesperus	28.7500	.6767*	oregonus	28.0000	.6667*
oregonus	28.0833	1.5833#	mazama	27.3333	1.3333#
pumilus	26.5000		pumilus	26.0000	

Hind foot length is taken from the extremity of the heel along the flattened extended foot to the tip of the longest toe, including the nail.

Significant interaction is present, therefore subspecies mean square and sex mean square are divided by interaction mean square yielding significant F-values. Individual F-tests in section C show the male means are significantly larger than the female means in mutabilus and mazama, accounting for the sexual significance revealed in the original factorial analysis of variance.

Analysis of the subspecies means in the presence of interaction necessitates separation of the males and females with independent application of Tukey's technique. For convenient reference the means and differences for males and females are tabulated in section D.

A. Analysis of subspecies populations, males only.

$$LSD = .8778 = 2.66 \sqrt{\frac{2(.653)}{12}}$$

where 2.66 is the student's t-value at the 1% level for 66 degrees of freedom, .653 the error mean square for the males and 12 the number of specimens in each sample. The gap between oregonus and pumilus exceeds the LSD, the later subspecies mean being separable from all others by smaller foot size. Further separation of oregonus is possible among the male means by test of the extreme mean.

(1) oregonus equals mutabilus, niger, mazama and hesperus.

$$v = \frac{1.0667}{.2333} = 4.57. \text{ Critical value } 3.14. \text{ Significant.}$$

(2) hesperus equals mutabilus, niger and mazama.

$$v = \frac{.6667}{.2333} = 2.86. \text{ Critical value } 2.95. \text{ Not significant.}$$

B. Analysis of subspecies populations, females only.

$$LSD = .8725 = 2.66 \sqrt{\frac{2(.646)}{12}}$$

The female population of pumilus is separable from all others by LSD.

Mazama is also separable by test of the extreme mean.

(1) mazama equals mutabilus, niger, hesperus and oregonus.

$$v = \frac{.9333}{.2320} = 4.02. \text{ Critical value } 3.14. \text{ Significant.}$$

(2) oregonus equals mutabilus, niger and hesperus.

$$v = \frac{.5000}{.2320} = 2.16. \text{ Critical value } 2.95. \text{ Not significant.}$$

The interaction is revealed as a discrepancy in separations between the subspecies. The population of pumilus males and females, is significantly distinct from all other subspecies. The males of oregonus are separable from the remaining subspecies but the females are not. The same is true with a distinct female population in mazama while the males are grouped with mutabilus, niger and hesperus.

VARIATION IN COAT COLOR

Coat color, the result of specific physiological activities affecting pigmentation with these activities being controlled by genetic factors, by its susceptibility to the impress of natural selection has produced such remarkable varieties of correlative hues, shades, and tints that it has long been recognized as a primary taxonomic mammalian trait. A certain amount of difficulty is experienced in discussing coat color: the physiological activities responsible for pigment have been the concern of the laboratory biochemist; the controlling factors which are inherited via the germ plasm fall to the geneticist; and the expression of colors has been allocated to certain admittedly crude guides. Until the perfection of some physical measuring device, which will provide a more exacting and critical analysis and comparison, a wholly satisfactory process apparently will not be available. An attempt to be exhaustive in each of these fields will not be undertaken here, but a general integration wherever possible will be utilized for the sake of clarity. Capitalized color terms are those of Ridgway's 1912 edition of Color standards and color nomenclature.

Hair structure, unmasked by pigmentation, is best discerned in colorless hairs wherein the macroscopic white appearance is the result of light refracted from the various surfaces. The hair consists of a central core of spongy cells, the medulla. The outer cell surface of the medulla is irregular as if the keratinized walls had become wizened, and in a regular manner pits or lacunae extend

radially into the medulla forming two ranked rows of alternating pits in narrow hairs, three visible rows in larger hairs and as many as four and five regular longitudinal rows in the broadest, these staggered in nearly transverse diagonals across the medulla. A relatively thin, transparent cortex sheaths the medulla. The outer surface is lightly embossed with shingle-like scales. Distally, as the hair narrows to the tip, the medullary cells lose their uniform appearance, becoming irregularly tapered to an interrupted line one cell thick terminating within the thickened cortex which continues to an acute point.

The appearance of all hairs, except white ones, is dependent upon pigmentation superimposed upon the structural cellular construction. Three pigments are recognizable in the gopher: (1) granular aggregations in the medullary lacunae appearing black, (2) a closely related but more diffuse pigment of sepia granules occurring singly or in lineal aggregations within the inner cortex giving a dark brown coloration, and (3) a diffuse yellow-orange pigment of the medullary cells. In general pocket gophers of the genus Thomomys exhibit the primitive hair pattern of rodents known as agouti.

The agouti pattern is best seen in dorsal overhairs. The greater length of the hair is pigmented only by dense black aggregations of sepia granules partially filling the lacunae of the medulla. The medulla itself is transparent in this region and the general macroscopic effect is one of dull Dusky Neutral Grey. Distal to this basal portion the black granules disappear, their place being taken

by the diffuse yellow-orange pigment of the subterminal band. Located in the periphery of the medullary cells the color is most intense in the lacunae where, on the surfaces paralleling the line of vision, light passes through more pigment. The terminal band is generally a black or brown attributable to the reappearance of the black granular aggregations in the lacunae plus, peripherally, a wash of sepia longitudinally arranged in lineal aggregations or lines of independent brown granules in the inner cortex which, at times, nearly or entirely masks the underlying black masses. The short fine hairs of the underfur generally possess a modified yellow-orange band but lack the dark terminal band. The paler appearance of the underparts of the species is due, at least in part, to the lack of a terminal dark band, the ventral overhairs having only a basal black pigmentation and a distal pale band of diffuse yellow-orange.

The hypothesis that the pigment melanin is an oxidation product of tyrosin or related products of protein metabolism has been well established and accepted. The exact color produced is dependent upon the action of specific enzymes oxidizing a general chromogen substance. These facts, and the genetic findings of experimenters, led Sewall Wright to postulate the presence of two hypothetical enzymes acting upon a basic chromogen substance to produce the variety of mammalian coat colors (28, pp.224-235). His enzyme I, acting alone upon the chromogen, would produce yellow, enzyme II acting alone would have no effect on either chromogen or yellow pigment but coupled with enzyme I would, below the threshold of enzyme

I alone, produce sepia and at a higher level black pigment. According to Wright's hypothesis the agouti hair developing from the papillae is colored by a fluctuating relationship between these two enzymes. As the terminal portion is formed enzymes I and II, available in limited quantity, would form the cortical sepia and, working in greater abundance, the black aggregations in the medullary lacunae. Then as the hair elongates, a lack of enzyme II would account for formation of the subterminal yellow-orange band. Renewed nuclear release in quantity of enzyme II coupled with continuing release of enzyme I would produce black masses in the forming proximal portion of the hair. With the variation possible in intensity and distribution of these pigments the constancy of overall mammalian coat color and pattern is truly amazing.

The inheritance of factors transmitted in the nuclei and acting through physiological processes, probably as outlined above, has been indisputably established by the geneticist. Unfortunately no one, to my knowledge, has successfully bred pocket gophers in captivity, and consequently genetic comparison to factors determined in other animals is the only evidence available. Limited as such inductions must be, they are nevertheless valuable in establishing provisional hypotheses, to be tested and accepted or eliminated wherever possible, explaining the observable variations.

Judging from specimens collected in northwestern Oregon, the coat color of pocket gophers may be modified at any one or more of several levels; these are classified as follows:

Class 1. Factors affecting the individual hairs, hence general coat color.

- a. Factors affecting distribution of pigments.
- b. Factors affecting intensity of pigments.

Class 2. Factors affecting the hairs of specific regions, hence general coat pattern.

- a. Factors producing bicolor pattern.
- b. Factors producing black patches.
- c. Factors producing white spotting.

CLASS 1. FACTORS AFFECTING THE INDIVIDUAL HAIRS, HENCE GENERAL COAT COLOR. Physiological factors controlling the sequence of pigment elaboration during hair formation over the entire body, except where interrupted by the pattern factors of Class 2, produce a uniformity of individual hair coloration.

Class 1a. Factors affecting distribution of pigments. The normal agouti pattern, as exemplified by dorsal overhairs of the brown gopher, has been described above. Albino and black specimens are marked deviations in pigment distribution.

(1) Albino. The only recorded white specimen of Thomomys monticola in northwestern Oregon was a mount, without skull, given to Bailey at Scottsburg, Oregon, and erroneously referred to T. m. niger (2,p.20). The specimen was more probably T. m. oregonus which occupies bulb farms and hillsides in the immediate vicinity. Albinos are known in other species of Thomomys, six being reported in

T. bottae of California by Storer and Gregory (25,p.308). The factor for albinism, the gene c, has been determined in laboratory mammals to be recessive to the gene C responsible for normal coloration. See dilution below for discussion of a third allelomorph g^d. In the presence of cc no appreciable amount of pigment is formed in the hair, skin or eyes. According to Wright albinism is due to the complete lack of enzyme I.

(2) Black. The general coat color of all individuals of T. m. niger is glossy black, as is that of seven of 47 specimens of T. m. mutabilis. Microscopic examination of the hairs reveals the complete absence of yellow-orange pigment, its place being taken by densely packed black masses of granules in the medullary lacunae which, in the distal region of the hair, extend over the surface of medullary cells between lacunae as short thickened strings looking most like deeply stained mitotic chromosomes. A distal wash of elongated dark sepia granules is present in the inner cortex, extending well beyond the terminal cells of the medulla.

The presence of a recessive gene a producing wholly black individuals has been demonstrated in the house mouse, rat, rabbit, and guinea pig. The dominant allele, A, results in the normal agouti coat of these rodents (25,p.309). The gene a could produce the black hair in case of failure in production of an inhibitor for enzyme II during the time the subterminal yellow-orange agouti band is normally formed in the follicle.

In addition to its occurrence in T. monticola the black coat

color is recorded for individuals of several species and subspecies. For example, Bailey states that, in T. orizabae of southern Mexico, 14 of 16 specimens from the type locality on Mount Orizaba are black and that five of 17 T. townsendii from southern Idaho are black. Additional records serve to show how common and widespread this variant is within the genus (2, pp. 21-22). It should be noted, however, that the phenomenon of "melanism" of the mammalogist does not differentiate between the non-agouti black and the dark brown extended coat discussed below. The two conditions are genetically distinct. The lapse of time necessary for phylogenetic establishment of an all black population and the evidence from intergradation with the brown oregonus are additional indications that, in niger at least, the gene is recessive. These will be discussed in detail later.

Class 1b. Factors affecting intensity of pigments. Clear cut examples of changes in intensity of pigmentation alone are rare in the subspecies under examination, being obscured by continuous variation wherever changes of intensity occur, or where discontinuous are coupled with distribution of pigments to give a darkening or lightening effect of general coloration. The most notable instance appears in mazana where, on the east flank of the central Oregon Cascades, some specimens tend to a paler, more yellowish subterminal band typical of T. m. nasicus which is contiguous to the east. Elsewhere the agouti band is a more intense yellow-orange.

Class 1a and 1b acting in combination. An intensification of color is coupled with an extension of dark pigment or vice versa.

(1) Extension. Over a period of several decades Alex Walker has made a collection of twelve selected "melanistic" individuals of T. m. hesperus from the upper Nestucca Valley, Tillamook County, Oregon. These specimens vary from a general intensification of brown pigment in a broad mid-dorsal line to an individual which might, at first glance, be mistaken for niger. Closer examination, however, reveals a discernable brownness, especially upon the hips. The extension of dark brown sepia has affected both dorsal and ventral hairs. Microscopic examination of dorsal overhairs from a moderately extended individual shows the extension of both granular cortical wash and medullary aggregations at the expense of the yellow-orange subterminal band. While certain hairs lack medullary aggregations, the remaining Apricot-buff band of other hairs show dark brown sepia granules scattered through-out. In the darkest specimen the yellow is greatly diluted by heavy sepia granulation, this uniformly so.

Extension of black or chocolate, in which the yellow band in the hair is completely lacking or else shows in only a comparatively few hairs, has been determined in the rat and rabbit. This extreme extension Ed is one of an allelomorphic series of four genes in which the wild type is represented as E. Extreme extension is dominant to wild-type or normal extension (25, p.305). While the phenotypic description of Ed agrees with the extreme condition in hesperus the assignment of this factor is purely tentative, dependent upon future breeding analyses of the pocket gopher or other mammal showing similar aberration. The graded series of extension argues for

multiple gene action.

(2) Dilution. A peculiarly aberrant specimen of T. m. oregonus was taken on Bull Mountain near Tigard, Oregon. Grossly the animal is a pale Sayal Brown. Closer examination shows the normal terminal wash of brown sepia granules to be missing, the agouti band is a pale brownish color, a mosaic of colorless medulla cells interspersed between lacunae with various shades of pale to deep yellow-orange and a scattering of dark reddish-brown granules. The long proximal band lacks pigmentation entirely in some hairs, in others the black aggregations are present but erratically disposed giving a Light to Pallid Neutral Grey basal color when examined grossly.

In the absence of breeding tests it is impossible to state with certainty the genetic mutation here represented. Tentatively, therefore, this condition will be referred to the allelemorphic g^d gene of the albino series as is done by Storer and Gregory for California specimens (25,p.307). In the mouse and guinea-pig, g^d causes a paling dilution of the black and red pigment. Regardless of the genetic mode of control, the physiological processes responsible for normal coat color have been remarkably interrupted.

CLASS 2. FACTORS AFFECTING THE HAIRS OF SPECIFIC REGIONS, HENCE GENERAL COAT PATTERN. Physiological factors acting upon the individual hairs of a particular region, regardless of whether limited or of broad extent, are placed in this class. The physiological actions may be similar or identical to those producing Class 1 colors but are of restricted nature and are inherited independently.

Class 2a. Factors producing bicolor pattern. Normal brown gophers display a color change from the dorsal to ventral surface, the transition appearing along a broad zone extending from the cheek pouches, above the forelegs, along the flanks, above the hind legs, and ending at the base of the tail. The ventral paling of the yellow-orange pigment is accompanied by loss of the dark terminal band, shortening of the hairs, and reduced density of pelage. The ventral surface is therefore some pale tone of buffy yellow-orange ticking overlaying a Dusky Neutral Grey. A similar but more spectacular coat pattern exists in the population of T. m. mutabilus of the Nehalem Valley. The back is a pure black with the glossy sheen of niger. In a narrow zone sweeping posteriorly on either side from the nose across the pouches, over the forelegs, thence along the flanks and above the hindlegs, and finally sweeping down to the base of the tail is a line of demarkation from the ventral brown coat. The ventral brown, varying from Apricot Buff to Ochraceous-tawny on gross examination overlays Dusky to Deep Neutral Grey basal fur.

The discontinuous nature of gene action responsible for the dichromatic pattern is indicated by: (1) the exact duplication of the pattern in 38 specimens, (2) the presence of two brown and seven black individuals in the same population with no sign of intergradation to either monochromatic phase, and (3) intergradation of brown oregonus and black niger that has not produced bicolored individuals. Unfortunately, determination of the mode of inheritance must wait upon experimental breeding.

Interestingly, the only recorded occurrence of the black and brown bicolor pattern in a gopher, as far as I could determine, is a specimen of Thomomys talpoides clusius taken 25 miles north of Fort Collins, Colorado (5,p.129).

Class 2b. Factors producing black patches. An oblong area of short black hairs extends posteriad from the ear, the postauricular patch. The hairs are normal in shape and types, but clumped granules, occupying the lacunae through-out the length of the medulla, are responsible for the black coloration. An admixture of hairs marks the region of blending of black and brown along the periphery. Here may be seen all black hairs with a reduction of granular black in the subterminal band, others where some black granules remain beneath the pale orange-yellow of a short subterminal band, and still others in which all the black has been lost in the yellow-orange band although the terminal band is still extended and dark at the expense of the former area. The hairs of the dilute example of oregonus are normal for the patch except for the absence of terminal band cortical granular wash which gives a general coloration between Deep and Dark Neutral Grey. The postauricular patch blends into obscurity in the darker extended hesperus coat and the black coat of niger and mutabilus. The genetic control is unknown but apparently the gene occurs only in the homozygous state in this species.

Class 2c. Factors producing white spotting. White spotting, inconspicuous enough to be overlooked on casual examination, is to be

found on the feet, often extending up onto the wrists, and the distal portion of the tail. Closer scrutiny invariably reveals white hairs lining the pouches and usually others around the lips. Additional white ventral spotting is of frequent occurrence although differing in incidence and extent among the several subspecies. There is no ventral spotting in 27 specimens of pumilus. Only two of the examined specimens of maxama show any spotting supplementary to the basic pattern, this limited to a small area on the throat. Of 47 examples of oregonus five have limited thoracic spotting and two others have rather extensive areas. A ratio of one in four hesperus have a white spot between or just posterior to the forelimbs. A thoracic spot is present in eight of 47 mutabilis with an additional area in one around the hind leg and extending antero-medially to cross the midline. Ventral spotting occurs most frequently in niger where the white areas stand in bold contrast to the surrounding black coat. This condition exists in 37 of 96 specimens examined; usually of limited extent, the spotting becomes extensive over the ventral surface in 12, sometimes coalescing with an enlarged chin patch and one or more of the feet. In one specimen the ventral white is expanded transversely on the right side as a wide and tapering band midway between the fore and hind limbs to the mid-dorsal line.

