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JOSEPH CURTIS MOORE
Research Fellow
Department of Mammalogy

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INTRODUCTION

THE FIRST LINE of evidence for a successful, natural classification of the diurnal squirrels (Sciurinae) was found in the characteristics of the os penis, or baculum (Thomas, 1915; Pocock, 1923). The second line of evidence was the number of bony transbullar septa, and other characteristics of the skull, offered by the present writer (1959). A third line of evidence is offered here.

While the writer was revising an Oriental squirrel genus, an alleged difference in the number of mammae between two species, which otherwise seemed to intergrade, came under scrutiny and was found to be wrong. The constancy of the quantitative data on the number of pairs of mammae obtained in the making of the test, however, stimulated a check throughout the genus. The constancy found in recognized intrageneric taxa stimulated a further check of other Oriental squirrel genera. The differences found between these higher taxa in the number of pairs of functional mammae showed a correspondence to taxonomic relationships that had already been demonstrated by the first and second lines of evidence, so that my interest was aroused in the Ethiopian relatives of the Indian *Funambulus* and Palearctic relatives of the Bornean *Reithrosciurus*. The results of these comparisons seemed to demand a consideration of the relationships that may be indicated by the number of mammae in all the available genera of the Sciurinae.

J. A. Allen, in his review of the squirrels of South America (1915), used the number of mammae as a taxonomic tool. If, however, the disapproval that Allen's rather excessively split classification of the South American squirrels has suffered among other students of mammals has permitted his line of evidence also to be scorned, it seems unfortunate. It is one thing to disapprove a judgment as to the rank of taxonomic categories and quite another to ignore evidence that categories of some rank exist. Some later authors on squirrel systematics, such as Arthur Howell (1938), have ignored the number of mammae as indicators of relationships. Others may be exemplified by Monroe Bryant (1945, p. 262) who, in his phylogeny of Nearctic Sciuridae, brushed off the use of the number of mammae as a taxonomic tool, saying that it was highly variable. Even so, many mammalogists have unobtrusively made a point of noting in their publications the numbers of pairs of mammae that seem to be characteristic for the various taxonomic units that they have considered. Such records have been descriptive rather than comparative and, although better than no treatment at all, represent a step backward from the study of South American squirrels by J. A. Allen (1915), in which the comparisons were obviously of some significance, whatever relationship one may decide they signify.

It is perfectly evident that the number of pairs of functional mammae is an inconvenient taxonomic tool. Data on this character are difficult to obtain. First, one must eliminate all the male specimens, then all the nonparous females, and, finally, all those specimens of parous females on which a mammae count is uncertain. The last category includes all those that were prepared in such a fashion that a pair of mammae were possibly hidden by folds of the skin, all those in which shot holes or dried blood clots may conceal mammae, and all those from which areas of the ventral epidermis and pelage have slipped. Nevertheless, after all these have been firmly disregarded, it is possible, at least in a study collection of several thousands of squirrel skins from many parts of the world such as is available in the American Museum of Natural History, to obtain some valuable results.

In the polytypic Oriental giant squirrel *Ratufa*, each of the 69 parous female specimens suitable for being counted had three pairs of mammae. In the North Amerlcan chickaree genus *Tamiasciurus*, there was no variation from four pairs in the 76 suitable specimens that were found. In the Holarctic squirrel genus *Sciurus* four pairs are the characteristic number, and, except for one Mexican species which varied in a manner that requires further consideration, four pairs were found in each of 132 specimens from many species. In the Neotropical taxon to which J. A. Allen (1915) gave the generic

TABLE 1

THE NUMBER OF PAIRS OF FUNCTIONAL MAMMAE IN SAMPLES OF PAROUS FEMALE SQUIRRELS

	Pairs of Teats					
	2	3	3[a]	4	5	6
Ratufini						
Ratufa	—	69	—	—	—	—
Protoxerini						
Heliosciurus	—	—	15	—	—	—
Epixerus	—	—	—	1	—	—
Protoxerus	—	—	—	17	—	—
Funambulini						
Funambulina						
Funambulus	12	—	—	—	—	—
Funisciurina						
Paraxerus	—	—	15	—	—	—
Funisciurus	16	—	—	—	—	—
Myosciurina						
Myosciurus	—	—	—	—	—	—
Callosciurini						
Callosciurina						
Callosciurus	191	135	—	—	—	—
Tamiops	—	17	—	—	—	—
Sundasciurus	—	19	—	—	—	—
Glyphotes	—	—	—	—	—	—
Nannosciurus	11	—	—	—	—	—
Dremomys	—	24	—	—	—	—
Lariscus	—	24	—	—	—	—
Paralariscus	—	2	—	—	—	—
Menetes	—	18	—	—	—	—
Rhinosciurus	1	—	—	—	—	—
Hyosciurina						
Prosciurillus	—	37	—	—	—	—
Rubrisciurus	9	—	—	—	—	—
Exilisciurus	10	—	—	—	—	—
Hyosciurus	—	—	—	—	—	—
Sciurini						
Sciurina						
Sciurus	—	17	—	139	—	—
Tenes	—	—	—	2	—	—
Guerlinguetus	—	—	—	23	—	—
Reithrosciurus	—	—	—	5	—	—
Microsciurina						
Microsciurus	—	21	—	—	—	—
Simosciurus	—	—	—	20	—	—
Syntheosciurus	—	97	—	1	—	—
Sciurillina						
Sciurillus	—	—	5	1	—	—
Marmotini						
Tamiina						
Eutamias	—	—	—	12	—	—
Tamias	—	—	—	9	—	—
Spermophilina						
Spermophilus	—	—	20	19	126	30
Ammospermophilus	—	—	—	—	26	10
Cynomys	—	—	—	10	14	—

TABLE 1—(*Continued*)

	Pairs of Teats					
	2	3	3[a]	4	5	6
Marmotina						
Marmota	—	—	—	9	20	3
Tamiasciurini						
Tamiasciurus	—	—	—	76	—	—
Sciurotamias	—	—	7	2	—	—
Xerini						
Xerus	6	—	—	—	—	—
Euxerus	—	13	—	—	—	—
Geosciurus	7	—	—	—	—	—
Atlantoxerus	—	2	—	11	—	—
Spermophilopsis	—	—	—	3	—	—

[a] Three pairs in the hiatus pattern.

name *Mesosciurus*, which Philip Hershkovitz (1947) reduced to the species *Sciurus granatensis*, and which the present writer (1959, p. 179) recognized as *Syntheosciurus* (*Mesosciurus*) *granatensis*, the characteristic number is three pairs. In 78 good specimens of *granatensis* there were only three deviations from that total. Although these four examples of constancy in the number of pairs of mammae within a taxon are among the largest samples of squirrels that were examined in the present study, the tendency is general for the number of pairs of mammae to be constant in the taxonomic units that are recognized at the present time. This is to say that only rarely in the Sciurinae does a difference in the number of pairs of functional mammae appear to distinguish units that have not already been recognized as natural taxonomic units (see tables 1 and 2).