Dorsal spotting is less common and has been found only in oregonus and niger. A blaze occupies the median line directly between the pinnas in 24 of 44 oregonus, a feature unique enough to this subspecies to be of aid in separating it from adjacent forms.

Six examples also have white hairs scattered along the mid-dorsal region of the anterior body as a scarcely discernible interrupted line. Ventral spotting and dorsal line appear to be more closely linked to blaze than would be expected by chance alone, this occurring with but one exception, a specimen with ventral spot but lacking the blaze.

Scattered white hairs interspersed among the black give a slightly grizzled effect in four specimens of niger. No definite spot is formed, however. Limited ventral spotting is present in two instances, absent in the other two.

The most spectacular spotting aberration found in the gophers of northwestern Oregon is represented in eight specimens of niger collected in two separate colonies, one on Tenmile Creek, the other on the Yachats River, both near Yachats, Oregon. Ventrally, patches of white frequently extend erratically from the legs to a mid-ventral area, the chin and throat are largely affected, and the white extends over the margins of the cheek pouches and around the nose to form a stripe running along the dorsal median line between the eyes to the level of the pinnae. A ninth specimen follows the pattern closely but the facial hairs are mixed black and white forming a grizzled stripe. While the termination and median orientation remain fixed, the width of the stripe and symmetry around the pouches is variable between particular individuals. This facial stripe is described by Storer and Gregory from a Thomomys perpallidus taken at Palm Springs, California (25,p.311).

Storer and Gregory (25,p.310) apply the Dutch spotting of Castle to the conditions they found in pocket gophers. The series in rabbits contains three alleles Du, du^w, and du^d. The gene Du produces the unspotted condition, du^w the white Dutch, and du^d the dark Dutch. The considerable phenotypic variation between the dark and light extremes is thought by Castle to be the expression of heterozygotes. According to Castle's chart of grades of Dutch spotting (6,Plate 1) most gophers are of grade 1, a few have the more extensive spotting of grade 2, while the examples of niger possessing a facial stripe correspond to grade 4 in the head region and grade 2 for the rest of the body.

Still another approach to the explanation of the observed condition is by homologizing the pocket gopher with mutations found in the house mouse Mus. The gopher and mouse are more closely related, phylogenetically, than are the gopher and rabbit. Grüneberg believes that spotting is the result of a recessive gene g acting in conjunction with a "k" complex of genes. He states (13,p.55):

"In the absence of the "k" genes, that is in the presence of their normal allelomorphs, g is almost completely recessive to its normal allelomorph. On the other hand, the "k" genes are almost recessive in the absence of g; however, on a s/s background they are semi-dominant. In other words the dominance of g is influenced by the presence or absence of the "k" genes, and the dominance of the "k" genes is influenced by the presence or absence of g."

In the mouse the "k" complex is thought to contain about three genes with major effect and possibly several others with minor effects. However, even the major genes have a limited effect singly, but combined may have a greater effect than g.

Particular areas are susceptible to an interference of the normal processes of pigment formation. However, these areas are not all equally liable to a certain interference since there is a singularity of effect not attributable to simple quantitative increase of the interfering factor. The presence of multiple genes with both modifying and cumulative effects has been advanced above. Nevertheless specific genes, either g or, more likely, a member of the "k" series is apparently responsible for a specific effect, at least in certain instances, although the phenotypic expression, admittedly, may be modified by other genes. This is especially true if, as Wright postulates, white hairs are the result of a deficiency in production of the hypothetical enzyme I by the nuclei of papillae cells. For example, white blaze of oregonus is independent of any other spotting except that basic type common to all the subspecies, yet blaze is absent in niger where white spotting of a different nature is prevalent. This does not negate the multiple nature of inheritance for the blaze pattern, but rather suggests that certain unique gene or genes must be present within the multiple accumulate. Barto and Huestis (4, pp. 245-248) analyzed a character, possibly identical, found in wild Peromyscus, called by them white star. The inheritance involved interaction of multiple genes.

Ventral spotting in oregonus may tentatively be thought of as due to a particular spotting gene in the heterozygous state which attains expression through the modifying influence of blaze. The single case of ventral spotting without blaze would be explained by

its occurrence in the homozygous state.

On the other hand, a graded series ranging from limited ventral spotting through extensive ventral spotting to facial stripe in niger seems to be a quantitative increase, the cumulative effect of several spotting genes. Facial stripe has not occurred independent of extensive ventral spotting.

MOLT. Certain pelage changes and coat markings are due to particular stages of molt. There are two molts in the gophers studied, one in summer, the other in late fall. In some extralimital species the winter pelage is darker or greyer than the summer condition. However, in the lowland subspecies of Thomomys monticola for which specimens are available from throughout the year practically no difference of color is discernible although the winter coat is generally softer and denser than the summer coat. The summer molt causes extreme disruption of normal color pattern by dark molt lines on brown gophers, by areas of thinned and worn hairs contrasting to adjacent fresh full coat, and, at times, by severe thinning to show patches of basal fur and even the skin.

The summer molt, in its various stages, is adequately represented by specimens; the time of molt has coincided nicely with the time of major collecting effort. The following sequence of events is based upon specimens of niger, hesperus and oregonus. The series of mazama, pumilus and mutabilus are in general accord at the equivalent times of collection. Bailey describes the spring molt as consisting

of up to five waves of partial replacement commencing on the face and progressing in succession posteriorly over the body (2, pp. 18-20). It is believed that the new interpretation given here, primarily based on careful examination of a series of skins taken from the same area throughout the summer months and secondarily by comparisons made to the manner of molt in other mammals such as the weasel, could be substantiated by observations on captive gophers whose fur had been stained or bleached.

The time of commencement of the first stages of molt is variable for different individuals in the same subspecies and even in the same colony. Some specimens show a thinning on the dorsum and signs of new hair growth just above the nose early in June while others maintain the winter coat intact into early July. After the middle of July, however, most gophers are well into the process. At least three regions along the mid-dorsal line are primary areas of initial hair growth. The first to appear is a spot immediately anterior to the eyes which, with time, extends its area by the emergence and growth of new hairs posteriorly and laterally. In the meantime a second center is activated between the pinnas. New growth radiates from this center as a wave posteriorly and to a lesser extent laterally causing an antero-posteriorly elongated crescentic line of demarkation from the thinning winter hair. Soon after the appearance of the centers of growth upon the head a third center is established along the back just posterior to the shoulders. Because of its elongate nature and the action of differential growth this center may

become broken into two or more sub-regions each of which, by posterior and lateral increase in size, form crescents which, in some cases, become erratic and run together. Growth, of course, ceases when a region collides with the one posterior and since the hairs were formed at different times a discrepancy in length leaves a faintly discernible line marking the junction. By late August the areas have joined to form a bright uniform coat over the entire anterior of the body, the old winter coat remaining over the rump and hips as well as anteriorly and ventrally to mid-body. On a single irregularly crescentic front the formation of new hair continues posteriad and ventrad during September, usually completing the coat replacement by October.

The fall molt is discernible in November specimens of oregonus and hesperus but insufficient specimens are at hand to fully interpret the process. Commencing again along the mid-dorsal region, a zone of growth appears to move both laterally and posteriorly as in the late summer molt. However, there is no thinning preceding the growth which is perceptible as a narrow band of short hairs of decreasing length, peripherally, sandwiched between the soft dense winter coat and the still plush summer coat. From the back this line may be readily traced, in some instances, anteriorly and ventrally along the flanks and inward across the abdomen. Whether this molt results in complete replacement of the summer coat or just adds a filling of additional hairs was not determined.

The young, leaving the nest to enter the tunnel system, and

traps, possess the dull dark plumbeous juvenile coat. Soon thereafter the first molt is initiated being similar in nature to the adult summer molt but proceeding less erratically and with greater celerity to completion by August.

COAT COLOR GENES AND PHYLOGENY. The preceding array of color variations is bound to set any field biologist to thinking on the evolutionary factors responsible for this unique display. One might think that pocket gophers, living continuously underground, would be of uniform color. Quite the contrary, there is throughout the genus a considerable variation. The colors are not entirely random, however. Those gophers whose range is limited to the light soils of the desert regions are correspondingly light colored and those occupying the dark soils of humid regions are, regardless of specific or subspecific relationships, generally dark. Grinnell has admirably illustrated this phenomenon as it occurs in California (19, pp. 179-180). The same trend is readily perceived among the Oregon gophers. How then are such outstanding abnormalities as the black population of niger, or the bicolor pattern of mutabilus, or for that matter the facial stripe of certain niger allowed to exist if natural selection, as is believed, tends to mold the gopher so like the substrate in which it dwells?

The most significant impress of natural selection on coat color is limited to the time the gopher appears at or above the ground surface, the few guarded moments when it is most available as food for any one of several predators. In the gopher's everyday habits this

surface appearance is mainly confined to two activities, mound building and feeding. In the Cascades, mazama is frequently seen outside the tunnel cutting and stuffing nearby herbs into cheek pockets with feverish celerity, retreating hastily to the safety of the burrow as soon as the pockets are full. The coat of mazama reflects the soil conditions with recognizable subgroups that can be correlated with soil types. Examples from the deep rich soils of the low level humid zone at Rhododendron, on the west base of the Cascades near Mt. Hood, are the darkest members of the subspecies; the pale arid pumice flats on the east flank of the Cascades south of Bend are inhabited by pale individuals; the intermediate soils of the alpine meadows of Crater Lake, Santiam Pass and Mt. Hood yield individuals intermediate in coloration.

Figuratively immersed in a bountiful food supply the coastal gophers have abandoned as unnecessary the above ground foraging. While still practiced on a restricted basis, as infrequently indicated by cut vegetation around a mound, only once have I seen one of these gophers above ground; it was carefully filling its pouches oblivious to any danger only six feet from where a trap was being set in another entrance to its tunnel system. On occasion I have witnessed a plant shake violently, then in a series of short quick jerks disappear into the ground leaving a small hole as the only evidence of where it had been. The selective forces, limited now to the instants of exposure in mound formation when the gopher thrusts out a load of dirt and, without using precious moments to turn around,

scurries tail first back to the safety of the burrow, are no longer as effective in pruning the populations of conspicuous aberrations. Nevertheless, natural selection does exist and does act upon the population.

The problems of how certain specific spotting genes or bicolor coat arose and became distributed are intriguing but the most interesting and significant illustration of population genetics and phylogeny concerns the relationship between brown and black coat. The general question of how the ancestral population of brown monticola stock gave rise to the black population of niger is too complex and requires knowledge not now available for adequate solution. However, without attempting spuriously exact conclusions, a clearer understanding of the taxonomic relationships may be gained by perusal of the data available.

Once a mutation occurs, if it has a selective advantage, the number of generations necessary for establishment of a given percentage frequency may be mathematically computed (9,p.220). If black had a selective advantage of one percent over its allele brown (for instance if one more black individual survives in a mixed population of 100 black and brown gophers than in the preceding generation through having escaped predation by owls better at night while casting out dirt from the tunnel mouth) over one million generations would be required to change the gene frequency from .01 to 99.99 regardless of whether the mutation be dominant or recessive. With only a single generation produced each year this would mean that the

mutation would have had to occur back in the middle Pleistocene.

Additional selective advantage, which is difficult to visualize, or additional mutation pressure, especially during the earlier generations, would speed up the process somewhat. The vagaries of chance, however, could do more to disrupt the mathematical model and accelerate evolution. Invasion of a new territory is not accomplished by a heterogeneous sample of the total ancestral population but rather by a small non-heterogeneous colony or colonies adjacent to the route of expansion or invasion which are thereafter intermittently or continuously isolated from the parent stock. There, in small colonies, chance alone could quickly establish or wipe out a gene independent of selective pressure. Of course if the character causes the organism to be incompatible with the environment then extinction may result.

It is impossible to ascertain with any degree of certainty just where along the phylogenetic line the mutation for black occurred, whether at the time the parent stock diverged from monticola or later by independent mutation after the subspecies were isolated. If the gene became established in the common ancestral population of the coastal gophers it seems that complete fixation had not occurred since a closely related brown population of hesperus is found just north of niger, while mutabilus, still further north, displays a population not yet genetically stabilized with both brown and black individuals. Each probably received a different labeling from the genetic pot fortuitously offering unique genes to each along with a

basic portion of identical genes. In view of the geographical proximity and ecological similarities of ranges it is doubtful that selection, acting alone, would favor black on the north and south while eliminating it in hesperus.

Therefore, it is entirely possible that black coat color was established by the action of chance but it seems probable that complete fixation did not result from chance alone in niger. Returning to the action of selection, in the absence of breeding tests we are handicapped in not knowing for certain if black coat color is dominant or recessive to its brown allele. For a dominant gene the initial frequencies are rapidly increased in a few generations whereas a greater number of generations are required to alter the frequency as it approaches 100. A dominant gene would have to be almost absolutely fixed in the population by chance; 900,230 generations are required just to shift the frequency from 99.90 to 99.99! On the other hand the initial stages of establishment proceed exceedingly slowly for a recessive gene, then accelerate rapidly as the higher frequencies are attained, a selective advantage of .01 being sufficient for a shift from 1.00 to 99.99 in 11,280 generations, a time lapse entirely compatible with the probable phylogenetic history (9,p.220).

A further indication that the gene for black may be recessive is discernible in the gophers inhabiting upper meadows of Marys Peak in Benton County where both black and brown individuals were obtained. A brown gopher, oregonus, has been collected on three sides of the

mountain and niger, the black gopher, only 15 miles southwest. It is reasonable that each subspecies may have populated the area at two separate occasions in the past, the present isolated colony resulting from consequent intergradation. In cranial features this population almost exactly matches niger as it does in body size. However, only seven black specimens were collected adjacent to and intermingled with burrow systems yielding 16 brown gophers. A white blaze, occurring in over one half the specimens of oregonus taken elsewhere, is exhibited by one of the brown gophers. The strong trend to niger in cranial characters and body dimensions while the coat color remains predominantly brown is adequately explained only by the assumption that the gene for black is recessive to its brown allele.

Thus we may speculate that along the Oregon coast incipient subspecific populations became established which contained the gene for black, either receiving that gene from the immediate common ancestral populations or from independent mutations after isolation from the ancestral stock which, through the action of chance alone, resulted in at least a moderate frequency for the gene in the subspecies of niger and mutabilus while eliminating it, if ever present, entirely from hesperus. Modified further by the continuing action of natural selection the genetic composition of the present populations gradually emerged.

DISTRIBUTION AND DIFFERENTIATION

Physiographically Oregon, west of the eastern flank of the present Cascade Mountain range and north of the Umpqua River, is the result of a long, somewhat involved and variable geological history. Ignoring earlier events which produced little effect on present day geography of the region we begin this brief summary with the Cretaceous seas encroaching the continental margins at least as far as Eastern Oregon then, by the close of the Eocene, receding to the western border of the present Cascades leaving behind a marginal area of low relief gradually rising to highlands eastward. In the Oligocene volcanism erupted along the present axis to produce the "First Cascade Range". Volcanic activity continued over much of Oregon in the Miocene, a "basaltic flood" poured forth east of the Cascades while the Pacific sea retreated to near its present shore in Western Oregon. In the Pliocene the region, assuming modern configuration, was marked by uplift of the marine sediments to form the Coast Range with its basaltic intrusions on the west. A new outbreak of volcanism and rejuvenation of the Cascades occurred to the east. Between the two areas and limited to the south by the Cascadian spur of the Calapooya Mountains lay the Willamette basin whose bottom of Eocene and Oligocene marine sediments has been partially buried beneath deposits of glacial filling and stream alluvium of the Pleistocene and Recent, forming a broad fertile valley. In the Cascades glaciation and erosion shaped the range, coupled with volcanism that has persisted to near present time. The western

slopes, cloaked in the humid transition forests of Douglas fir, cedar and hemlock below the band of high altitude conifers, are sharply dissected by streams flowing into the Willamette drainage along the northern half and the Umpqua and Rogue basins in the south. Beds of lava and pumice along the crest and eastward, some of recent origin, display every stage of ecological succession interrupting the zonal climax forest. The now silent volcanoes extend upward above tree-line, the peaks scoured by permanent glaciers and exposed rugged sides partially clothed with arctic-alpine vegetation. Eastward a zone of arid transition yellow pine forest blends gradually into the sagebrush-juniper plateau country. To the west, the Coast Range was affected by heavy rainfall, abundant swift flowing streams carved deep narrow valleys, eroded the softer sediments and exposed the basaltic intrusions as higher peaks. Dense stands of humid transition forests cloaked much of the region except for a few exposed mountain tops, precipitous slopes, stream courses, and a narrow coastal strip that extended inland at most only a few miles. The coastal shoreline shows evidence of recently rising land but a still more recent subsidence has drowned the stream mouths.

The pollen analyses of Hansen from Pacific Northwest bogs have been carefully interpreted by him to substantiate descriptions of forest distribution and succession since the retreat of the last (Wisconsin) glaciation. Northwestern Oregon lay well south of the continental ice sheet, which extended as far as southern Puget Sound during maximum glaciation, and therefore received only the secondary

effects of colder climate and extension of montane glaciation in the Cascades. Of the ensuing period he states: (15,p.114)

"Along the Pacific Coast those profiles that possibly represent all of postglacial time reveal that the earliest forests consisted of species of the same identity and of about the same proportions as those of the climax forests of today. As most of this area lies well beyond the glacial boundaries and under the dominating climatic influence of the adjacent ocean, the former presence of forests of modern aspect eliminates any possible interpretation of a climate essentially different from that of the present."

Lodgepole pine, an arboreal primary successional pioneer, was more widespread then than now, invading unforested areas left by retreating montane glaciers, on pumice or lava deposits, and in areas denuded by disease, fires or other causes.

A period of gradual warming with increased dryness culminating in a period of maximum warmth and dryness between approximately 8,000 and 4,000 years ago is indicated by an oak expansion in the Willamette Valley coupled with significant findings elsewhere in the northwest. This period, followed with a cooler, moister climate continuing to the present, probably had little major effect upon the distribution of climax vegetation in the Coast Strip or Coast Range, due to the marine influence, and likewise did not in itself cause any great change in the dominant species of the Cascades.

Concurrent with the outlined geological events was the ebb and flow of mammalian evolution, with the present distribution an end product of integration of the two factors which has been further modified in recent time by human activity. The geomyoid rodents, arising from primitive sciuriomorph ancestors, are limited to the

North American continent where they are found from Oligocene times on. Archaic genera appear in the Oligocene John Day formation of Eastern Oregon as well as in various localities elsewhere during the Lower and Middle Miocene ultimately giving rise to the modern genus Thomomys in the Upper Miocene (24,p.80) or lower Pliocene (23,p.196). It seems probable the present day species had been delimited either immediately before or early in the Pleistocene. The tempo of subspeciation which has resulted in recognition of a tremendous number of geographic races within the several species of the genus over western North America is not easily defined. A slow tempo is indicated by Grinnell (19,p.181) who states:

"From the Rancho La Brea asphalt deposits near Los Angeles there have been exhumed an abundance of excellently preserved skulls of Thomomys intimately associated with remains of certain mammals, now extinct, of known Pleistocene age. And those gophers show cranial characters identical with not only the species bottae, but with the subspecies pallescens as it exists in the vicinity of Los Angeles today. In other words, in upwards of 200,000 years which it is thought have passed since those Rancho La Brea gophers lived and died, there have been no changes in cranial features such as the systematist would recognize in separating geographic races existing today in different part of southern California."

On the other hand Dalquest and Scheffer in examining the distribution of pocket gophers in the state of Washington postulated migration, isolation, and subspeciation having taken place since the Vashon-Wisconsin glaciation, evidenced by the populations on glacial outwash prairies around southern Puget Sound, in "less than ten thousand generations" (8,p.329).

If the degree of differentiation, determined by examined cranial

characters, is indicative then the subspecies of T. monticola did not all arise from a single stock at precisely the same time and we may assume these divergences are the end results of independent evolution in isolated populations for a period of time varying from ten thousand to two hundred thousand years.

The pocket gophers of western Oregon belong to three distinct species, the large uniquely aberrant Thomomys bulbivorous of the Willamette Valley, T. bottae with northerly extensions of the range terminating in tongues across the border into the upper Rogue River valley and north along the coast to Pistol River, Curry County, from the Californian center of differentiation, and in the area under consideration the most widespread and adaptable form Thomomys monticola (it may be said the special habitat required by monticola is more widespread in western Oregon).

Thomomys bulbivorous, probably indicating a highly specialized development of adaptive characters, shows closest affinity with Thomomys bottae yet differs sufficiently to be accorded unquestionable specific rank through divergence to a degree accountable only by a great lapse of time since isolation from the ancestral bottae stock. If, as has been suggested (10,p.453), the Willamette Valley was a great inland lake clogged with ice floes depositing glacial erratics along the shores during the disappearance of the ice sheet, where then were the populations of bulbivorous? Drainage of the lake allowed expansion of the species from remnant populations along the higher valley margins outward over the deposited sediments and the

forming alluvial plains of the bottom, or else the supposed rate of evolution of the genus since the last period of glaciation is grossly in error. Acceptance of the more ancient origin is mandatory in view of all other accumulated data. Therefore, it seems the ancestors of bulbiverous were isolated from bottae stock which extended northward to the Willamette Valley in suitable habitat provided by an ameliorated interglacial climate early in the Pleistocene, possibly in the interglacial period between the Nebraskan and Kansan or Kansan and Illinoian glaciations.

The present subspecies of T. bottae can be considered the products of more recent immigration from the south which made the passage across the Klamath Mountains (Siskiyou) possibly in the arid phase of the warm dry period recorded some eight to four thousand years ago, (15,p.113), and an equally recent invasion along the coast.

Arising from early northern talpoides stock T. monticola has long been isolated in the western mountains, centering largely in the Cascades of Oregon and northern California, and over this period accumulated distinguishable character differences sufficient to satisfactorily set it off from any present adjacent populations of talpoides. The monticola stock, molded by the vicissitudes of the fluctuating early Pleistocene climate, and therefore changing and shifting habitats, apparently experienced isolation only temporarily, if at all. A continual intermixing maintained constancy throughout the range.

The earliest permanent isolation was in the extension of populations along the margins of the Willamette Valley possibly by way of alluvial fans building outward and coalescing from the Cascades on the east and the Coast Range on the west during the interglacial period between the Illinoian and Vashon-Wisconsin glaciations. Prior occupation of the valley by T. bulbivorous would restrict, but not necessarily impede, the expansion of the early T. m. oregonus stock; at present the two species are generally well separated but have been found, in a few instances, in adjacent interdigitating but not intermingling colonies. Postglacial isolation of a portion of this race in the northwestern part of the valley gave rise to the well differentiated subspecies that now inhabits the gravelly Columbia River alluvium at Scappoose, T. m. pumilus. Due to habitat extensions in the warm dry period, some four to eight thousand years ago, oregonus surmounted the crest of the Coast Range and invaded the upper valleys of the Alsea and Yaquina Rivers and made its way southward across the low divide between the Willamette and Umpqua valleys, then westward as far as Scottsburg.

Sometime in the immediate postglacial period other pocket gophers migrated from the Cascades into the Coast Range, most likely by way of the Calapooya mountains, there spreading northward as well as westward throughout the area. Isolation brought about differentiation of T. m. niger in the southern portion of the region, T. m. hesperus centrally and T. m. mutabilus further north. T. m. niger has evidently experienced at least a moderate period of

geographical isolation from hesperus on the north and has only recently intergraded with T. m. oregonus on Marys Peak, an isolated population which today is not continuous with either subspecies, and possibly also at Siltcoos Lake just south of the mouth of the Siuslaw River. Similarly hesperus and mutabilus, differing from each other markedly in body size and cranial features to an extent expected only with a fair degree of isolation, meet and intergrade at Cedar Butte in the Wilson River section of the Tillamook burn.

A certain degree of isolation from parent mazama stock has resulted in slightly differentiated and somewhat isolated populations being recognized as the subspecies T. m. nasicus, inhabiting part of the Deschutes drainage and Paulina Mountains, and T. m. helleri, known only from near the mouth of the Rogue River.

In the Cascades the particular habitat has been continuously available to T. m. mazama even though the areas of plant succession have been altering the local conditions throughout glacial and post-glacial times as reflected in the extensive range uninterrupted by any outstanding divergence of isolated regional gopher populations. The herbaceous cover beneath lodgepole pine, beneath yellow pine, bordering stream and lake shores, in mountain meadows, even above tree-line suffices to meet the ecological requirements of the subspecies. Likewise in the Willamette Valley, where the presence of extensive areas of grasslands is recorded by early explorers and settlers, the habitat requirements of T. m. oregonus have been readily and constantly fulfilled, at least since the end of the

Pleistocene. However, as one surveys the coastal region today, mentally restoring the extensive and sometimes wanton or at least ill considered alterations made in the last century by white man, the question immediately arises: Where was habitat suitable for gophers?

The three coastal subspecies display certain definite habitat requirements, first adequate food, largely grasses and herbs, must be available in clearings, and second a tunnel system to be constructed in a well drained site free from danger of rising water table below or flooding from above. It is indeed difficult to visualize extensive areas fulfilling these basic requirements prior to the coming of white man. The climax vegetation that once extended over most of the area was a dense coniferous forest, entirely unsuitable for pocket gophers. In flat wet areas along the streams conifers were excluded, but because of excessive water, so were gophers. The narrow border of herbaceous vegetation on exposed headlands, where conditions are too rigorous even for lodgepole pine or Sitka spruce, have not been found to support any gophers along the central and northern Oregon coast. Certain peaks of the Coast Range support natural meadows although only Marys Peak is known to be colonized. It is doubtful if a habitat of meadows and clearings was ever available to these animals as it was to their kindred inland subspecies. Through vegetational succession, initiated by such natural causes as floods, slides, fires or disease, a wending thread of the necessary transitory habitat sufficed to maintain population continuity.

The Indian, it is reported, burned areas of forest to improve

hunting. However, fire succession, as observed today, would not yield extensive habitat for the gophers, and then it could be utilized only if individuals were in the immediate vicinity. Food would be lacking on the barren fire scorched earth. Once vegetational invasion has commenced the brake-fern, Pteridium, shades out most grasses and small herbs that gain a temporary foothold, then the fern loses to dense brush, and this in turn gives way to tree species.

Only attendant upon the activities of white man has succession been held in check. The areas most easily cleared for agriculture were settled first, then the forests were pressed further and further back from the fertile valleys and low hills. Grazing of livestock and cultivation kept the fields clear as more fields were added. Today a huge stump of Douglas fir or western red cedar still stands here and there in the middle of a cultivated valley, a fire scarred, rotting, desolate reminder of the forest giants that once dominated the area. Attempts to wrest a living from less fertile marginal lands have sometimes failed; in the span of a few years the small fields, potential homesites for gopher colonies, vanish beneath a closed canopy of fern, brush and small trees. Logging operations, often followed by slash fires, have produced cleared areas throughout much of the Coast Range. If unattended the vegetational succession soon sets upon its inevitable course. The interference by grazing of domestic stock and reseeding with imported grasses may alter or retard this succession, well drained hillsides are frequently maintained in this manner, offering the gophers most excellent habitat.

It seems, at first glance, an incongruous fact that actually more areas, seemingly suitable in every way, are unoccupied than support gopher populations along the coastal valleys. Upon consideration of the sudden transformation wrought in less than one hundred years it is not surprising that small isolated colonies, existing under natural conditions, have occupied only the readily available contiguous areas. The coming of white man has been beneficent to the coastal gophers at least! But formation of potential habitat has outstripped the inherent expansive capacity of the gophers. Just what is the reproductive potential of the species and what is the realizable population increase available for expansion responsible for the present distribution?

The press of late spring activities on campus has resulted in a hiatus in critical collecting records during the breeding season. At least the three subspecies along the coast appear to breed from late March to early May with birth of young occurring from May to early July. The only geomyid gestation period recorded by Asdell (1,p.229) is for Thomomys talpoides quadratus and there is little reason to doubt that 40 days approximates the duration for T. monticola. The average young per litter probably lies between three and four as indicated in the following data:

<u>T. m. oregonus</u>	Scottsburg	June 8	3 embryos
<u>T. m. oregonus</u> X <u>T. m. niger</u>	Marys Peak	May 21	4 embryos
Same	Marys Peak	June 5	4 uterine scars
<u>T. m. niger</u>	Mercer Lake	July 3	3 embryos

Concentrated collecting after July 1st without demonstration of reproductive activity proves only a single litter is produced each season. In the Cascades the breeding season is undoubtedly retarded by lingering snow cover at higher altitudes. Discussing observations on T. monticola at 7,000 feet in Fresno County, California, Ingles states:

"No lactating females were taken later than the middle of August, and no external evidence of sexual activity in either sex was observed before the middle of May nor later than the middle of June. It seems safe to assume, therefore, that the mountain pocket gopher has but one litter each year, born in late spring, and that the young do not breed until the following spring." (16,p.35)

The male gopher willing to abandon the safe shelter of his own tunnel system surely finds no difficulty in selecting a mate should he be fortunate enough to escape predation while seeking about from mound to mound for a suitable scent for there exists a ratio of three females to each two males. Certain females probably fail to reproduce during the short breeding season. Thus, at the time of parturition, the population just little more than doubles.

In addition to the low reproductive potential the population is decimated by the loss of males and young venturing forth above ground even at night, by predation of hawks and owls at the tunnel entrance, by accidents and diseases, and at times by curious museum collectors. Eight or ten systems were found opened, the passages partially enlarged by additional digging, at the north end of the Scappoose airport. In the brush nearby the distress calls of several birds attracted attention to an ermine (Mustela erminea) slipping along

down a log. With all due regards for the fabulous ferocity of the little weasel the author wondered if facing the sharp incisors of a pugnacious gopher within the confines of his own home was not a harder way of making a living!

The young are extremely vulnerable when they leave their parental system to establish tunnels of their own, yet in these young lies the potential motility of the colony. One youngster met the challenge very resourcefully, if only temporarily, in a colony of T. m. niger on Tenmile Creek. In an attempt to determine if more than one animal occupied a system twelve trap sets were left in place for a week. Two days after removal of a mature male from a particular system the trap pan was found pushed inward and a light plug of dirt pushed back from inside. Reset, the trap held an immature gopher when inspected a few hours later. Except for the interference of the trap he would have successfully avoided the labor of constructing a new system. The spacing of systems is indicative of the hostility which exists between neighbors and is extended to the young. In a mature colony, occupying limited suitable area, the young will fill gaps left by earlier loss of a member or less favorable situations to the periphery and may wander into unfavorable regions of dense brush or, still further from the colony, into dense coniferous forest. To argue that the gopher cannot exist in these regions is unsound. Provided the animal fortuitously escapes predation there is ample vegetational sustenance available. Nothing is known of the behavior of gophers in this situation because it would be nearly

impossible to detect their presence due to the plant growth and, furthermore, attention is always focused upon the more productive habitat by investigators. Continued wanderings could take the gopher to new, uninhabited, perfectly desirable areas but it seems the likelihood of success would vary inversely with the distance from the parent colony. The fact that a gopher of the opposite sex must also make the trek during the first pioneer's reproductive lifetime cannot be ignored. A potential homesite one hundred yards removed from a saturated colony might be colonized in one or two years but an area one mile away could remain unoccupied for one hundred years or more awaiting the chance occurrence of circumstances that leads to colonization. A new colony, with potential room for absorption of the low annual population increase for many years before attaining the carrying capacity, is slow to contribute to overall expansion of the subspecies in a discontinuous habitat. Barring coordinated vermin control measures instituted by human inhabitants, the pocket gopher populations in northwestern Oregon seem destined to an inevitably slow and gradual but continuous increase in the years to come.

SYSTEMATIC ACCOUNTS

The accounts of subspecies of Thomomys monticola of northwestern Oregon include four forms previously recognized, mazama, oregonus, niger and hesperus, and in addition two undescribed forms, mutabilus and pumilus. Necessitated by lack of time and specimens the restricted area examined in this investigation does not include the following extralimital subspecies:

Thomomys monticola monticola Allen. Sierra Nevada of California and Nevada from Lassen Peak south to Mammoth Pass and the mountains along west side of Sacramento Valley from Mt. Shasta to the Yolla Bolly Mountains. (= Thomomys monticola pinetorum Merriam and Thomomys monticola premaxillaris Grinnell. See Goldman (12,p.147.)

Thomomys monticola nasicus Merriam. Paulina and Yamsey Mountains and along the Deschutes River, Deschutes, Klamath and Lake Counties, Oregon.

Thomomys monticola helleri Elliot. Mouth of the Rogue River, Curry County, Oregon.

In the synonymy no attempt is made to list every published reference to the subspecies, rather it is designed to give citations of each name combination and the most important references. No comma is placed between the zoological name and the name of the author who first used the name, otherwise a comma is inserted. The condition of type skin and skull are those of Poole and Schantz. The salient features of the skull are listed in "Characters for ready recognition" and are supplemented by comparisons to other subspecies under

the heading "Description: Skull.--". Fifteen such comparisons need be made between the six subspecies; to conserve space and reduce repetition the comparison is made only once, the reader is referred when it is under the account of the other subspecies. For the sake of clarifying past alignments a comparison to Thomomys talpoides douglasii is included in the account of pumilus. All measurements are standard, in millimeters, and have been defined in the accounts of statistical analyses. Capitalized color terms refer to Ridgeway's (1912) Color standards and color nomenclature. In the paragraphs headed "Remarks" pertinent historical material affecting the systematic position of the subspecies is discussed when warranted, the habits and habitats are considered, geographical variation is mentioned, and any other information thought to be useful is included.

Thomomys monticola mazama Merriam.

Mazama Pocket Gopher

Thomomys mazama Merriam, Proc. Biol. Soc. Wash. 11:214, July 15, 1897.

Thomomys monticola mazama, Bailey, N. Amer. Fauna 39:123, November 15, 1915. Bailey, N. Amer. Fauna 55:256, June, 1936.

Type: Head of Anna Creek, near Crater Lake, Mt. Mazama, altitude 6,000 feet, Klamath County, Oregon. Number 80502, U. S. Nat. Mus. Biol. Surv. Coll. Collected September 3, 1896 by E. A. Preble. Original number 1485. Adult male, well made skin in good condition

with grade A skull.