There are indications in the literature of the variability in the number of mammae within a species or subspecies of diurnal squirrel, recorded from fresh specimens. Hamilton's (1934, p. 139) record of only two occurrences of a single supernumerary nipple in 500 woodchucks, *Marmota monax rufescens* (and of no occurrence of more than one), is an extraordinary record of constancy. Much higher individual variation is suggested by Linsdale's (1946, p. 324) sample of 38 females of *Spermophilus beecheyi* from one locality in California. Here only 26 had neither more nor fewer than the usual six pairs. Four more had a single additional supernumerary teat. Six individuals lacked a single teat of having six pairs. Two had seven pairs of mammae. Linsdale's counts were not restricted to individuals with mammae that had been functional (hence of parous females). Linsdale

TABLE 2

TAXONOMIC LEVELS AT WHICH TAXA ARE DISTINGUISHABLE BY DIFFERENCES IN THE NUMBER OF PAIRS OF FUNCTIONAL MAMMAE

Tribes of Sciurinae	Subspecies	Species	Subgenus	Genus	Subtribe	Tribe
Ratufini	—	—	—	—	—	x
Protoxerini	—	—	—	x	—	—
Funambulini	—	—	—	x	—	—
Callosciurini	?	x	x	x	—	—
Sciurini	?	?	x	x	—	—
Marmotini	?	x	x	x	—	—
Tamiasciurini	—	—	—	x	—	—
Xerini	—	—	x	x	—	—

TABLE 3

THE TOTAL NUMBERS OF DIFFERENCES IN SKULL CHARACTERS THAT DISTINGUISH 11 TRIBAL AND SUBTRIBAL UNITS OF THE SCIURINAE[a]

	No. of Genera	Ratufini	Protoxerini	Funambulini	Callosciurina	Hyosciurina	Sciurina	Microsciurina	Sciurillina	Marmotini	Tamiasciurini	Xerini
Ratufini	1	—	10	8	7	9	8	7	13	10	10	13
Protoxerini	3	—	—	4	4	5	2	4	12	2	3	8
Funambulini	4	—	—	—	2	2	2	3	8	2	3	6
Callosciurina	8	—	—	—	—	1	1	4	6	5	4	10
Hyosciurina	4	—	—	—	—	—	5	4	7	5	4	8
Sciurina	3	—	—	—	—	—	—	1	11	4	2	3
Microsciurina	2	—	—	—	—	—	—	—	10	4	1	8
Sciurillina	1	—	—	—	—	—	—	—	—	9	12	14
Marmotini	6	—	—	—	—	—	—	—	—	—	2	5
Tamiasciurini	2	—	—	—	—	—	—	—	—	—	—	4
Xerini	3	—	—	—	—	—	—	—	—	—	—	—

[a] The influence of ecological niches is pertinent (see Moore, 1959, p. 193).

(*op. cit.*, p. 312) mentions that on one female with seven pairs of mammae, one nipple of the supernumerary two appeared to be "not functional." In the present writer's examination of a series of museum specimens of parous females, a record was kept of deviations during preliminary stages of the study, but these, as indicated above, were slight. No such variation as Linsdale tabulates was found in the present study of *parous* females in any species. It should be noted that in the present study only *pairs* are counted for the taxonomic purpose, thus dampening the variation by the exclusion of any single, unpaired, supernumerary teat.

One of the most puzzling aspects of squirrel geography is the occurrence in Borneo of a highly differentiated but close relative of the Holarctic tree-squirrel genus *Sciurus*. This displaced member of the Sciurini is a monotypic genus endemic in Borneo. It is a very rare squirrel and possesses a distinctively bushy tail (of hairs 11–12 cm. long) and enormously long (5–6 cm.) ear tufts. The general character of its skull is so peculiar, moreover, as to arouse an interest at once in its relationships. Oldfield Thomas (1915), in his pioneer work on the relationships within the Sciurinae as indicated by the os penis, made the arresting observation that an os penis of *Reithrosciurus* indicated closer relationship of *Reithrosciurus* to *Sciurus vulgaris* than to any Oriental squirrel. This os penis from Thomas' *Reithrosciurus* specimen then became lost, and, when Pocock (1923) offered a classification of the Sciuridae on further study of the baculum (as Thomas had named the penis bone), he had found no other squirrel in the rich squirrel fauna of the Oriental Region which possessed a baculum like that of *Sciurus*. If *Reithrosciurus* did possess the *Sciurus* kind of baculum, then the animal was more than 3000 miles from its nearest relative. Lacking further material of the baculum of *Reithrosciurus*, Pocock questioned Thomas' observation.

Subsequent authors have shared Pocock's doubt, but recently the present writer (1959, p. 163, figs. 3, 4) was able to show that, also unlike any other diurnal Oriental squirrel, *Reithrosciurus* possesses two bony septa across the auditory bulla and a low squamosal, and that these skull characters demonstrate the relationship of *Reithrosciurus* to *Sciurus*. Of course, the baculum of *Reithrosciurus* examined by Thomas (1915) was not illustrated or minutely described and has since been lost, and the present writer's report of the skull characters was from a sample of only two. It is therefore still a question of

some significance whether or not any other line of evidence will be found to support the relationship of *Reithrosciurus* to *Sciurus*. In the number of pairs of functional mammae the sample of *Reithrosciurus* is five parous females. Although no other genus of diurnal squirrel (Sciurinae) in the entire Oriental Region has more than three pairs of mammae, the Bornean tassel-eared squirrel, *Reithrosciurus*, has the number of pairs that is characteristic of *Sciurus*, four.

Together, the three lines of evidence must be considered definitive. Thomas (1915) is vindicated. *Reithrosciurus* unquestionably belongs in the tribe Sciurini. And the geographic location of *Reithrosciurus* with respect to that of its relatives has become a fundamental fact which any scheme that attempts to explain the squirrel geography of the Oriental Region cannot afford to ignore.