Range: From near the Columbia River south along the crests and east and west flanks of the Oregon Cascades, westward in the Siskyou Mountains and south into the Trinity Mountains of California.

Characters for ready recognition: A medium sized rich Hazel colored gopher with a relatively slender skull. Skull narrow across zygomata and mastoid relative to basilar length; nasals spatulate, posteriorly emarginate; premaxillae extending moderately (1.2 mm.) or less behind nasals; interparietal inflated, tending to suborbicular in shape, extending well into supraoccipital; zygomata parallel or diverging posteriorly; interpterygoid space usually V-shaped; pterygoids with low to moderate arching, diverging posteriorly; bullae moderately inflated, angled to rounded antero-ventrally.

Description: Size.--Significant sexual dimorphism is displayed in the body dimensions. Averages of 22 males and 34 females, adults from the length of the Oregon Cascades, are respectively: Total length 218, 208; length of tail 69.7, 65.6; length of hind foot 29.0, 27.6.

Color.--Only summer specimens are available. Adults dorsally generally Hazel with some variation throughout the range, a paling occurs on the eastern flank of the Cascades where specimens of a lighter tint of Hazel are taken east of the Three Sisters Mountains, these approaching the Cinnamon-rufous of the adjacent subspecies nasicus. In the vicinity of Mt. Hood, at Rhododendron on the west and Parkdale to the north, the coat darkens to a deeper shade of

Hazel and approaches Russett. Ventrally usually near Light Ochraceous-buff darkening to pale Cinnamon-buff in the more intense northern specimens. Postauricular patch black, two to three times length of pinna. Feet and distal part of tail whitish, pigmentation more extensive over dorsal than ventral surface of tail. Juveniles more grayish before first molt, comparable to adults thereafter.

Skull.--Significant sexual dimorphism exists between males and females in most cranial dimensions. Averages for 22 males and 34 females respectively are: Basilar length 31.2, 29.9; zygomatic breadth 20.5, 19.8; mastoid breadth 17.1, 16.6; least interorbital breadth 6.4, 6.5; height of brain case 10.9, 10.9; length of nasals 13.7, 13.1; palatilar length 18.0, 17.4; alveolar length of maxillary tooth row 8.1, 8.0.

The skull of mazama is very similar to those of niger and hesperus but may be distinguished from niger by narrower zygomatic breadth; shorter alveolar length of maxillary tooth rows; deeper extension of interparietal into supraoccipital; shorter extension of premaxillae behind nasals; interpterygoid space usually V-shaped instead of invariably U-shaped; ventral face of pterygoids light and narrow instead of broad and heavy. Mazama differs from hesperus in shorter alveolar length; greater interorbital breadth; shorter palatilar length relative to basilar length; greater extension of interparietal into supraoccipital; zygomata parallel or diverging posteriorly instead of parallel or diverging anteriorly.

Compared to oregonus the skulls of mazama are narrower across

the zygomata and mastoid, the brain case is lower; alveolar length of the maxillary tooth row is less; relative to the basilar length the palatilar length is less; relative to the length of nasals the alveolar length is less; the nasals not narrowing as acutely posteriorly; premaxillae narrowly emarginate rather than broadly emarginate or rounded; arch of the pterygoids low to moderate instead of high; maxillary root of zygomata forming less of an angle from the longitudinal plane.

Comparisons with pumilus and mutabilis are made in the accounts of those subspecies.

Remarks: This mountain inhabiting pocket gopher was described as a full species by Dr. C. Hart Merriam in 1897. Vernon Bailey, in the monographic revision of the genus Thomomys, recognized the affinity with the mountain pocket gopher of the Sierra Nevadas of northern California and Nevada which had been described as the species monticola by Allen in 1893. Thus the Oregon gophers, mazama, nasicus and helleri, became subspecies of Thomomys monticola.

The form mazama successfully occupies a greater diversity of habitat than any other Oregon pocket gopher. Living mainly in meadows, open park-like places, and occasionally open timber, they may be found in the Humid Transition life zone on the western flank of the Cascades, in the Canadian-Hudsonian zone of the crests and ridges up to timberline on the higher peaks, and in the Arid Transition zone of the eastern slopes. From Cloud Cap Inn, elevation nearly 6,000 feet on Cooper's Spur, northeastern flank of Mt. Hood,

these gophers, like the pika, range downward to an elevation of 750 feet at Rowena Crest on the Columbia River between Hood River and The Dalles only 20 miles north and 10 miles east. Along the western border of the range they have been taken near Rhododendron at 1,300 feet, McKenzie Bridge on the McKenzie River between 1,400 and 1,600 feet, and near Prospect at 2,200 feet. The range is limited to the east, except where a gradual intergradation occurs with nasicus in the highlands between the Cascades and the Paulina and Yamsey Mountains, where the Arid Transition yellow pine forests give way to the Upper Sonoran juniper-sagebrush climax of the Central Oregon high plateau country.

Geographic variation is evident in the examined material. The dark-colored gophers from Rhododendron and Parkdale were first noted for the broadly emarginate or truncate posterior border of the nasals. Further examination revealed this condition prevailed in the paler specimens taken at Government Camp and Cloud Cap Inn. In view of the inconstancy of color variation and the constancy of other cranial characters with the populations to the south it seems advisable, therefore, to recognize the character as a cline rather than fruitlessly describing a weakly defined race.

Specimens examined: Wasco County: Rowena Crest, 2 mi. E, 4; Hood River County: 3 mi. S. Parkdale, 8; Cloud Cap Inn, Tilly Jane Creek, NE slope Mt. Hood, 9. Clackamas County: 2 mi. S. Government Camp, 5; Salmon River, 2 mi. W. Rhododendron, 14. Jefferson County: Jack Lake, 2 mi. NE Three Fingered Jack, 1. Linn County: Lost Prairie,

Santiam Pass, 9. Lane County: Scott Lake, McKenzie Pass, 4; Frog Camp, 2 mi. S. Scott Lake, 1; Belknap Springs, McKenzie River, 1. Deschutes County: Sparks Lake, 20. Klamath County: Davis Lake, 8; Annie Springs, Mt. Mazama, near Crater Lake, 1; Rocky Point, Upper Klamath Lake, 2. Douglas County: Diamond Lake, 4. Jackson County: Rogue River, 8 mi. SW Prospect, 6. Possible mazama X nasicus intergrades: Deschutes County: 6 mi. E. Sisters, 12; 6 mi. N. Lapine, 5.

Thomomys monticola oregonus Merriam.

Oregon Pocket Gopher

Thomomys douglasii oregonus Merriam, Proc. Biol. Soc. Wash.

14:115, July 19, 1901. Bailey, N. Amer. Fauna 39:117,

November 15, 1915. Bailey, N. Amer. Fauna 55:254, June, 1936.

Thomomys monticola oregonus, Goldman, Jour. Wash. Acad. Sci.

33:146, May 15, 1943.

Type: Ely, near Oregon City, Clackamas County, Oregon. Number 56939, U. S. Nat. Mus. Biol. Surv. Coll. Collected October 24, 1893 by C. P. Streater. Original number 3340. Adult male, well made skin in good condition with grade A skull.

Range: The Willamette Valley from the vicinity of Portland south along both sides of the valley, across the summit of the Coast Range into the upper comparatively dry reaches of the Yaquina and Alsea Valleys, and on the south extending into the Umpqua drainage and west

at least as far as Scottsburg.

Characters for ready recognition: A smallish Hazel colored gopher with a relatively shorter, broader and higher skull, specifically: Zygomatic and mastoid breadth greater; brain case higher; nasals more narrowed posteriorly, spatulate, posterior border emarginate; pre-maxillae broad, extended moderately behind nasals, posterior border broadly emarginate or rounded; zygomata parallel or diverging posteriorly; interpterygoid space U- or V-shaped, hamular processes divergent posteriorly, arch generally high, ventral face light and fragile; bullae strongly inflated anteriorly reducing antero-lateral angularity.

Description: Size.--Sexual dimorphism slight and not significant. Averages of 15 males and 24 females, adults from throughout the range, are respectively: Total length 205, 203; length of tail 64, 60; length of hind foot 28, 28.

Color.--Upperparts an even expanse of rich Hazel in summer, winter pelage slightly darker, dorsal color blending smoothly but quickly along sides to the ventral pale Ochraceous-tawny wash of ticking over Dusky Neutral Grey basilar fur. Postauricular patch large and blackish. Distal two-thirds and underside of tail white as are the feet. A white chin patch is frequently present, some specimens display additional ventral white spotting. A blaze of hairs white to base occupies the midline between the pinnae in over one half of the specimens. Two aberrant dilute specimens were taken on Bull Mountain, 4 miles west of Tigard, Yamhill County, Oregon. Juveniles

duller, more greyish before first summer molt.

Skull.--Average measurements for adults, 15 males and 24 females, are respectively: Basilar length 30.8, 30.3; zygomatic breadth 21.4, 21.2; mastoid breadth 18.0, 17.7; least interorbital breadth 6.6, 6.6; height of brain case 11.6, 11.3; length of nasals 13.2, 13.2; palatilar length 18.3, 18.1; alveolar length of maxillary tooth row 8.3, 8.3.

Comparisons are made in accounts of each of the other subspecies.

Remarks: Concentrating on a realignment of the species Thomomys talpoides Goldman reduced T. douglasii douglasii (Richardson) to a subspecies under the earlier name talpoides. He included the statement (11,p.233) "The lower course of the Columbia River, however, appears to be an effective barrier for pocket gophers. Thomomys monticola and allied forms inhabiting areas near the Pacific coast south of the Columbia River are similar to the talpoides series in general characters, and should be assigned to the same group, even though differential features clearly point to specific distinction." The status of T. douglasii oregonus was not precisely determined, by rules of nomenclature it should be a subspecies of talpoides, but he recognized it as a form closer to monticola. Four years later Goldman aligned the forms "near the Pacific coast south of the Columbia River..." including oregonus, as subspecies of T. monticola (12,p.146).

Unique in cranial characters, oregonus positively differs also

in habits from the other monticola subspecies. When Streater collected the original series, locating the burrows by his feet breaking through or by thrusting a cane into the ground until it penetrated a burrow, the lack of mounds was laid to washing effect of heavy rains. It is more probable, however, that he was experiencing the frustrating proclivity of these gophers to refrain from building mounds whenever, and for as long a time as possible. In the range of this subspecies one cannot successfully drive leisurely along the road scanning the adjacent one or two hundred yards on either side for mounds; a likely pasture or hillside must be covered on foot with concentrated attention to locate the few old, spaced, weathered mounds or the small holes, just large enough to accomodate the small gopher reaching for nearby food plants, neatly plugged flush with the surface. When one system is found others are near. The twisting and turning burrow frequently must be torn up for three to twelve feet before one either loses it or breaks into a portion thought to be currently occupied, this distance being filled with packed soil, debris from earlier meals, and short open spaces. Herein lies the secret to the singular lack of mounds; as a tunnel is extended the dirt is pushed to a less desirable portion of the system and carefully tamped into place. I have watched captive monticola, given firm dirt between two sheets of plate glass with a ledge above on which to discard dirt, dig a short tunnel, plug the opening, then zig-zag back and forth, up and down, within the confines of a ten inch tube shifted by digging from one end, scooting the dirt to the

other and with a rapid patting of the forefeet in unison tamping it securely in place.

Professor C. Andresen Hubbard of Tigard tells of several occasions where a young peach tree in the yard would wither; withdrawing the rootless stem and setting a trap in the thus exposed runway a gopher was invariably taken--after the damage had been done. A farmer near Noti, Lane County, told of similar happenings, the gophers destroying young plum, apple and pear trees. To emphasize his point he pulled up a dying six foot peach, the roots were cut short to the crown with the bark partially removed up to the ground line. In both cases mounds were wanting.

The clayish nature of the soils over much of its range may partially explain this behavior, the gopher limiting tunneling activity to that endeavor which will yield necessary food. However even in more friable soils mound building is not nearly as extensive as that carried on by the other subspecies. A snowfall is immediately seized upon as a time for feverishly extending the system, the casts left a few days later by melting snow are the most easily discerned evidence of gopher occupancy until washed out by ensuing winter rains.

The large camas pocket gopher, Thomomys bulbivorous, also ranges through the Willamette Valley and, across the low divide, into an adjacent portion of the Umpqua drainage. Generally oregonus occurs along the sides of the valley above bulbivorous but systems of the two forms have been found within one hundred yards of each other.

Whether or not actual competition exists between the two is unknown.

While the proximal region of the nasals is narrower than in other subspecies, this character is most pronounced in the sample from bulb farms and adjacent hillside pastures at Scottsburg. The rostrum is not narrower, rather the nasals appear as if pinched and distorted by expansion of the broader premaxillae. This seems to be one of the aberrant characters that are typical of semi-isolated populations of any wide ranging subspecies of pocket gopher.

Intergradation with niger on Marys Peak, Benton County, and near Siltecoos Lake, Lane and Douglas Counties, is discussed in the account of that subspecies. On a geographical basis the specimens listed by Bailey as hesperus from Philomath and Alsea should be referred to oregonus as is true also, probably, for the albino specimen from Scottsburg listed as niger.

Specimens examined: Washington County: Beaver Creek, 2 mi. S. Timber, 8; Bull Mountain, 4 mi. W. Tigard, 7; 2 mi. S. Tigard, 1. Clackamas County: Oregon City, 1; 3 mi. SE Molalla, 11. Linn County: Lyons, 1. Polk County: Falls City, 2. Lincoln County: Little Elk Creek, 5 mi. E. Eddyville, 2. Benton County: Summit, 1; 3 mi. W. Alsea, 6. Lane County: 5 mi. N. Noti, 7. Douglas County: Umpqua River, 2 mi. E. Scottsburg, 11.

Thomomys monticola pumilus new subspecies.

Thomomys douglasii douglasii, Bailey, N. Amer. Fauna 55:254,

June 1936 (part).

Range: Known only from the vicinity of Scappoose, Columbia County, Oregon.

Characters for ready recognition: A small Russet brown monticola gopher with a lightly constructed skull which is characterized by shorter basilar, palatilar and alveolar lengths; greater interorbital breadth; brain case elevated relative to basilar length and mastoid breadth; nasals generally spatulate, posterior border emarginate; premaxillae moderately extended behind nasals, narrowly emarginate; interparietal slightly inflated, antero-lateral border seldom angular, posterior border usually flush with occipito-parietal suture but sometimes slightly extended into supraoccipital; zygomata parallel or divergent posteriorly, squamosal root flaring abruptly anterior to external auditory meatus; interpterygoid space usually V-shaped; pterygoid processes generally divergent, moderately or well arched, ventral face light and fragile; bullae well inflated, ventro-lateral outline convex, antero-lateral angularity wanting.

Description: Size.--A significant sexual dimorphism is exhibited in these very small gophers, the males being larger than the females. Average measurements of 10 males and 12 females are respectively: Total length 196, 189; length of tail 58, 55; length of hind foot 26.5, 26.0. In each of these dimensions pumilus is significantly

smaller than any of the five other subspecies of monticola under consideration.

Color.--Upperparts a deep shade of Russet shading to a lighter tint of Russet laterally and blending ventrally into a sparcer layer of Ochraceous-tawny tips overlaying and partially concealing the dull Dark Neutral Grey underfur. Postauricular patch black. Feet, ventral and distal portion of tail whitish, proximal dorsal and lateral portion of the tail Fuscous. White hairs usually about lips and within cheek pouches, a white chin patch is generally present.

Skull.--The sexual dimorphism exhibited in body measurements is significantly reflected in most lineal cranial measurements. Averages for 10 males and 12 females are respectively: Basilar length 29.7, 28.5; zygomatic breadth 20.3, 19.4; mastoid breadth 16.8, 16.1; least interorbital breadth 6.9, 6.7; height of brain case 11.2, 11.1; length of nasals 13.3, 12.6; palatilar length 17.2, 16.4; alveolar length of maxillary tooth row 7.9, 7.8.

In cranial features pumilus is distinct from all considered subspecies of monticola by: Shorter basilar and palatilar lengths; greater interorbital breadth and a more highly elevated brain case relative to the mastoid breadth. The bullae are more inflated; the antero-lateral surface, as viewed in outline from the rear, is somewhat convex rather than flat. Further, it differs from all but mazama by a shorter alveolar length and from all but oregonus in a more elevated brain case relative to basilar length. Additional differences will be discussed as comparisons with each subspecies.

From oregonus, which pumilus most closely resembles, it differs by narrower zygomatic and mastoid breadths; less elevation of the brain case; relative to the basilar length the mastoid breadth and palatilar length are less; the nasals are not so pinched, posteriorly, between the premaxillae which are, in pumilus, narrower and more acutely emarginate; pterygoid arch generally moderate but sometimes high rather than generally high but sometimes moderate.

Compared to the north central coastal form, hesperus, pumilus is broader across the mastoid region and shorter in palatilar length relative to basilar length; interparietal less inflated, less frequently angular along antero-lateral border; arch of pterygoids sometimes high instead of usually low or moderate; zygomata parallel or posteriorly divergent rather than sometimes anteriorly divergent.

In comparison to the black pocket gopher, niger, pumilus is narrower across the zygomata; relative to the basilar length the mastoid breadth is less, however relative to the zygomatic breadth the mastoid breadth is greater; the interparietal is less inflated, the antero-lateral border less angular; the interpterygoid space generally V-shaped rather than U-shaped, the hamular processes usually divergent instead of often parallel, arching often high rather than always low or moderate, ventral face light and fragile compared to broad and heavy.

Compared to the mountain gopher, mazama, pumilus is broader across the mastoid region relative to basilar length; the alveolar length is greater relative to length of nasals; interparietal less

inflated, not as frequently or deeply extended into supraoccipital; extension of premaxillae posterior to nasals usually greater; arch of pterygoids often high rather than generally low or moderate; anterio-lateral surface of bullae rounded instead of angular.

Comparison with mutabilus, adjacent to the southwest, is made in the account of that subspecies.

Since this small gopher on the Oregon side of the Columbia has been confused with Thomomys talpoides douglasii from the Washington side a comparison seems advisable. A sample of 7 males and 7 females was taken 10 miles northeast of Vancouver, Washington, March 29 and 30, 1953. In every instance the body and cranial measurements cited above are decidedly less than those for T. t. douglasii. The skull of douglasii is much more heavily constructed than any monticola, noticeably so in broader interorbital constriction and rostrum. To compare selected characters, in pumilus the interparietal is not decidedly extended into the supraoccipital; the zygomatic arches parallel or divergent posteriorly rather than divergent anteriorly; interpterygoid space generally V-shaped instead of U-shaped; pterygoid processes more divergent, more highly arched; bullae robust, more inflated along anterior border, ventro-lateral outline convex rather than flat when viewed from the rear; posterior surface of skull more rounded and less truncated; dentition decidedly lighter.

Remarks: -The presence of this form from the vicinity of Scappoose was first noted by Bailey (3,p.254) who, while recognizing its

distinction from oregonus, erroneously referred specimens taken during 1926 and 1927 by A. W. Moore to Thomomys douglasii douglasii (Richardson). (This form has since been designated as Thomomys talpoides douglasii by Goldman (11,p.234).) Critical examination of a longer series shows undeniable affinity with the other monticola gophers of northwestern Oregon, the broad lower Columbia River serving, as would be expected, an efficient barrier to the water abhorring pocket gopher. Darker coloration and presence of a large black postauricular patch may be added to the characters distinguishing pumilus and douglasii, the postauricular patch is comparatively small and a deep shade of Neutral Grey in the latter form.

Despite the smaller size and corresponding cranial dimensions, pumilus, while distinct, is most closely related to oregonus. This relationship is displayed particularly in the configuration of the interparietal and pterygoids. An early monticola stock apparently invaded the Willamette Valley from the Cascades, since undergoing considerable evolution as a rather extensive but isolated form. Sometime later a portion of this basic oregonus stock managed to cross the hills along the northwestern end of the valley to occupy the alluvium which was able to support a thriving population. Continuous isolation of both forms since has resulted in the significant differentiation.

These small gophers are always energetic mound builders having inherited neither the proclivity nor the habitat of their oregonus ancestors. Their habitat is, nevertheless, one demanding strenuous

work, a base of gravel deposited first by the Columbia River, then topped and percolated with rich black loamy sediments is their home. A rain-washed mound is frequently neatly capped with pebbles. Trap sets are complicated by the lack of straight tunnels, the gopher being inclined to readily change course to dodge the larger stones. The threat of broken fingernails and trowels is always present. As the gravel is a nuisance, so the interspersed loam is a boon for it supports an herbaceous growth more than adequate to fulfill the diligent gopher's food requirements. And the gravelly nature of the soil is undoubtedly responsible for the exclusion of extensive dense coniferous forests which would have, previous to the agricultural practices of man, forced the eventual loss of food supply. Perhaps this is why these gophers are only found on the lowland aluvium; a careful search of nearby upland hills and valleys, even well into the mountains westward, did not reveal a single system, nor did anyone contacted have knowledge of their existence in these apparently favorable situations. Grazed hillsides and cultivated fields, however, are a recent innovation; under the original stands of dense coniferous forests the gophers have for centuries been excluded.

Specimens examined: Total of 27 from the immediate vicinity of Scappoose, Columbia County, Oregon, and from the airfield 1 mile northeast.

Thomomys monticola niger Merriam.

Black Pocket Gopher

Thomomys niger Merriam, Proc. Biol. Soc. Wash. 14:117, July 19,
1901. Bailey, N. Amer. Fauna 39:121, November 15, 1915,
Bailey, N. Amer. Fauna 55:256, June, 1936.

Thomomys monticola niger, Goldman, Jour. Wash. Acad. Sci. 33:146,
May 15, 1943.

Type: Seaton, 2 miles northeast Mapleton, Lane County, Oregon.

Number 69407, U. S. Nat. Mus. Biol. Surv. Coll. Collected October 6,
1894 by J. E. McLellan, original number 1147. Adult male, well made
skin in good condition with grade B skull.

Range: Central Oregon coast from the Alsea River south to the
Siuslaw River west of the summit of the Coast Range.

Characters for ready recognition: A medium-sized pocket gopher
entirely black except for white spotting. Skull of about average
dimensions for the species with the mastoid breadth less relative to
zygomatic breadth; interparietal inflated, suborbicular or broadly
angular anteriorly, posterior border flush with occipito-parietal
suture or extended slightly into supraoccipital; nasals spatulate,
posteriorly emarginate; premaxillae extended well behind nasals
(.6 mm. or more), emarginate; zygomata parallel or diverging posteri-
orly; interpterygoid space U-shaped, lateral borders often parallel,
ventral face of hamular processes broad and heavy, low to moderate
arching; bullae moderately inflated, rounded rather than angular

anterio-ventrally.

Description: Size.--While sexual dimorphism is present it is not sufficient to be deemed significant. Average for 21 males and 27 females are respectively: Total length 221, 214; length of tail 65.7, 64.4; length of hind foot 29.6, 28.8.

Color.--Adults of winter and summer, except where hairs are being molted, a uniform black with glossy sheen above becoming dull dark plumbeous below. Microscopically the dorsal hairs lack the agouti band, the procession of dense granular aggregations in the medullary lacunae continuing to the tip, terminal region with a wash of dark sepia granules in inner cortex. Ventrally the overhairs have a lesser concentration of lacunar pigment and the distal wash is missing, as is the thick clear cortex of the tip, resulting in the lessened intensity of pigmentation and a reduction of gloss. Feet and distal portion of tail whitish, black pigmentation more extensive on upper surface of tail. Juveniles black but duller, molting to glossy black summer coat soon after emergence from the nest. Additional white spotting on underparts noticeable in nearly 40 percent of the specimens, becoming more extensive in about 10 percent in which a facial stripe is frequently displayed.

Skull.--Average measurements for 21 males and 27 females, adults, are respectively: Basilar length 32.0, 31.0; zygomatic breadth 21.6, 20.9; mastoid breadth 17.3, 17.1; least interorbital breadth 6.4, 6.5; height of brain case 11.3, 10.9; length of nasals 13.7, 13.3; palatilar length 18.7, 18.1; alveolar length of maxillary tooth row

8.5, 8.5.

Compared with hesperus the skull of niger is very similar but differs in having greater zygomatic breadth and greater interorbital breadth; the palatilar length is longer relative to basilar length; the mastoid breadth less relative to zygomatic breadth; extension of premaxillae behind nasals averaging slightly more; interpterygoid space U-shaped instead of often V-shaped, 50 percent of lateral processes parallel instead of all divergent; zygomata parallel or diverging posteriorly rather than sometimes diverging anteriorly.

In addition to the black coat color niger differs from the smaller brown oregonus by having narrower zygomatic and mastoid breadths; less elevated brain case; mastoid breadth, palatilar length and height of brain case less relative to basilar length; mastoid breadth less relative to zygomatic breadth; nasals not so pinched by premaxillae posteriorly; premaxillae narrow and emarginate rather than broadly emarginate or rounded; interparietal more inflated along antero-lateral border, posterior border convex, cordate, or angular instead of usually truncate; interpterygoid space U-shaped instead of frequently V-shaped, ventral face heavily thickened instead of light and fragile; arch low to moderate rather than generally high; anterior portion of bullae moderately rather than strongly inflated.

Comparisons with mazama, pumilus, and mutabilis are made in the accounts of those subspecies.

Remarks: This unique black pocket gopher was described as a full species by Dr. C. Hart Merriam in 1901. In 1943, E. A. Goldman

suggested that, with oregonus and hesperus, niger should be reduced to subspecies of Thomomys monticola without further elaboration. In niger, as well as the other two forms, the facts of this investigation support the validity of this suggested alignment.

A lesson on the necessity of properly designating locality on data accompanying any specimen is offered in the confusion surrounding the type locality. To quote from Merriam's original description (18,p.116): "Type from Seaton, near mouth of Umpqua River, Oregon...". In the 1915 Revision of the Genus Thomomys Bailey, believing Seaton to be on the Umpqua River, referred an albino specimen, without skull, to the species niger (2,p.20). Then in the Mammals and Life Zones of Oregon conflicting statements appear, first correctly: "Type.--Collected at Seaton, near mouth of Siuslaw River, Oreg....", then under "distribution and habitat" incorrectly: "Known only from near the mouth of the Umpqua River, at Seaton and Scottsburg, and in the Siuslaw Valley...". Since the locality was no longer on available maps an inquiry into the exact location was launched in 1948. An unidentified elderly lady at Mapleton, on the Siuslaw River, said in effect: "Yes, I was in Mapleton years ago when there was a post office at Seaton about two miles upriver from here." Other examples of disappearing locales occur in the range of niger; Mercer is still to be found on U. S. National Forest Service maps, there stands a decrepit farm house on the north end of Mercer Lake seven miles north of Florence. Deadwood was near the confluence of Deadwood and Lake Creeks four miles northeast of Swisshome. These

place names date back to the era when farm houses along the few routes of access to the back areas became post offices to accomodate those nearby and to increase the family earnings. With changes in economy and transportation these have fallen into oblivion. Seaton has vanished completely beneath a dense growth of salmonberry, thimbleberry and alder; there has been no habitat favorable to gophers left in the vicinity by the quickly encroaching vegetation.

The black pocket gopher is to be found in well drained situations accorded by clearing and grazing along the coastal stream valleys from the Yachats to the Siuslaw Rivers and inland to Lobster Valley of the Alsea drainage and into the vicinity of Triangle Lake which feeds the Siuslaw through Lake Creek. However, much suitable habitat lies unoccupied by gophers due to the rapid clearing of the past century which has outstripped their capacity for expansion. Little variation in altitude is possible, the higher peaks are generally less than 3,000 feet in elevation.

An interesting population of gophers inhabits natural meadows on Marys Peak, Benton County, at an elevation of about 3,800 feet where a series of 23 examples were taken over a period of years to prevent undue decimation of the colony. Sixteen are brown like oregonus which has been taken around the base of the mountain, at Summit and Eddyville on the north, Philomath on the east and Alsea on the south. Seven are black as niger which occurs in Lobster Valley, 15 miles southwest. In characters where niger and oregonus differ these specimens agree remarkably with niger deviating in favor of oregonus.

only in having, in addition to brown color, a longer palatilar length in relation to basilar length and the ventral face of the pterygoid processes not as heavily constructed as in niger. In arching of the pterygoids these examples are intermediate but tend towards niger. It is postulated that the two subspecies attained the peak by separate invasions sometime in the past, the present isolated colony resulting from consequent interbreeding. The specimen, referred to hesperus, listed by Bailey (2,p.131 and 3,p.255) as from Chintimini Mountain undoubtedly was from this colony, Chintimini being the Indian name for the mountain now called Marys Peak.

A second population of mixed colors exists near the coast just south of the Siuslaw River. Richard Pimental reported to me on trapping a brown gopher, which he took to be Thomomys m. helleri, in a stand of timber on the north shore of Siltcoos Lake in the summer of 1949. Unfortunately the specimen was discarded. Later, July of 1952 in fact, William Scott collected nine black and one brown gopher for the Oregon State College Museum of Natural History, these from Ada on the east shore of Siltcoos Lake. The series is too short to allow adequate diagnosis but it may be assumed the brown strain is also derived from oregonus, a colony of which is to be found at Scottsburg, 21 miles southeast. However, no gophers were found in an examination of the intervening Smith River valley, although this does not exclude the possibility of their presence.

Specimens examined: Lincoln County: Lobster Creek, 8 mi. SW Alsea, 6; North Fork Yachats River, 7 mi. E. Yachats, 7. Lane County:

Temple Creek, 7 mi. SE Yachats, 19; Big Creek, 10 mi. S. Yachats, 22; China Creek, 11 mi. S. Yachats, 2; Paris, Five Rivers, 14 mi. N. Swisshome, 4; Alpha, Deadwood Creek, 8 mi. NE Swisshome, 1; Indian Creek, 13 mi. N. Mapleton, 3; Shoemaker Creek, 3 mi. N. Mapleton, 6; Mercer Lake, 6 mi. N. Florence, 27.

Possible niger X oregonus intergrades: Benton County: Marys Peak, 23. Lane County: Ada, Siltcoos Lake, 10.

Thomomys monticola hesperus Merriam

West Coast Pocket Gopher

Thomomys hesperus Merriam, Proc. Biol. Soc. Wash. 14:116, July 19,

1901. Bailey, N. Amer. Fauna 39:131, November 15, 1915.

Bailey, N. Amer. Fauna 55:255, June, 1936.

Thomomys monticola hesperus, Goldman, Jour. Wash. Acad. Sci.

33:146, May 15, 1943.

Type: Tillamook, Tillamook County, Oregon. Number 69825, U. S. Nat. Mus. Biol. Surv. Coll. Collected by J. E. McLellan, November 9, 1894, original number 1189. Juvenile female, well made skin in good condition with grade A skull.

Range: Stream valleys and adjacent ridges of Tillamook County on the northcentral Oregon coast and near Devils Lake, northern Lincoln County.

Characters for ready recognition: A medium sized light Russet brown pocket gopher with a slender skull very similar to that of the

subspecies mazama and niger. The zygomatic breadth is relatively narrow; the interorbital constriction very narrow; relative to the basilar length the mastoid breadth is less as is the palatilar length; nasals spatulate, posteriorly emarginate; premaxillae generally extended moderately behind nasals (.6 to 1.2 mm.); interparietal inflated, generally angular on antero-lateral border, posterior border flush with occipito-parietal suture or slightly extended into supraoccipital; zygomata of about 25 percent divergent anteriorly, 60 percent parallel and 15 percent divergent posteriorly; pterygoids either U- or V-shaped, wings lightly constructed, diverging posteriorly, low to moderately arched; bullae moderately inflated, antero-lateral angularity reduced.

Description: Size.--Sexual dimorphism not marked. Average measurements of 23 males and 33 females, adults from Tillamook County, are respectively: Total length 220, 212; length of tail 71.4, 69.7; length of hind foot 29.0, 28.2.

Color.--Upperparts usually Russet but variable, some individuals lightening to Hazel, others darkening to a deeper shade of Russet. Underparts Cinnamon-buff to Pinkish Buff ticking over Dark Neutral Gray underfur. A series of 12 selected "melanistic" specimens taken in the upper Nestucca Valley by Alex Walker show various degrees of extension of melan pigments ranging from examples with a dorsal median stripe of Mars Brown through ones showing increasing stages of darkening over cheeks, ears, sides and abdomen to a nearly black individual which, nevertheless, is a deep dark rich brown rather than

true black. Microscopically the dorsal hairs have a restricted yellow agouti band diluted by a uniform extension of heavy sepia granulation. Feet whitish, tail white below, also above for distal one-half or two-thirds of length, white hairs usually lining pouches and around lips, a ventral white spot lies on the midline between or just posterior to the forelegs in 25 percent of the specimens examined. Postauricular patch large and blackish. Juveniles duller, more greyish, before first molt, resemble adults thereafter.

Skull.--Average measurements for 23 males and 33 females are respectively: Basilar length 31.4, 30.2; zygomatic breadth 21.0, 20.2; mastoid breadth 17.3, 16.8; least interorbital breadth 6.3, 6.3; height of brain case 11.2, 11.0; length of nasals 14.2, 13.4; palatilar length 18.6, 17.9; alveolar length of maxillary tooth row 8.5, 8.3.

Compared to the smaller brighter oregonus the skull of hesperus is narrower in zygomatic, mastoid and interorbital breadths, the brain case is less elevated giving lesser mastoid breadth and brain case height when related to basilar length; the nasals are not as pinched posteriorly by the premaxillae which are posteriorly narrowly emarginate rather than broadly emarginate or rounded; interparietal less inflated, posterior border less frequently truncated; 25 percent of zygomata diverging anteriorly instead of all parallel or diverging posteriorly; pterygoids with low to moderate arch compared to pterygoids generally highly arched; bullae only moderately inflated anteriorly rather than strongly inflated.

Comparison to mazama, niger, mutabilis and pumilus is made in the accounts of those subspecies.