SCOPE

The present paper undertakes to report on the nearly world-wide, diurnal squirrel subfamily Sciurinae in several ways:

1. Samples of as many genera of the subfamily as possible were examined in order to determine whether the variation in the number of pairs of functional mammae is regularly geographic.
2. How this new line of evidence conforms with the relationships of the numerous phyla within this subfamily as understood from the older two lines of evidence is treated.
3. Evidence on the variation in the number of mammae was scrutinized for indications of a substantial relationship to latitude.
4. When the number of pairs of mammae proved to be generally reduced in the low latitudes, a search of the literature was made to ascertain whether sizes of broods of young correspondingly decreased, or not.
5. When it was found that brood sizes also decreased in low latitudes (which might, other things being equal, reduce the evolutionary potential of tropical species below that of temperate-climate species), a search was made for any indication as to whether, in the advantageous climate, individuals of southern species produced more litters of young per annum than do those of northern species.

The materials examined were for the most part restricted to the Archbold collections and the general study collections in the American Museum of Natural History, but study materials representing taxa not available, or very scarce, were also examined at the United States National Museum in Washington. For three rare genera, authorities of the British Museum (Natural History) provided information.

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The author wishes to acknowledge some indebtedness to the late Dr. G. H. H. Tate for the part his work had in stimulating the present study. In his incomplete manuscript of a review of the Oriental Sciuridae, which the present writer has been turning into a revision, Dr. Tate had recorded the mammary formula whenever he had observed it for types that were parous females, and in some instances for parous females that he examined in the general collections of European museums. He presented these formulas as description, however, rarely stating the size of his sample, and only vaguely implying any taxonomic importance to them, even in a preliminary summary of the data that was intended for the introduction to his review, doubtless feeling that the review method of gathering data warranted no firmer voice.

Dr. Richard G. Van Gelder has critically read the manuscript at two stages and offered helpful suggestions that influenced its development.

RELATIONSHIPS SUGGESTED BY MAMMAE

TRIBE RATUFINI

SQUIRRELS OF THIS MONOTYPIC, Oriental, giant-squirrel tribe possess three pairs of functional mammae, evenly spaced. The sample is as follows: *Ratufa affinis*, 20; *R. bicolor*, 41; *R. indica*, two; and *R. macroura*, six. One deviation from the norm of three pair was noted: an example of *bicolor* possessed one additional right anterior mamma.

Of the five genera of Ethiopian squirrels (and *Euxerus* and *Geosciurus* are such distinctive subgenera as to make it virtually seven) that the writer examined for this character (no observations were made on *Myosciurus*), only *Euxerus* possesses mammae of this number and this arrangement. Half of the 10 genera of the Callosciurini that were examined for this character (no data for *Glyphotes* or *Hyosciurus*) share with the Ratufini the number and the arrangement of the pairs of functional mammae. Consequently the number and the arrangement of the pairs of functional mammae support the relationship between the Ratufini and the Callosciurini that has been reported for the characters of the skull.

The only other members of the Sciurinae in which this number and this arrangement are important are the Neotropical genera of the Sciurini (Microsciurina). Because the Neotropical Sciurini certainly derived this number and this arrangement by a reduction from the four pairs that characterize the Holarctic Sciurini, and did so in the Neotropical Region, the similarity is no indication of a close relationship of the Ratufini to the Microsciurina. The difference between the skull characters of the Ratufini and those of the other 10 tribes and subtribes, however, is shown in table 3 to be least in the Microsciurina and the Callosciurina. The indication that the Ratufini may have as close a relationship to the Microsciurina as to the Callosciurina in respect to skull characters surely must be interpreted as convergent adaptation to tropical forest life of two phyla, the separation of which may not be very ancient, or the evolution of which may have been marked by much parallelism, the Microsciurina and the Callosciurina.

In sum, then, the Ratufini show the closest relationships to the Callosciurini in mammae as well as skull characters, although they are also sharply separated from the Callosciurini by skull characters and by the character of the baculum.

TRIBE PROTOXERINI

In the Ethiopian tribe Protoxerini the sun-squirrel genus *Heliosciurus* possesses three pairs of functional mammae, but they are not regularly spaced as are those of *Ratufa*. The two posterior pairs are located as in *Ratufa*, but the anterior pair is thoracic and corresponds to the fourth (or anteriormost) pair of *Sciurus*. The arrangement of the pairs of functional mammae in *Heliosciurus* thus leaves a hiatus between the anterior pair and the two posterior pairs. The hiatus is of such a length that, on an assumption of regular spacing, would indicate the absence (or nonfunction) of one pair of mammae. This discontinuous pattern occurs in other genera also and for convenience is here called the "hiatus pattern." The hiatus pattern is more likely to represent a reduction from four pairs of functional mammae than is the pattern of three pairs regularly spaced, for the latter pattern may with equal likelihood represent an increase from a pattern of only two pairs. The pattern of functional mammae in the African giant-squirrel genera *Protoxerus* and *Epixerus* (table 1) is four pairs. J. E. Hill provided the datum on *Epixerus wilsoni*.

The pattern of four pairs observed in *Protoxerus* and *Epixerus* is the commonest in the tree-squirrel tribe Sciurini, but (as shown in table 1) occurs in the ground-squirrel tribe Marmotini, and characterizes the two Palearctic genera of the African ground-squirrel tribe Xerini. *Protoxerus* and *Epixerus* are the only squirrel genera in the Ethiopian Region known to the author to have the pattern of four pairs. Thus the mammary pattern of *Protoxerus* and *Epixerus* suggests a close relationship of the wholly Ethiopian tribe Protoxerini to the geographically distant, principally Holarctic Sciurini and possibly the Marmotini. Perhaps such a relationship is

supported by the weak differentiation between the Protoxerini and the Sciurini and the Marmotini that is shown in table 3.

The peculiar hiatus pattern of the sun-squirrel genus *Heliosciurus* appears also to characterize the African tree-squirrel genus *Paraxerus* of the Funambulini, the Chinese montane, rock-squirrel genus *Sciurotamias* of the Tamiasciurini, and possibly the Neotropical pygmy-squirrel genus *Sciurillus* of the Sciurini. No other evidence links these four genera into a relationship closer than that of the subfamily, and it seems necessary to infer three or four independent origins of the hiatus pattern in the Sciurinae.

The sun squirrel *Heliosciurus* and the other African tree-squirrel genus with the hiatus pattern of mammae, *Paraxerus*, are considered to be tribally distinct (Moore, 1959, pp. 169–171) but to belong to tribes that are perhaps more closely related to each other than either is to any other tribe. The mammary patterns here reported for other genera in these two tribes (Protoxerini and Funambulini) differ from those of *Heliosciurus* and *Paraxerus* in no more than one pair of functional mammae. The hiatus pattern in *Heliosciurus* and *Paraxerus* may, therefore, be the basic mammary pattern of these two phyla in having been the pattern of the parent species from which the two lines diverged.