Remarks: This pocket gopher was described as a full species in 1901 by Dr. C. Hart Merriam, one of approximately 660 new mammals described by him during an extraordinary lifetime. Field collectors of the Division of Economic Ornithology and Mammalogy, concentrating not on any particular mammal, obtained the first small pocket gophers of northwestern Oregon; oregonus in 1893, niger and hesperus in 1894, and mazama in 1896. Short series, usually of less than a dozen specimens, were forwarded to the United States National Museum Biological Survey Collection where they underwent careful examination by the Chief. Recognizing substantial differences in geographically isolated localities each was assigned, by him, a separate specific rank except oregonus which was placed as a subspecies of douglasii. Only with continued collecting, facilitated with improving access to new areas, have the series and ranges been extended, allowing a gradual emergence of new concepts. Goldman, recognizing this relationship, reduced hesperus to a subspecies of monticola, along with niger and oregonus, in 1943.

If one were to select the most average monticola gopher of northwestern Oregon it would have to be hesperus. Undeniably accorded distinction on the basis of coloration and geographic isolation, only a single conspicuous cranial feature, the lesser interorbital breadth, distinguishes hesperus from all other subspecies, however separation is facilitated by utilizing combinations of characters.

The range of this coastal pocket gopher is spotty but they are locally common in well drained sites of Tillamook Valley and extend inland with the Wilson and Trask Rivers as the valley floors raise and narrow. While occupying important dairy land the damage done is not great. The more abundant mole, Scapanus townsendii, is the unheeding recipient, rightfully or wrongfully, of vehement epithets when a mower blade fouls in a mound. In fact, farmers who are cognizant of the gopher's presence generally choose to ignore them. An instance to the point: Having tended a series of sets in a certain pasture in Tillamook Valley, just below the mouth of the Wilson River Valley, I was startled by the roar of a car racing across the field and whirling to a stop between me and my own vehicle parked beside the nearby highway. Out jumped a highly indignant farmer; having seen no house close I had neglected to obtain permission from the landowner. A vitriolic flood was cut short with the exclamation "What's those?" when he noticed the gophers dangling in my hand. After examination of the specimens, the likes of which he vowed he had never before seen, and following an explanation of the distinction between gopher and mole mounds plus instruction on how to make proper sets we parted friends with his rejoinder: "Come back to trap--anytime--and welcome."

Just into the Coast Range from Tillamook one enters the Tillamook Burn, thousands of acres of mountain and forests ravaged three times by fire. At present suitable habitat for gophers is to be found scattered throughout the area where thin soil and exposure

has retarded vegetational succession along ridges and on higher peaks, providing, of course, the gophers escaped the conflagrations. Three were taken in 1950 on the North Fork Wilson River, in the heart of the burn, by Wesely Batterson, Oregon State Game Commission Biologist. A population of hesperus X mutabilus intergrades inhabit Cedar Butte, four miles north of the Wilson River and 14 miles east of Tillamook, where the fire burned to the clearing surrounding the lookout but left it unscorched.

Further south these gophers are to be found on the summit of Mt. Hebo, the highest peak in Tillamook County, elevation 3,200 feet, towering above the upper Nestucca Valley 3,000 feet below and four miles north. It is from both the valley and mountain colonies that the "melanistic" or extended specimens come.

Eighteen specimens taken at Devils Lake, northern Lincoln County, are tentatively referred to hesperus. These gophers are much smaller, total length averaging about 190 mm., but basically retain the features of hesperus, for example the interorbital breadth is very narrow and the zygomata of some diverge anteriorly. Since these were all collected in August, additional specimens from other months are desirable lest this sample, as the series from which hesperus was originally described, include only immatures.

Several specimens referred to hesperus by Bailey (3,p.255) may be reassigned on a geographical basis. The specimen from Elsie, Clatsop County, should be referred to mutabilus, those from Philomath and Alsea in Benton County to oregonus, and the one from the top of

Chintimini Mountain (Marys Peak) to the population of niger X oregonus intergrades.

Specimens examined: Tillamook County: Tillamook, 2; Wilson River, 4 mi. E. Tillamook, 2; Wilson River, 7 mi. E. Tillamook, 9; North Fork Wilson River, 18 mi. NE Tillamook, 3; Trask River, 5 mi. SE Tillamook, 7; Trask River, 10 mi. SE Tillamook, 6; Beaver, 25; Blaine, 1; Mt. Hebo, 7 mi. E. Hebo, 20. Lincoln County: Devils Lake, 18.

Thomomys monticola mutabilis new subspecies.

Thomomys hesperus, Bailey, N. Amer. Fauna 55:255, June, 1936
(part).

Range: Known only from the Nehalem Valley, Clatsop County, Oregon, in the vicinity of Elsie and Jewell.

Characters for ready recognition: A large bicolored gopher, upper-parts black, underparts brown, of which both all black and all brown examples are known, which distinctly displays characteristics of the monticola group. Greater total body length and longer tail are coupled with significantly larger cranial values of the ruggedly constructed skull for basilar, palatilar, nasal, and alveolar length, and correspondingly greater zygomatic and mastoid breadths. The brain case is low compared to the mastoid breadth; nasals usually cuneate, posterior borders as often round or truncate as emarginate; premaxillae narrowly emarginate posteriorly, extending moderately to

well behind nasals; interparietal inflated, antero-lateral border angular, posterior border flush with occipito-parietal suture or slightly extended into supraoccipital; zygomatic arches parallel or diverging posteriorly; interpterygoid space U-shaped, hamular processes usually divergent posteriorly, ventral face moderately broad and heavy, arch low to moderate; bullae strongly inflated anteriorly, antero-lateral border rounded or only weakly angular.

Description: Size.--A large monticola gopher showing significant sexual dimorphism. Average measurements of adults, 16 males and 31 females, are respectively: Total length 233, 220; length of tail 78, 70; length of hind foot 30, 29.

Color.--Bicolor phase: Upperparts a glossy black as in niger, underparts a tone of brown varying between individuals from Apricot-Buff to Ochraceous-tawny, ventrally becoming a ticking over Dusky to Dark Neutral Grey underfur. A narrow zone of transition, separating black fur from brown, sweeps posteriorly from the pouches, over the forelegs, along the flanks, above the hindlegs, thence down to base of the tail. There is a remarkable constancy in the extent of black and brown in the bicolor pattern, one that is displayed by juveniles just leaving the nest and old adults alike. Black phase: Black all around, glossy sheen on upperparts, duller ventrally. Brown phase: Dorsum a deep rich shade of Russet blending smoothly along the flanks to a ventral Ochraceous-tawny ticking over dark underfur. Of the 47 specimens before me 37 are bicolor, 8 black and 2 brown.

Feet whitish, undersurface and distal upper surface of tail

white, proximal dorsal surface of tail black or splotted with black in bicolor and black phases or brown in brown phase. Cheek pouches and lips frequently with white hairs, thoracic spotting occasional.

Skull.--The significant dimorphism of body measurements between the sexes is not reflected in the skull. Averages of 16 males and 31 females judged adults are respectively: Basilar length 32.1, 31.0; zygomatic breadth 21.9, 21.2; mastoid breadth 18.0, 17.7; least interorbital breadth 6.6, 6.5; height of brain case 11.2, 11.1; length of nasals 14.1, 13.6; palatilar length 19.1, 18.4; alveolar length of maxillary tooth row 8.7, 8.6.

This large gopher differs significantly from all five other forms of the species monticola in northwestern Oregon by the greater basilar, palatilar, alveolar and nasal length and by a lower brain case relative to the mastoid breadth. In addition it differs from hesperus, adjacent to the south, as follows: Least interorbital, zygomatic, and mastoid breadths greater; mastoid breadth greater relative to basilar length; nasals generally cuneate rather than spatulate, posterior border as often round or truncate as emarginate instead of all emarginate; ventral face of pterygoids moderately broad and heavy rather than light and fragile; zygomata parallel or diverging posteriorly compared to some diverging anteriorly in hesperus.

From oregonus on the east mutabilis differs as follows: Brain case less elevated actually and relatively when compared to basilar length; nasals generally cuneate instead of generally spatulate,

posterior border frequently rounded or truncate rather than always emarginate; nasals less pinched proximally; premaxillae narrow instead of broad, emarginate; interparietal more inflated; interpterygoid space U-shaped rather than U- or V-shaped, ventral face of pterygoid broader and heavier, arch low or moderate rather than generally high.

When compared to the little pumilus the skulls of mutabilus, in addition to differences listed above, are broader in zygomatic and mastoid breadths but narrower in least interorbital breadth; height of brain case is less relative to basilar length; palatilar length is greater relative to basilar length; nasals generally cuneate rather than generally spatulate; interparietal more inflated; zygoma with a smooth flaring of squamosal root instead of an abrupt flaring; interpterygoid space U-shaped compared to generally V-shaped; ventral face of pterygoids broader and heavier; bullae moderately inflated with flat ventro-lateral outline instead of convex.

Mutabilus, when compared to niger of the central Oregon coast, differs, in addition to the general distinctions listed above, by: Greater zygomatic and mastoid breadths; relative to the basilar length the mastoid breadth and palatilar length are greater; relative to the zygomatic breadth the mastoid breadth is greater; nasals usually cuneate instead of generally spatulate, posterior border often round or truncate rather than usually emarginate; hamular processes of pterygoids generally divergent posteriorly rather than frequently parallel, ventral face not as broad and heavy.

Additional distinctions from mazama are: Mastoid breadth broader actually and relative to basilar length; greater zygomatic breadth; relative to basilar length the palatilar length is greater; alveolar length of maxillary tooth row greater relative to length of nasals; nasals generally cuneate rather than spatulate; premaxillae usually more extended posterior to nasals; interparietal more angular on anteriolateral border, less constantly and deeply extended into supraoccipital; interpterygoid space generally U-shaped instead of U-tending to V-shape; ventral face of pterygoids broader and heavier; bullae more inflated anteriorly with a comparative reduction of antero-lateral angularity.

Remarks: The larger size and presence of three distinctive color patterns immediately set this gopher apart from any other subspecies of monticola, yet it is unmistakably related to the species as proven by comparable cranial features. Despite size differences, one finds a constancy in the ratio of parts, the architectural form of the cranium, and in the general configuration of the particular bones of which the skull is composed; to be sure differences do exist but with no more frequency than in the other subspecies. Considering cranial features, coat color, ecological preferences, and geographical distribution the closest phylogenetic affinity of this form appears to be with hesperus and niger. A common ancestral stock of monticola, independent from that which earlier diverged as the oregonus-pumilus line, may be visualized as having invaded the Oregon Coast Range, there to be differentiated into three subspecies through isolation.

What action of chance has resulted in the fixation of coat color and pattern genes? What factors of natural selection are molding the variability and in what direction? Unfortunately, positive answers to these intriguing questions must await further evaluation, comparison and testing.

An instance of dichromatic pattern, apparently parallel to the bicolor phase of mutabilis, has been reported from a specimen of Thomomys talpoides clusius trapped 25 miles north of Fort Collins, Colorado. If of more widespread occurrence, published records of the fact were not found.

These active gophers are to be found along the Nehalem River from Jewell southward to two miles south of Elsie. They are most populous in fertile loam bottomlands, especially preferring fields of the legume Lotus major cultivated for dairy herds, but range into hill pastures and scrub lands of the valley sides. Energetic mound builders, their presence is easily determined by fresh and extensive systems wherever the vegetation is kept short by mowing or grazing. Trampling cattle cause constant cave-ins of the burrows requiring the gopher to exercise continuous attention and repair. A more extensive range is indicated by the presence of a hybrid population of mutabilis X hesperus intergrades found on Cedar Butte, 18 miles south. However, a search of favorable areas on Saddle Mountain, elevation 3,283 feet, 9 miles west of Jewell was of no avail. The Tillamook Burn area undoubtedly offers mutabilis, as it does hesperus, suitable habitat along ridges and peaks potentially

available to those individuals that escaped the fires or have more recently successfully invaded the area. The sample from Cedar Butte, 4 bicolor, 2 black, and 3 brown, are unfortunately mainly young of the year; the three adults favor hesperus in having spatulate nasals which are posteriorly emarginate, mutabilus in greater interorbital breadth, and are intermediate in shape of interpterygoid space and construction of the ventral face of the pterygoid.

The specimen from Elsie, referred to hesperus by Bailey (3,p.255), should be reassigned to mutabilus on geographical basis.

Specimens examined: Clatsop County: Jewell, 37; Elsie, 10.

Possible mutabilus X hesperus intergrades: Tillamook County: Cedar Butte, 14 mi. E. Tillamook, 9.

Plate 1

Above ground the pocket gopher, Thomomys monticola, readily assumes a pugnacious attitude at any approach. Notice the general stocky build, the small eyes and ears, and the large forefeet heavily armed with sickle-shaped claws. These claws and the large sharp incisor teeth provide formidable defensive weapons. Specimen photographed in captivity.

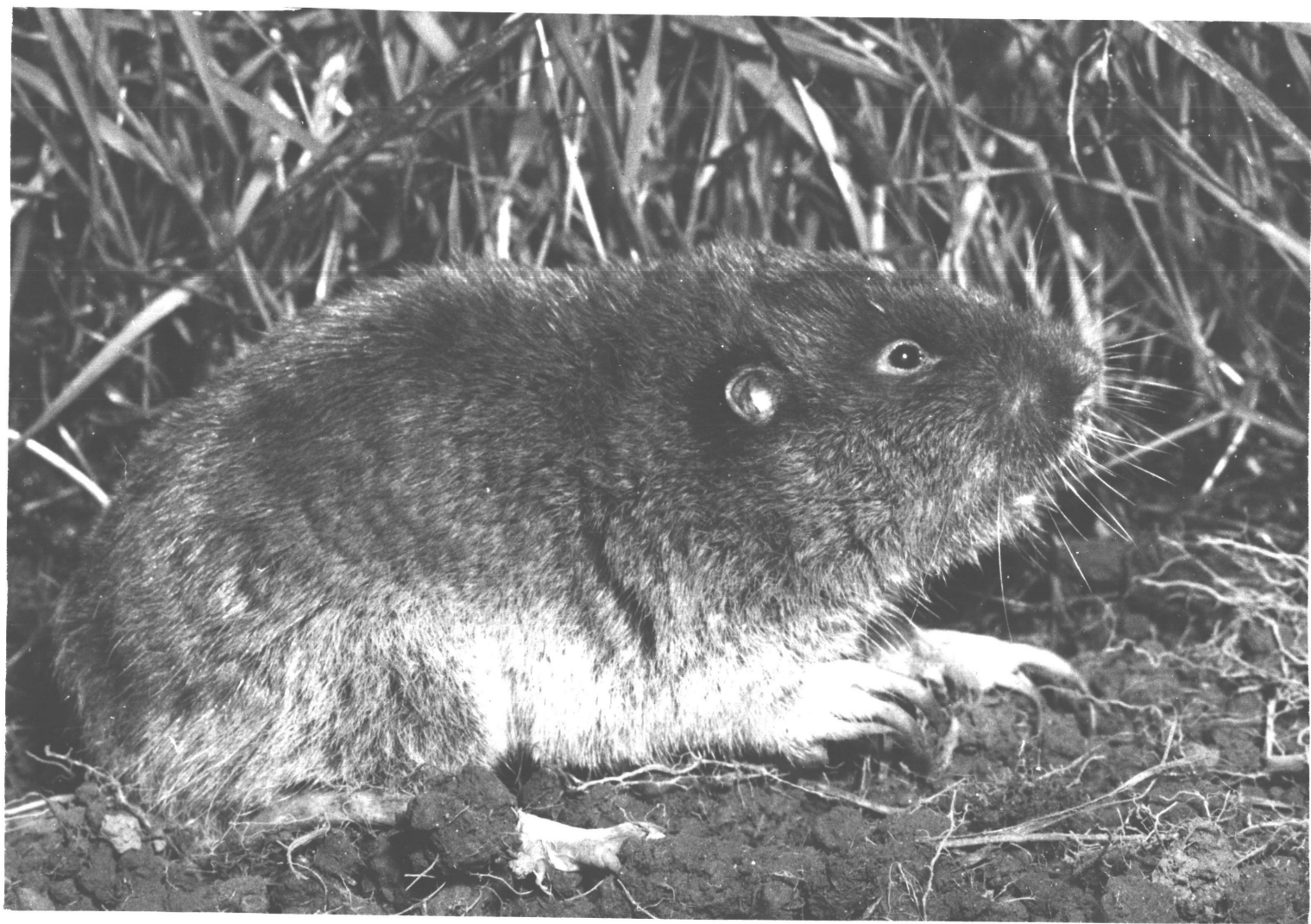


Plate 2

Range of the six subspecies of Thomomys monticola examined in this study.

1. pumilus, new subspecies.
2. mutabilus, new subspecies.
3. hesperus, West Coast pocket gopher.
4. niger, black pocket gopher.
5. oregonus, Oregon pocket gopher.
6. mazama, mountain pocket gopher.