TRIBE FUNAMBULINI

The Ethiopian and Indian tree squirrels and pygmy squirrels of the four genera that constitute this tribe seem specialized in having small numbers of functional mammae. *Funambulus* and *Funisciurus* have only two pairs, located posteriorly as if any anterior pairs in the locations corresponding to those on other tree squirrels had become lost (or had not yet developed?). *Paraxerus* has three pairs in the hiatus pattern and is adequately discussed above. No counts were obtained from the pygmy squirrel *Myosciurus*.

The correspondence of the Indian striped squirrels, genus *Funambulus*, with the African genus *Funisciurus* in the number of functional mammae appears to support their classification in the same tribe, which had previously been based on the other two lines of evidence. However, this new support is equivocal, for several genera of the Oriental Callosciurini are also characterized by having two pairs of functional mammae. Only three of the five species of *Funambulus* (*layardi*, *palmarum*, and *pennanti*) provided the data on mammae for the genus that are given in table 1.

TRIBE CALLOSCIURINI

The 12 genera of this strictly Oriental squirrel tribe (see table 1) are divided into two subtribes. The smaller, the Hyosciurina, includes three genera, which are endemic on Celebes, and one pygmy genus, *Exilisciurus*, which is distributed on Borneo and the southern Philippine Islands but not on Celebes. The number of pairs of functional mammae does not distinguish these two subtribes, for there are exceptions on both sides, but there seems to be a tendency, at least in the Malaysian Subregion, for the Callosciurina to have three pairs of functional mammae regularly spaced, and for the Hyosciurina to have but two.

No natural division of the long-nosed squirrel genera of the Oriental Region from the other genera of the Callosciurina has been suggested in the published reports on squirrel bacula. The possibility of such a natural division was mentioned in a consideration of the second line of evidence by the present writer (1959, p. 174), but no evidence was advanced in its support. In Pocock's (1923, figs. 21, 22) account, the difference of the baculum of *Menetes* from the bacula of *Lariscus*, *Dremomys*, and *Rhinosciurus* is rather great. The difference in the number of pairs of functional mammae in *Rhinosciurus* from that in *Lariscus*, *Menetes*, and *Dremomys* may militate further against recognition of these long-nosed squirrel genera as a natural group.

The sample of *Callosciurus* shown in table 1 is rather evenly divided into individuals with two and others with three pairs of functional mammae. An analysis of the division of this genus (table 4) reveals that *Callosciurus* is separable by species into two geographic groups which, if one exclude the subgenus *Tamiops*, is rather well divided geographically at the Isthmus of Kra on the Malay Peninsula, which approximately separates the

TABLE 4

SAMPLES OF *Callosciurus* SPECIES WITH THE NUMBER OF PAIRS OF MAMMAE RELATED TO THE ZOOGEOGRAPHICAL SUBREGIONS

	Pairs of Mammae	
	2	3
Indo-Chinese Subregion		
Callosciurus erythraeus	88	1
Callosciurus pygerythrus	32	1
Callosciurus quinquestriatus	4	—
Callosciurus flavimanus	—	—
Callosciurus finlaysoni	65	—
Callosciurus caniceps	38	—
Malaysian Subregion		
Callosciurus prevosti	—	100
Callosciurus nigrovittatus	—	29
Callosciurus notatus	98	205
Callosciurus melanogaster	18	—

zoogeographic Malaysian and Indo-Chinese subregions.

In the low number of pairs of functional mammae, but contrary to the first and second lines of evidence, one sees some suggestion of relationship between some Callosciurini and the geographically adjacent Indian striped-squirrel genus *Funambulus*. This correspondence with *Funambulus* in the number of mammae does not apply to the striped ground squirrels of the Callosciurini, *Lariscus* and *Menetes*, which, prior to Thomas (1908), were in the genus *Funambulus*. Nor does this correspondence in pairs of mammae apply to the striped tree-squirrel subgenus *Tamiops* which one author recently classified as a subgenus of *Funambulus* (Zahn, 1942), for all three of these taxa of the Callosciurini possess three pairs of functional mammae. It seems probable in view of the evidence from skull characters and bacula that the possession by *Funambulus* and some of the Callosciurini of a common mammary pattern represents convergence and not close relationship.

As nothing is known of the male genitalia of the montane rock-squirrel genus of China, *Sciurotamias*, it is interesting to note that the mammary patterns observed in *Sciurotamias* in no case agree with those of the Callosciurini, a fact that supports the very important evidence of the skull characters against a close relationship of *Sciurotamias* with the Callosciurini. The mammary patterns in the Callosciurini, furthermore, do not correspond in any case with those observed in either the Sciurina or the Marmotini and thus support both earlier lines of evidence on relationships.

Although the Neotropical Microsciurina generally possess the same number and arrangement of functional mammae that characterize most of the Callosciurini (three pairs regularly spaced), the evidence from the bacula (Didier, 1955, particularly as cited in Moore, 1959, p. 179) and skull characters shown in table 3 will not admit close relationship.

The extraordinary conformity between the pattern of the mammae observed in the Ethiopian Xerini and that of the mammae of the Callosciurini is also presumed to represent convergence, because of differences in the bacula and, especially abundant, in the skull characters (see table 3). The relationship to the Ratufini is discussed above under that tribe.

As indicated in table 1 and further elucidated in table 4, on the number of pairs of functional mammae, the subgenus *Callosciurus* is divided. There are some points of special interest here. One is that this wide divergence occurs primarily between the species of the two subregions. Indo-Chinese species characteristically have two pairs, and most Malaysian species have three pairs, as does the closely associated Malaysian genus *Sundasciurus*. Another especially interesting point is the variation within the presumably good species *C. notatus*, a matter expected to be dealt with further in revisionary work. Of course, the possession of only two pairs by *Callosciurus melanogaster* of the Mentawi Islands west of Sumatra is interesting in its implications regarding the geographic spread of the character for three pairs (within the phylum that is now recognized as the subgenus *Callosciurus*).

Attention should be drawn at least to the suggestion in tables 1 and 4 that the subgenus *Tamiops* may be more closely related to the Malaysian species of the subgenus *Callosciurus* than to the species of the Indo-Chinese Subregion with which it is fully sympatric.

On the Indonesian island of Celebes, which is one of the easternmost to which squirrels have attained, is an endemic species of squir-

rel which is very large and partly red. Ellerman (*in* Laurie and Hill, 1954) gave this squirrel a subgeneric name, *Rubrisciurus*, although he found no other diagnostic character in the skull than its large size. The present writer (1959, p. 176) has shown that *Rubrisciurus* has, however, distinctive skull characters, and that these appear to justify its elevation to the rank of genus. Table 1 reveals that the nine available good specimens of *Rubrisciurus* possess only two pairs of functional mammae each. This fact may be said to add another piece of evidence against certain similarities that indicate a close relationship between *Rubrisciurus* of the Hyosciurina and *Sundasciurus* (*Aletesciurus*) *hippurus* of the Callosciurina (Moore, 1959, p. 176). However, the number of mammae appears to relate *Rubrisciurus* to the Oriental genus of pygmy squirrels *Exilisciurus*, rather than to the endemic Celebesian genus *Prosciurillus* to which it has been supposed to be more closely related.

Although this is a paper that stresses relationships rather than distinctions, an important point of differentiation may also be emphasized here. This point is that the number of pairs of functional mammae, just as does the number of transbullar septa, distinguishes all the Callosciurini, which have two and three pairs, from all the Holarctic Sciurini, which have four pairs.

TRIBE SCIURINI

The Holarctic subtribe Sciurina shares with the Holarctic ground-squirrel tribe Marmotini a tendency towards having high numbers of mammae, four pairs or more. Although the numbers of mammae range only from three to four pairs in the Sciurini, whereas in the Marmotini they range from three to six pairs, the Sciurini are as close to the Marmotini as is any other tribal unit in this line of evidence. Such general close correspondence between these two tribes is also quite evident in the number of pairs of transbullar septa (Moore, 1959, p. 163). Also, a greater similarity to the character that distinguishes the Sciurini may be seen in the bacula of several genera of Marmotini (Wade and Gilbert, 1940, pp. 55, 58, 60) than in those of other tribes (Pocock, 1923). Thus, the tribe Sciurini, although clearly distinct from the tribe Marmotini, shows close relationship to it in all three lines of evidence.

Although the range in the number of functional mammae in the Sciurini completely includes that in the Tamiasciurini, which might otherwise be taken as evidence of close relationship, the earlier two lines of evidence witness strongly against close relationship. Probably the same thing may be said of the similarity that can be seen in table 1 between the Sciurini and the Protoxerini.

The distinctions already well drawn between the Sciurini and the tribes Ratufini, Funambulini, and Callosciurini by the first two lines of evidence tend to be supported by the third line.

The number of functional mammae in the subgenus *Simosciurus* (table 1) suggests a relationship to *Guerlinguetus* rather than to *Microsciurus*. On the basis of the number of mammae and the absence of the third upper premolars, J. A. Allen (1915) evidently considered *Simosciurus* to be more closely related to *Guerlinguetus*, a genus that is at the present time (Moore, 1959, p. 177) considered to include Allen's genera *Hadrosciurus* and *Urosciurus*. The possibility should be considered here that Allen (1915) was right about the relationships of *Simosciurus stramineus*. In addition to its lack of PM^3 and the possession of four pairs of functional mammae, its opisthodonty also suggests a relationship to *Guerlinguetus* rather than to *Microsciurus*. These three characters combined must be weighed against the single important one of the lack of a low squamosal which otherwise characterizes the Sciurina (*Sciurus*, *Reithrosciurus*, and *Guerlinguetus*) throughout the Palearctic, Nearctic, and Neotropical regions and Borneo. If *Simosciurus stramineus* represents a branch of *Guerlinguetus*, it has of course become separated from its relatives of the Amazon Basin and reached the western slope of the Andes around the Gulf of Guayaquil in Ecuador and Peru, where its only squirrel neighbors are the Microsciurina. Somewhere along the line it must have evolved the higher squamosal which makes it difficult to identify as a member of the Sciurina. Yet such a history may seem more reasonable to postulate than an alternative one, that *S. stramineus* evolved

locally around the Gulf of Guayaquil from a group of the Microsciurina, and independently evolved another pair of mammae and opisthodont upper incisors, and lost the third upper premolar teeth (if it were from the *Microsciurus* group), or lost the ability to complete ankylosis of the sutures bounding the interparietals (if it were from the *Syntheosciurus* group). It seems important that a low squamosal is a character known to have occurred only once in the Sciurinae and to be constant over a great geographic range and in a large number of species, including relicts such as *Sciurus* (*Tenes*) *anomalus* of Asia Minor and *Reithrosciurus macrotis* of Borneo. It must be pointed out that the failure of adults to complete ankylosis of the sutures demarking the interparietal bone, the lack of third upper premolars, and opisthodonty, if not the four pairs of functional mammae, are all characters that seem to have been acquired independently in several taxa of the Sciurinae. The question is, Is it more likely under the circumstances that a species of the Microsciurina evolved the three characters of Sciurina type, or that a geographically disjunct species of the Sciurina lost the low squamosal? Possibly the best answer lies in our waiting to see what additional evidence can be brought to bear by the next investigator to grapple with the problem. *Simosciurus* is in the Microsciurina according to the existing arrangement.

In a brief report abstracted from part of the present paper for the 1959 meeting of the American Society of Mammalogists, the writer drew attention to the discovery that 14 specimens of *Sciurus deppei deppei* and three specimens of *Sciurus deppei matagalpae* each have three pairs of functional mammae, whereas nine individuals of *Sciurus* (*deppei*?) *negligens* possessed four pairs (see Hall and Kelson, 1959, vol. 1, p. 382, for range maps, all in tropical North America). Although left quite unresolved taxonomically, this problem is discussed with some biogeographic details elsewhere (Moore, 1960, p. 360). *Sciurus deppei* accounts, thus, for all 17 instances of deviation from the norm of four pairs in *Sciurus* that are shown in table 1.

It should be noted here that the 96 specimens of *Syntheosciurus* in table 1 are *Syntheosciurus* (*Mesociurus*) *granatensis*.

The significance of the mammary count in *Reithrosciurus* is such that discussion of it is placed in the Introduction of the present paper.

TRIBE MARMOTINI

The indications of close relationship between the Marmotini and the tribe Sciurini are discussed above.

Although the range of numbers of mammae characterizing the various genera and species of the Marmotini includes that of the Tamiasciurini and thus suggests close relationship, the known male genital characters differ trenchantly (Mossman, Lawlah, and Bradley, 1932), and the number of pairs of transbullar septa differs (Moore, 1959, p. 163). The scarcity of differences in the skull characters that is indicated in table 3 derives from certain similarities of *Sciurotamias* to rock squirrels and chipmunks of the Marmotini, which, owing to a lack of knowledge of the male genital characters of *Sciurotamias*, are tentatively ascribed to convergence. The differences in skull characters between *Tamiasciurus* and the Marmotini are more numerous. No very close relationship is admitted between the tribe Tamiasciurini and the tribe Marmotini, therefore, in the present state of knowledge.