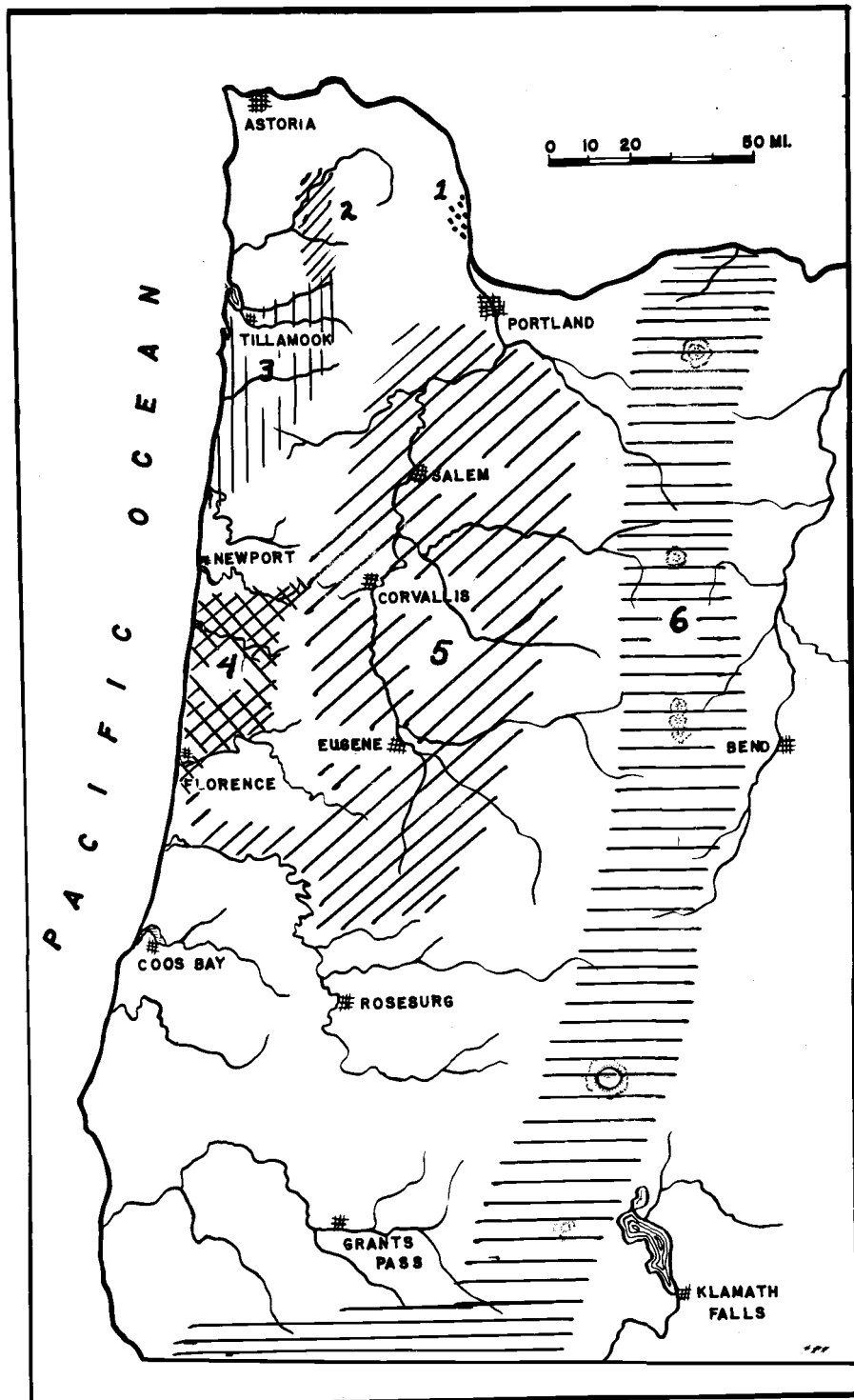


Plate 3

Possible routes of expansion of Thomomys monticola in northwestern Oregon. An invasion of the Willamette Valley during the interglacial period between the Illinoian and Wisconsin glaciations from the primitive stock inhabiting the Cascade range probably gave rise to oregonus. A more recent postglacial extension of the Willamette Valley stock across the mountains and hills along the northwestern border of the valley developed into the pumilus population in inhabiting alluvial plains of the Columbia River at Scappoose. A second major expansion in the postglacial, presumably by way of the Calapooya mountains at the south end of the valley, resulted in the coastal populations which have been since broken up into three distinct subspecies, mutabilis, hesperus and niger. The ancestral mountain population is currently represented by mazama.

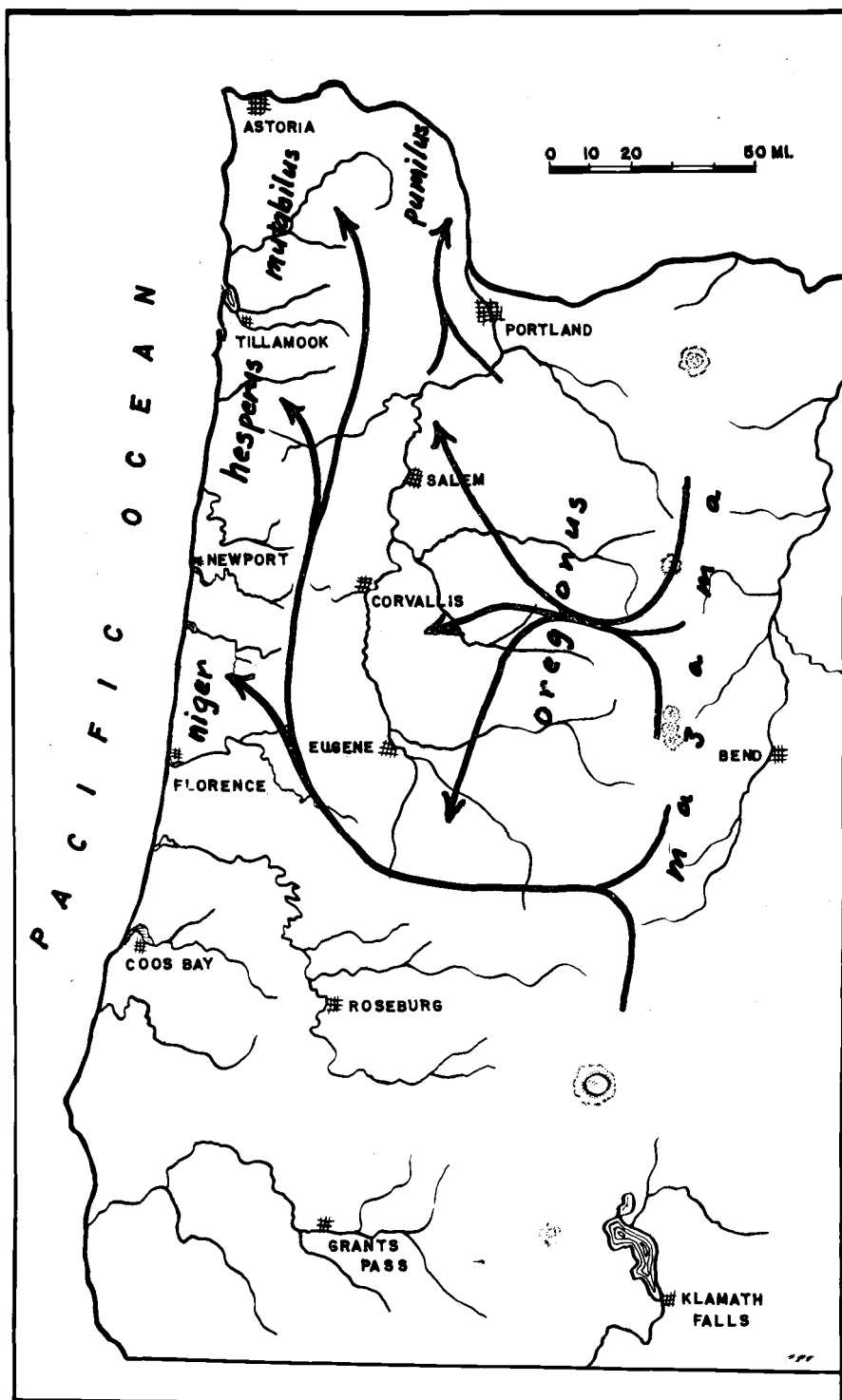


Plate 4

Distribution of pocket gophers in Western Oregon excluding the six subspecies of Thomomys monticola illustrated in Plate 2.

1. Thomomys bulbivorus, camas pocket gopher.
2. Thomomys bottae leucodon, white-toothed pocket gopher.
3. Thomomys bottae laticeps, Humbolt Bay pocket gopher.
4. Thomomys monticola helleri, Heller's pocket gopher.
5. Thomomys monticola nasicus, Deschutes pocket gopher.

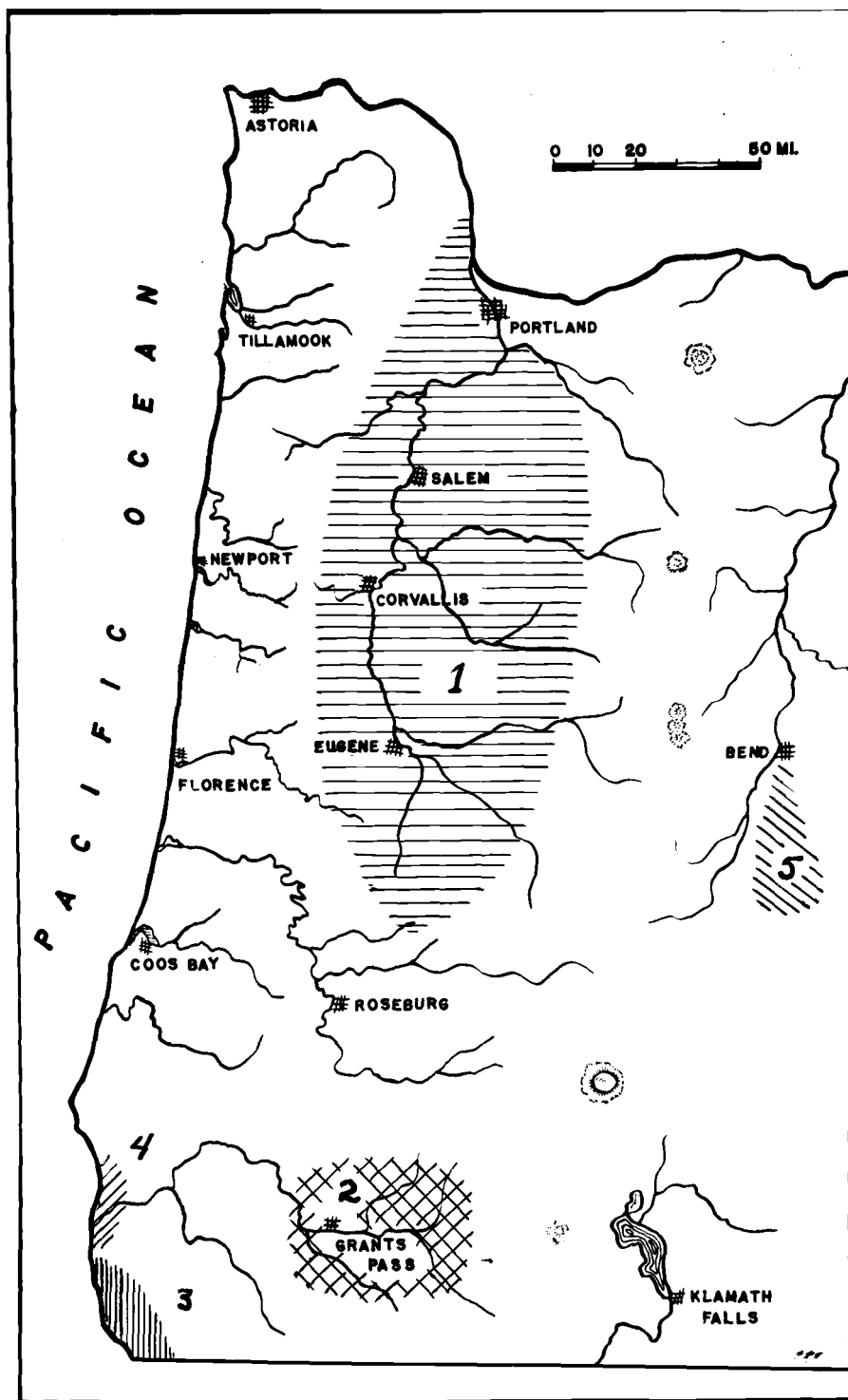


Plate 5

Cranial bones and measurements of a typical Thomomys monticola skull. Illustrated lineal measurements are:

- A. Length of nasals.
- B. Least interorbital breadth.
- C. Zygomatic breadth.
- D. Mastoidal breadth.
- E. Basilar length.
- F. Palatilar length.
- G. Height of brain case.
- H. Alveolar length of upper molariform teeth.

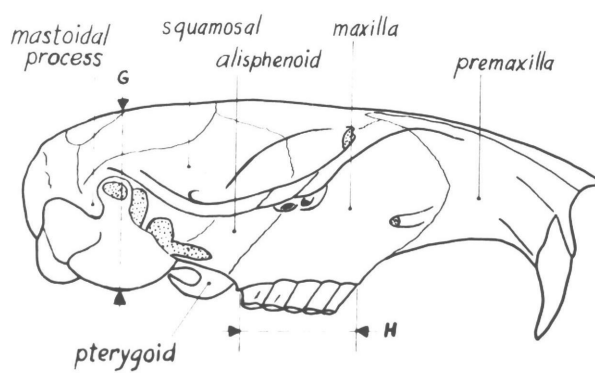
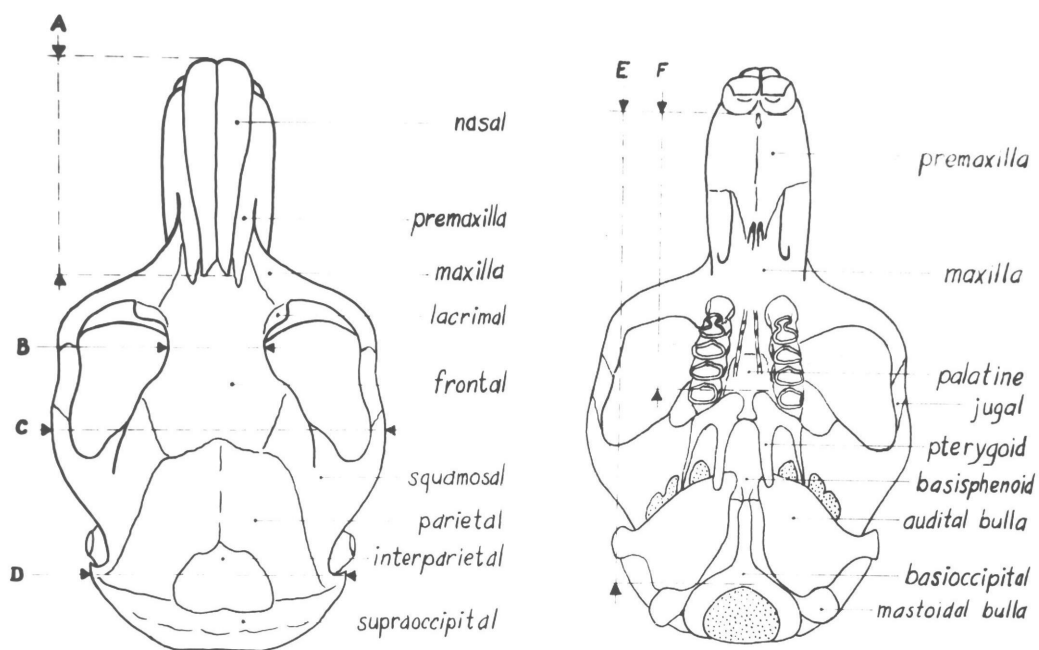


Plate 6

Excellent coastal gopher habitat occupied by Thomomys monticola niger. The slopes insure ample drainage and, due to abundant rainfall, support abundant green vegetation for food throughout the year. Following initial clearing the hillside vegetation has been maintained largely by livestock grazing. On the far side of Tenmile Creek the deciduous alder stand represents a serial stage of vegetational succession initiated years ago by the logging of Douglas fir. Seven miles southeast of Yachats, Oregon.



Plate 7

Typical of the submarginal lands bordering many of the small coastal streams is this abandoned farm with its buildings fallen to ruin. The roof of the farmhouse lies to the right, a barn once stood to the left rear. Since the land was first cleared continuous grazing has held vegetational succession in check thus preserving excellent habitat for Thomomys monticola niger. Big Creek, 14 miles north of Florence, Oregon.



Plate 8

The coastal gophers also inhabit certain broader valleys such as this meadow on a dairy farm on the Tillamook lowlands. The gopher, locally abundant, is seldom recognized or controlled by the farmer. In fact there is reason to believe that the gopher, by preferring succulent weed roots to grasses and by increasing soil fertility and aeration may actually exert a beneficial effect upon the land. Four miles east of Tillamook, Oregon.



Plate 9

Ten miles northeast of the prosperous farmland illustrated in Plate 8 is this area of destruction and desolation, the Tillamook Burn. Retarded vegetational succession has produced apparently suitable gopher habitat along many of the ridges. However, the area is too extensive for the low motility and limited expansive capacity of the few gophers that may have escaped the conflagrations, consequently most of it lies unoccupied. A population of hesperus has been found on the North Fork Wilson River and a population of hesperus X mutabilis intergrades occurs on Cedar Butte near which this photograph was taken.