The mammary patterns known to occur in the Protoxerini are included within the range of those observed in the Marmotini. However, there is no particular resemblance in their bacula (Howell, 1938, pl. 13; Pocock, 1923, figs. 19, 23), and the number of pairs of transbullar septa differs (Moore, 1959, p. 163). Despite the scarcity of other skull characters which nicely separate these two tribes (see table 3), and the correspondence of patterns of mammae, close affinity is not inferred for these two tribes.

There appear to be many differences in the pattern of the mammae in the Marmotini at the specific level. For example, in *Marmota monax* a sample of nine proved constant in the possession of four pairs of mammae, while 11 specimens of *M. flaviventris* and nine of *M. caligata* all had five pairs, and three suitable specimens of *M. bobac siberica* had six pairs. (The four-pair and five-pair patterns are interrupted ones, curiously, with a hiatus separating the posterior two pairs from the

TABLE 5

NUMBERS OF MAMMAE IN THE SPERMOPHILINA

	Pairs of Mammae			
	3	4	5	6
Spermophilus (Spermophilus) richardsoni	—	—	4	—
Spermophilus (Spermophilus) beldingi	—	—	6	—
Spermophilus (Spermophilus) undulatus	—	—	29	6
Spermophilus (Spermophilus) columbianus	—	—	12	—
Spermophilus (Spermophilus) washingtoni	—	—	12	—
Spermophilus (Spermophilus) citellus	—	—	12	—
Spermophilus (Ictidomys) tridecemlineatus	—	—	—	9
Spermophilus (Ictidomys) mexicanus	—	10	1	—
Spermophilus (Ictidomys) spilosoma	—	—	3	—
Spermophiilus (Poliocitellus) franklini	—	—	12	3
Spermophilus (Otospermophilus) variegatus	—	—	9	—
Spermophilus (Otospermophilus) beecheyi	—	—	—	12
Spermophilus (Otospermophilus) annulatus	20	—	—	—
Spermophilus (Xerospermophilus) tereticaudatus	—	—	8	—
Spermophilus (Callospermophilus) lateralis	—	9	18	—
Ammospermophilus leucurus	—	—	15	—
Ammospermophilus nelsoni	—	—	—	10
Ammospermophilus harrisi	—	—	11	—
Cynomys ludovicianus	—	10	—	—
Cynomys leucurus	—	—	5	—
Cynomys parvidens	—	—	3	—
Cynomys gunnisoni	—	—	6	—

anterior two or three.) In the prairie-dog genus *Cynomys*, the patterns of the mammae appear to separate the two subgenera, for in samples of six individuals of *gunnisoni*, five of *leucurus*, and three of *parvidens*, all of which are included in the subgenus *Leucocrossuromys*, five pairs of functional mammae are constant. In *ludovicianus*, however, which constitutes the subgenus *Cynomys*, the available sample of 10 is constant in having four pairs of mammae. (Hollister, 1916, pp. 12, 23, originally gave the number of mammae as one of the distinguishing characters of the subgenera.)

In the ground-squirrel genus *Spermophilus* the number of functional mammae ranges from three pairs to six pairs, and, although there are six subgenera in current use, the polytypic ones display little constancy in mammary pattern. (See table 5.)

TRIBE TAMIASCIURINI

The contribal relationship between *Sciurotamias* and *Tamiasciurus*, postulated principally on the number of transbullar septa, appears to be mildly supported by the numbers of pairs of functional mammae. Although the skull characters suggest a relationship as distant, for example, as that between *Spermophilopsis leptodactylus* and *Xerus rutilus*, which are unquestionably contribal, the number of mammae is much closer between the two members of the Tamiasciurini than is that between the two members of the Xerini. The variation in the numbers of pairs of functional mammae in *Sciurotamias* may indicate a relatively recent and still incomplete change from four to three pairs and invites further investigation. No data were obtained from the interesting subgenus *Rupestes*.

The intertribal relationships of the Tamiasciurini that are obviously suggested by the numbers of functional mammae alone would be to the Protoxerini, the Sciurini, and the Marmotini. In view of the possibility of a relationship to the Xerini that is suggested by the common possession of three pairs of transbullar septa, however, it is to be noted

that the genus of the Xerini that is geographically closest to the Tamiasciurini (*Spermophilopsis* in Turkmen) also has four pairs of functional mammae. Of the various possibilities, therefore, relationship with the Xerini seems somewhat the best supported, even though no species of the Xerini is known to have three pairs of functional mammae in the hiatus pattern.

TRIBE XERINI

Quite in keeping with the pronounced differences in skull characters among the genera of the Xerini reported earlier (Moore, 1959, p. 184), and with the strong differences also observed among the subgenera (?) *Xerus*, *Geosciurus*, and *Euxerus*, the divergence in the numbers of pairs of functional mammae is fairly extreme.

The "African" ground-squirrel tribe Xerini is like the Ethiopian tree-squirrel tribe Protoxerini and the Ethiopian and Indian tree-squirrel tribe Funambulini in having a range of variation of from two pairs to four pairs of functional mammae. It seems less similar in this character to the Holarctic ground-squirrel tribe Marmotini, for in that tribe most genera have the modal number of five pairs.

The discovery that both Palearctic genera of the Xerini, *Spermophilopsis* of Turkmen and *Atlantoxerus* of Morocco, seem to have four pairs of mammae as the characteristic number, whereas the one Ethiopian genus, *Xerus* (constituted by three very distinct subgenera), has fewer may be of some taxonomic interest. The present writer (1959, p. 185) noted evidence of considerable importance in the skull characters which associates *Spermophilopsis* and *Atlantoxerus* and distinguishes the two from the genus *Xerus*. If study had at that time been brought to bear on whether or not *Euxerus* and *Geosciurus* merit distinction as genera, and the conclusion had been favorable, the present writer would have placed the two Palearctic genera in one subtribe distinct from the three Ethiopian ones. The observed relationship in the number of mammae seems to strengthen the evidence that the two genera north of the Sahara are more closely related to each other than either of them is to the genus *Xerus* south of the Sahara. That some other factor may enter into this relationship of the number of mammae is shown below in the present paper.

On the occurrence of two specimens with only three pairs of functional mammae in the sample of 13 individuals of *Atlantoxerus*, J. E. Hill (letter of February 2, 1960) comments: "I have examined the two anomalous skins, and they prove to be *Atlantoxerus*. Neither is there evidence [that this difference is one] of geographical variation: we have other skins with four mammary pairs from the same or nearby localities. Nor does there appear to be reason for miscounting—there are clearly three mammary pairs in each case. It seems therefore that *Atlantoxerus*, while usually endowed with four mammary pairs, has on occasion three."

CLIMATE AND NUMBER OF MAMMAE

WHETHER OR NOT CLIMATE may influence the number of pairs of functional mammae in diurnal squirrels should at least be considered. The range recorded here in table 1 is from two pairs to six pairs. (Two specimens of *Ammospermophilus harrisi* clearly have six and one-half pairs, but no squirrel was observed to have fewer than two full pairs.) Some tendency is apparent for those with fewer mammae to be tropical, and it should prove worth while to consider the numerical variation within each of the several tribes in respect to climate.

The montypic tribe Ratufini is tropical (Oriental) and consistently has a low number (three pairs). The Protoxerini, although tropical (Ethiopian), may be considered equivocal with three pairs in the hiatus pattern and four pairs. The Funambulini are tropical (Ethiopian and Indian) and have preponderantly only two pairs, but one genus has three pairs in the hiatus pattern.

The Callosciurini are tropical (Oriental), with three pairs of mammae the most common, but four of the genera seem to have only two pairs. The number of species characterized by three pairs of functional mammae in the Indo-Chinese Subregion exceeds the number of species in that area that are known to possess only two pairs (nine species to about five). The number of species with only two pairs of functional mammae is greater in the Malaysian Subregion (seven, including extraterritorial *Rubrisciurus*) than in the Indo-Chinese Subregion (about five). Because the Indo-Chinese Subregion is the more northern and less tropical [particularly when one considers the ranges of *Dremomys pernyi*, *Callosciurus erythraeus*, and *C.* (*Tamiops*) *swinhoei* to latitude 35° and latitude 40° N.], these differences in the number of mammae of the Callosciurini suggest an influence of climate on the number of mammae.

The Sciurini are temperate and boreal (Holarctic) for the most part but have also spread throughout the American tropics. It is, therefore, especially interesting to note that, although four pairs are the characteristic number throughout the Holarctic for this predominantly tree-squirrel tribe (and four pairs are the greatest number attained by any tree squirrel), some Neotropical genera and species of Sciurini have only three pairs. Also, all the reductions in the number of mammae in the tribe Sciurini, excepting *Sciurus deppei*, occur altogether in the endemic Neotropical subtribes Microsciurina and Sciurillina.

In the Sciurini one bit of contrary evidence is worthy of special note. The Bornean tassel-eared squirrel *Reithrosciurus*, which is the only member of the Sciurini in the tropics of the Old World, has the four pairs of mammae that are characteristic of the Sciurini of temperate and boreal climates rather than the reduced number so common in Neotropical members of the tribe. However, *Guerlinguetus*, the widespread, polytypic, and only Neotropical genus of the subtribe Sciurina to which *Reithrosciurus* belongs, also retains four pairs.

The Marmotini are a temperate and boreal (Holarctic), entirely ground-squirrel tribe that contributes especially interesting evidence of an effect of climate on the number of mammae. Although data obtained on *Ammospermophilus* and *Cynomys* are equivocal, in the very large genus *Spermophilus*, in which the mode is five pairs of functional mammae and the variation from it is more often higher than lower (see table 5), the only species characterized by the smaller number of four pairs is *S. mexicanus*, and it seems significant that *S. mexicanus* is one of the four species (of the 16 species sampled) that range south as far as the twentieth parallel of latitude. Further, the only species of *Spermophilus* that characteristically has the still lower number of three pairs is *S. annulatus*, the only sampled species of *Spermophilus* the entire range of which lies south of the Tropic of Cancer. (*Spermophilus adocetus* and *S. perotensus* are unsampled "species" with minute known ranges that lie below latitude 20° N. See range maps in Hall and Kelson, 1959, vol. 1.)

In the American species of the genus *Marmota* the range in pairs of functional mammae is from three to six. Between latitudes 30° and about 45° N. nine examples of the species *M. monax* have four pairs. The

range of the species *M. flaviventris*, which is the mountain form of western North America, occupies about the same latitudes as the bulk of *M. monax*, but at *higher* elevations. The whole sample (11) of *flaviventris* has five pairs. The most northern American species, *M. caligata*, ranges from about latitude 45° to 70° N. and is a high-mountain form in the more southern parts of its range. *Marmota caligata* (sample of nine) has five pairs of functional mammae. The small sample (three) of *M. marmota sibirica* has six pairs. Thus there is the suggestion of a relationship between climate and the number of functional mammae in this genus.

In the Tamiasciurini all the large sample (76) of the genus *Tamiasciurus*, the northernmost tree-squirrel species of North America, have the highest number of mammae (four pairs) that is known to characterize any tree squirrel. (But, of course, all the Nearctic tree squirrels and even all the Neotropical *Guerlinguetus* species have four pairs.) *Sciurotamias* ranges from latitude 25° to latitude 40° N. in China but apparently occurs at high altitudes in the more southern of these latitudes.

The entirely ground-squirrel tribe Xerini has two entirely Palearctic genera, the Barbary ground squirrel, *Atlantoxerus*, and the Turkmen ground squirrel, *Spermophilopsis*, and each appears to be characterized by four pairs of functional mammae. In the Ethiopian genus *Xerus*, however, the endemic tropical subgenus *Euxerus* has three pairs, the endemic tropical subgenus *Xerus* has only two pairs, and the third subgenus, *Geosciurus*, which ranges south out of the tropics to latitude 35° S., also has two pairs. Thus there is a strong north-to-south relationship to the number of functional mammae in this tribe.

To summarize, the evidence that the smaller numbers of mammae are related to warmer climate may be seen in the tribes wholly constituted by tropical endemics (the Ratufini, the Protoxerini, and the Funambulini) in which the genera are observed to be characterized by the possession of few functional mammae (two or three pairs), although two specialized genera, *Protoxerus* and *Epixerus*, have four pairs. In the one tribe that is predominantly tropical but has some considerable extension into a temperate region, the Callosciurini, the smaller number of mammae seems more prevalent in the south. The tribes with ranges predominantly in temperate and boreal climates (the Sciurini, the Marmotini, and the Tamiasciurini) each has in its temperate and boreal forms a greater number of pairs of functional mammae than is prevalent in the endemic tropical tribes. Each of these tribes of predominantly temperate and boreal climates also shows a tendency towards a reduction in the number of mammae in its own tropical or most southern taxa. In the one tribe that is about half tropical and half temperate in distribution, the Xerini, there is between the two "halves" the most notable positive relationship of all between warm climate and smaller numbers of mammae. Other factors must enter in, of course, but climate very clearly influences to some extent the number of pairs of functional mammae in the diurnal squirrel subfamily Sciurinae.