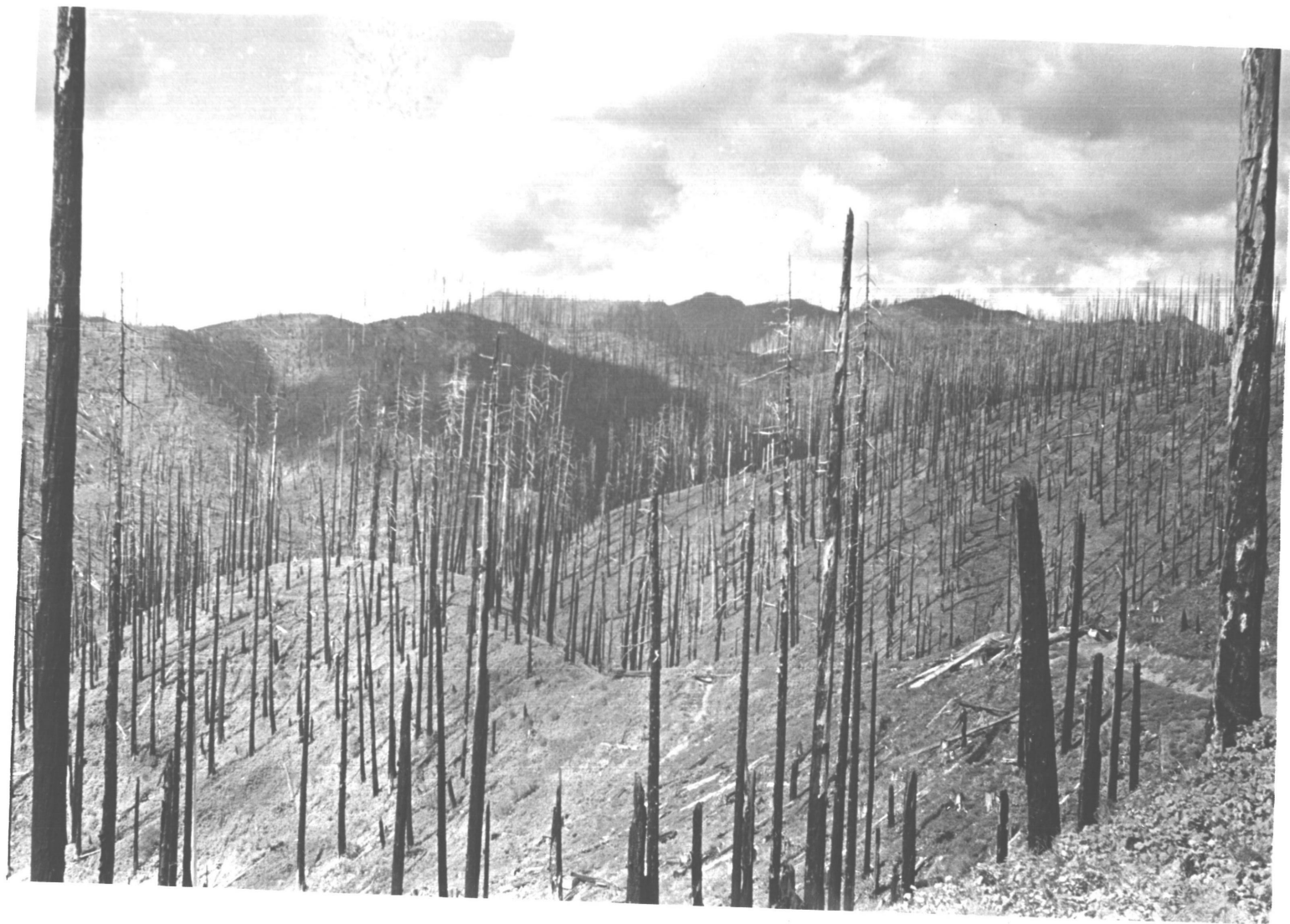


Plate 10

It is difficult to visualize suitable habitat of meadows and clearings in the heavily forested coastal areas before the coming of white man, nevertheless gophers were there and in the succeeding generations have successfully expanded into some of the newly provided areas. The top of Marys Peak, Benton County, exhibits one of the few natural meadows to be found in the region. It supports an interesting hybrid population thought to be the result of intergradation between brown oregonus and black niger populations which attained the summit at two different times in the past. Marys Peak is the highest mountain of the Oregon Coast Range with an elevation of 4,097 feet at base of the lookout.



Plate 11

Whereas the coastal gophers were faced with a lack of favorable habitat the mountain gophers of the Cascades were supplied with an abundance of suitable areas. This broad natural meadow bordering Sparks Lake is densely inhabited by mazama. South Sister Mountain rises in the background, and to the left the bare lava of the Devil's Garden reaches nearly to the lake.



Plate 12

Lodgepole pine, a pioneer coniferous invader in the Cascades, here forms a stand open enough to allow establishment of sufficient herbaceous vegetation for gopher food. The soil has been only slightly modified from a thick layer of pure pumice. Similarly along the eastern flank of the Cascades the dominant yellow pine forest is also open enough to permit pocket gopher occupancy.

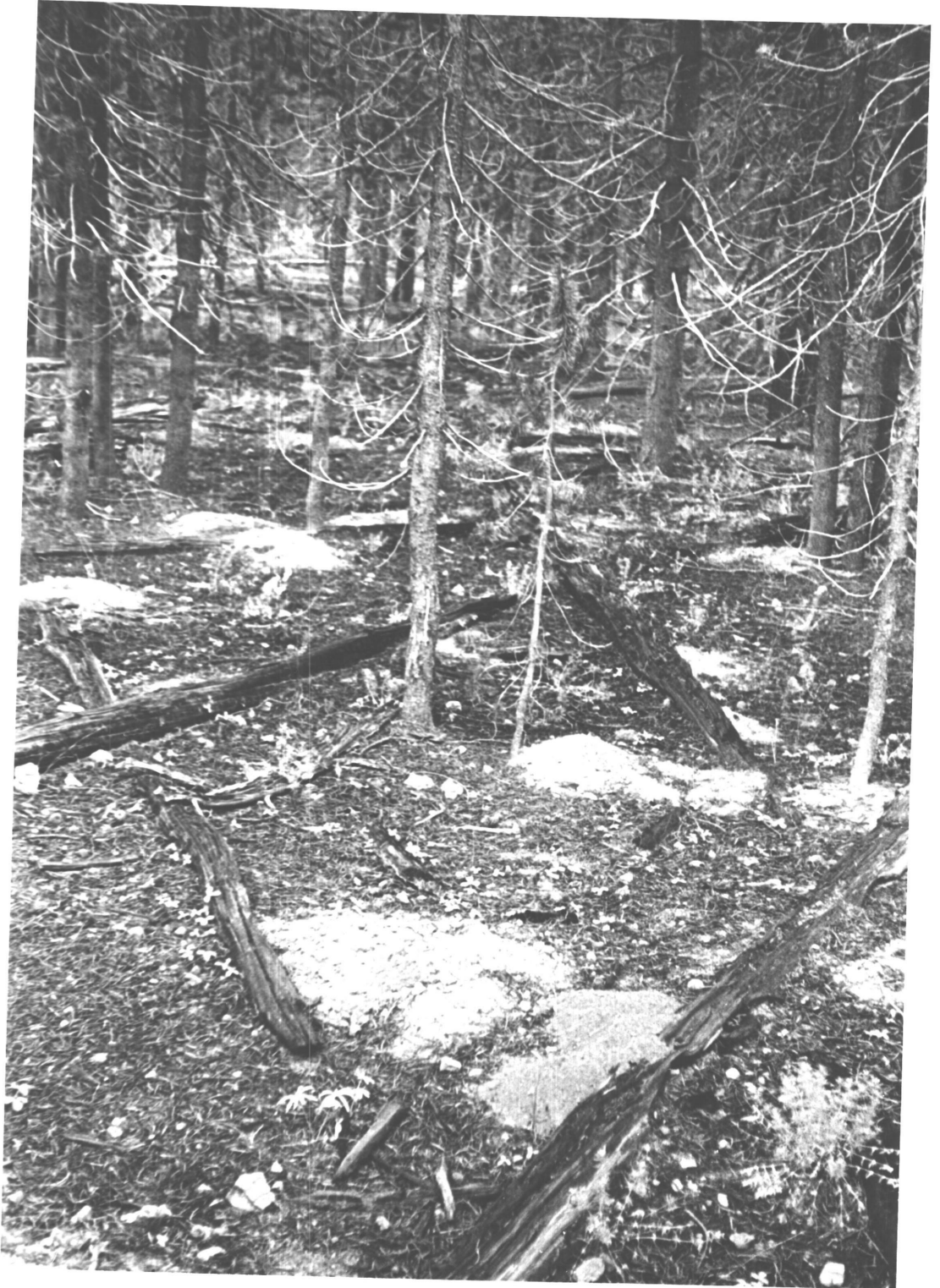


Plate 13

A golf course, with its well drained slopes and closely clipped vegetation is an ideal place to search out gophers. The collector usually receives full cooperation of the operator who is happy to rid himself of the nuisances. Here at Welches, two miles west of Rhododendron, the mountain pocket gopher mazama is found at an elevation of only 1,300 feet.



Plate 14

This beautiful mountain meadow lying beneath the dominance of towering Mt. Hood is located beside old Cloud Cap Inn near timberline on the northeastern flank of the mountain. While the snow-free duration is shorter at this high elevation the snow casts attest to the continuous wintertime activity of the gopher busily engaged in either foraging about beneath the snow blanket, which efficiently affords protection from predators, or enlarging and extending the underground tunnel system.



Plate 15

The gopher mound is crescentic in shape and low in outline. It is formed as numerous loads of dirt are thrust outward from the tunnel opening which is plugged from within by a final load. This plug is visible centered in the front edge of the mound. The gravel indicates the nature of the soil, an alluvial gravel percolated with and thinly topped with silt, in which pumilus thrives. Scappoose, Oregon.



Plate 16

In northwestern Oregon the mole is far more abundant than the pocket gopher. Comparison of these mole mounds with the mounds constructed by gophers reveals distinctive differences. The mole mound is higher in outline, circular rather than crescent-shaped, the tunnel opening is in the center instead of at one side, and the dirt, firmly compacted as it is pushed through the tunnel, emerges from the top and tumbles off in rough clods rather than being well fluffed.



Plate 17

Above ground the movements of the pocket gopher appear awkward. Because of the fossorial adaptations it is ill provided to a terrestrial existence compared to other rodents. For instance a comparison of eye and ear size with the white-footed mouse, Peromyscus, indicates the lesser dependency upon these receptors. Photograph of specimen in captivity.



Plate 18

A juvenile Thomomys monticola niger at the mouth of a burrow. The black coat color certainly does not contrast with the dark brown freshly expelled soil in daylight and is undoubtedly of greater advantage as protection from predators at night. Unlike the mountain form mazama which ventures out of the burrow for forage even in daylight the Willamette Valley and coastal gophers emerge only for the instant necessary to cast out dirt. During this investigation only two untrapped individuals were seen. This photograph was posed with a dead specimen.



Plate 19

While white spotting is found in all subspecies studied it is most frequent and marked by greater contrast in the black niger. The top individual displays the normal amount of spotting, only the distal portions of the feet and tail are white as is the lining of the cheek pouches. Variants ranged from a single additional ventral spot to extensive white areas on the ventral surface and a medial stripe on the face as in Plate 20.

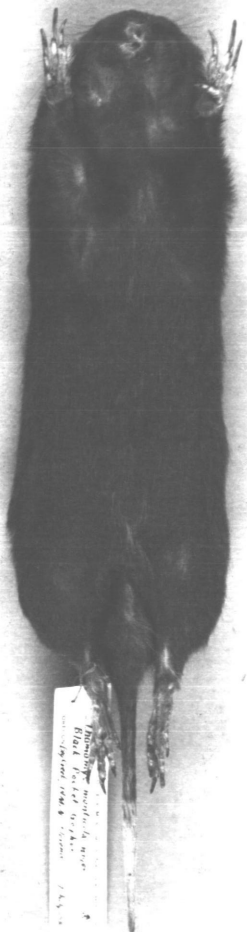


Plate 20

In the specimens examined the facial stripe occurred only in niger. At left is the normal condition, center a restricted stripe, and right an extended stripe. In each of the nine specimens the stripe terminates approximately at the level of the pinnae. The stripe, in each case, is accompanied by extensive ventral spotting.

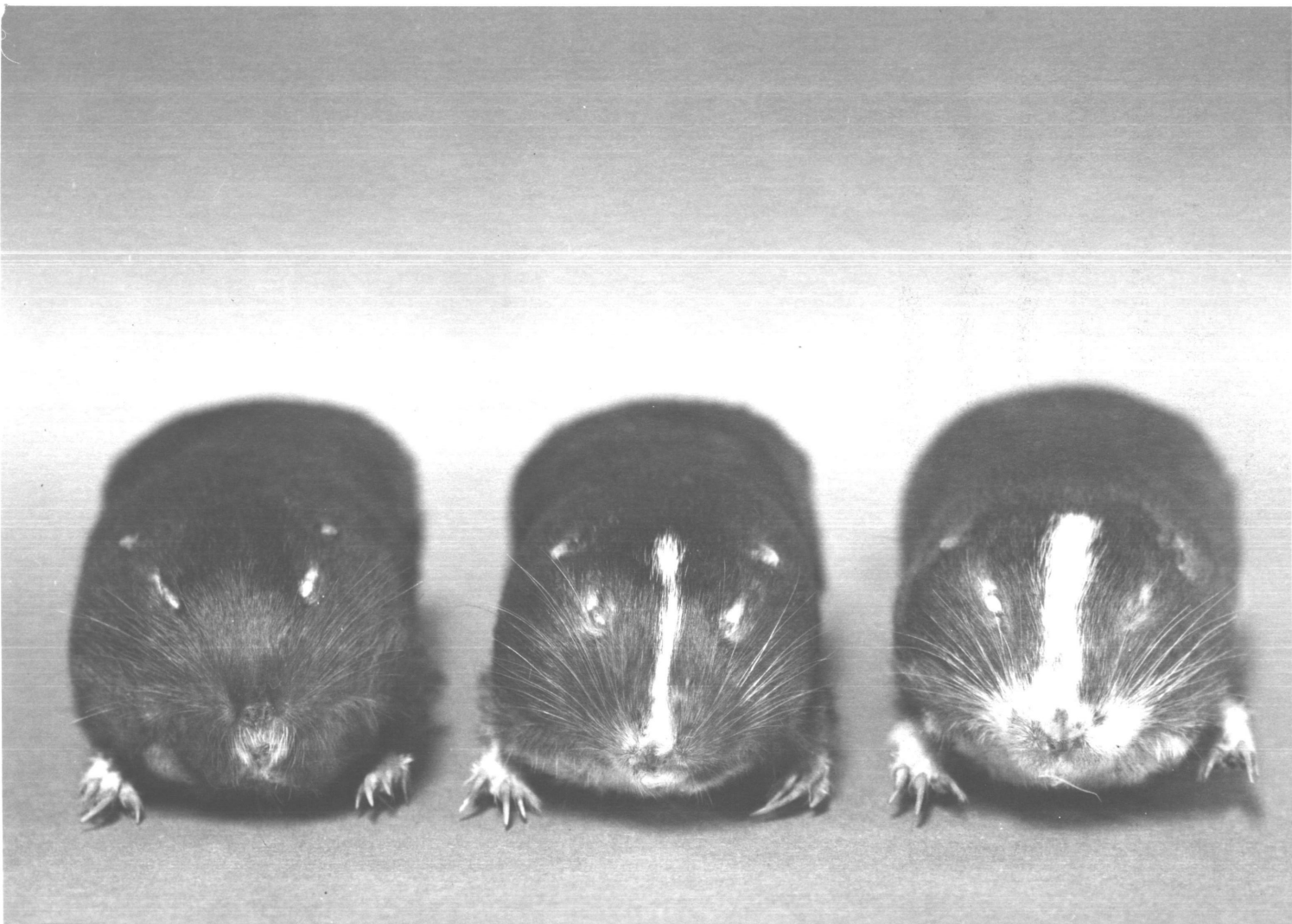


Plate 21

Thomomys monticola oregonus and a damaged fruit tree.

The white blaze on the midline at the level of the pinnæ in over one half of the examined specimens of this subspecies is somewhat more extensive than usual in this individual. The stump of a killed peach tree is from a farm at Noti, Lane County and attests to the voraciousness with which these gophers attack young fruit trees. A characteristic reluctance to construct mounds makes control of these gophers, where damage is being inflicted, most difficult.



Plate 22

This and the following two photographs illustrate how the pocket gopher moves dirt within its burrow. With the hind quarters firmly anchored, one foot low, the other well up on the opposite side of the tunnel and the thick stubby tail forming a prop to the rear, the body is in a contracted position preparatory to thrusting forward the dirt held beneath the chin and the laterally spread forefeet.



Plate 23

Sudden extension of the body thrusts the dirt forward one or two inches. At the instant the photograph was taken the feet were already moving back into position for the next thrust.



Plate 24

The hind feet are drawn forward and the forefeet are withdrawn slightly to scoop up any particles that may have slipped out. Note the amount of recovery that has been accomplished while the dirt is still moving forward from the impetus of the thrust. Stiff hairs, extending between the toes and increasing their efficiency, are to be seen on the forefoot. The scooting action, observed as a very rapid series of short jerks, would be difficult to analyze without the stoppage by speed flash photography. These photographs are the result of an exposure of $1/2500$ second duration. The captive specimen was given firm moist soil packed between two sheets of glass with a shelf above onto which to thrust the spill.



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