CLIMATE AND SIZE OF BROOD

TREE SQUIRRELS

FOR THE TREE-SQUIRREL GENUS *Tamiasciurus* of boreal North America, which has four pairs of mammae, Layne (1954, p. 248) reports an average of 4.9 (two to eight) young per litter.

For the tree-squirrel species of the temperate deciduous forests of North America with four pairs of mammae (*Sciurus niger*), Baumgartner (1940, p. 3) reported an average of 3.23 young for "92 sets of embryos and litters of very young squirrels" examined during a three-year period in Ohio. Monica Shorten (1951, p. 457) reports that 203 litters of *Sciurus carolinensis* in Britain averaged 2.87 (one to five) young per litter. The average of nine litters of *Sciurus griseus* (Ingles, 1947, p. 150) is 2.66 (two to four) in northern California. According to Shorten (1954, p. 32), for the Palearctic red squirrel, *Sciurus vulgaris*, in Britain three young per brood "is a good average."

For the tree squirrel of the subtropical, arid climate of India, *Funambulus pennanti*, Banerji (1955, 1957) reports the breeding of one individual whose 10 broods averaged 2.8, and ranged from two to four young (in the present author's interpretation of her data).

Among the species of tree squirrels of tropical America with four pairs of mammae, Hall and Kelson (1959, p. 372) report a female of *Sciurus aureogaster* from Potrero, Veracruz, with two fetuses at nearly full term.

Of the tree-squirrel species of tropical America with three pairs of mammae [*Syntheosciurus* (*Mesosciurus*) *granatensis*] *morulus*, Enders (1935, p. 449) records, "The usual number of embryos is two." Olalla (1935, p. 430) writes of *Sciurillus pusillus* that, "In the month of June on the Tapajos River [Brazil] I collected pregnant females, their embryos numbering two" (translation).

Among the tropical tree squirrels, Allen and Loveridge (1942, p. 185) report the finding of two minute embryos in a female, taken December 2, of *Protoxerus stangeri centricola*, which is a giant squirrel of the Ethiopian Region with four pairs of functional mammae.

Of tropical tree squirrels of the Ethiopian Region with three pairs of functional mammae the data are scattered and few. In eastern Africa, Loveridge (*in* Allen and Lawrence, 1936, p. 81) recorded taking a female sun squirrel (*Heliosciurus rufobrachium nyansae*) with a single large embryo, and another with two, on December 12. In the Misuku Mountains in Nyasaland, Lawrence and Loveridge (1953, p. 33) report a female of [*Heliosciurus*] *Aethosciurus lucifer* taken on September 23 which contained three embryos. Verheyen (1951, p. 155) says that *Heliosciurus gambianus* has two to four young per brood. Of *Paraxerus cepapi*, Haagner (1920, p. 87) reported that a female in the National Zoological Garden collections at Pretoria "gave birth to two young ones." Loveridge (1923, p. 699) obtained a pregnant female of *Paraxerus palliatus suahelicus* on August 24, 1921, and it contained "a single diminutive fetus." Allen and Loveridge (1942, p. 183) record the finding of a single quite small young of *P. flavivittis exgeanus* in a nest in a tree hollow on April 1. Lawrence and Loveridge (1953, p. 34) report two well-developed embryos in a female of *P. cepapi sindi* taken January 14. Allen and Loveridge (1942, p. 185) report a female of [*Paraxerus*] *Tamiscus e. emini* with a single embryo of medium development, taken December 13.

In tropical squirrels of the Ethiopian Region that have two pairs of mammae, Allen and Coolidge (1930, p. 593) mention a brood of two young of *Funisciurus pyrrhopus leonis* with eyes still unopened, when received on August 6 in Liberia, and they note that Büttikofer (*in* Jentink, 1888) found nests of this species in Liberia each containing but two blind young.

Among tropical tree squirrels of the Oriental tribe Callosciurini near Kuala Lumpur, Malaya, Harrison (1955, p. 458) found the average number of embryos per pregnant female to be 2.2 (one to five) in 14 *Callosciurus caniceps*, 2.2 (one to four) in 25 *C. notatus*, 2.2 (one to four) in 23 *C. nigrovittatus*, 3.0 (two to four) in four [*Sundasciurus*] *tenuis*, and 2.2 (two to three) in four [*S.*] *lowi*. The first and second species have two pairs of functional mammae; the other species, three pairs.

It is apparent enough that published data

are still very limited on the numbers of young in broods of tree squirrels from many parts of the world. The data that are available and that are arranged above (and in table 6) by climate from most cold to most warm indicate a north-to-south trend from larger to smaller broods. This north-to-south reduction in brood size is also correlated with north-to-south reduction in the number of pairs of functional mammae.

Apparently quite contrary to the above trend is a generalization by Hall and Kelson (1959, vol. 1, p. 381) that another tropical American tree squirrel, *Sciurus deppei*, has "2 to 8 (usually 4) young." Hall (in letter, April 17, 1960) assures me that the comment does not stem from original field observations. The present writer finds no full support earlier in the literature for it, but only the single observation by Gaumer (1917, p. 103) of the giving birth to five young in February by a female of *deppei* in captivity. *Sciurus deppei* is the only species of the genus *Sciurus* and the subtribe Sciurina (as recently redefined and diagnosed by the present author, 1959, p. 177) that characteristically has fewer than four pairs of functional mammae, however, and it is at least worth noting that the peculiarity of larger broods is discordant with the peculiarity of fewer mammae.

GROUND SQUIRRELS

Nearctic Only

The Holarctic ground-squirrel tribe Marmotini occupies the northernmost points of the mainland of Alaska and Canada above latitude 70° N. and ranges south to latitude 18° N. in the western end of the state of Guerrero, Mexico (Hall and Kelson, 1959, vol. 1, pp. 344, 356). The Holarctic ground-squirrel tribe is represented by some 41 species in North America compared to about 10 in the Palearctic Region. The great north-to-south range of nearly 3800 miles and the large number of species invite an investigation of the possible relationship of the size of a litter to latitude within the Nearctic Marmotini alone.

TABLE 6

Climate and the Size of Broods in Tree Squirrels
(A indicates approximate average; x shows range; figures in parentheses are sample sizes; authorities are given in the text.)

	Brood Size							
	1	2	3	4	5	6	7	8
Nearctic Region								
Tamiasciurus (many)	—	x	x	x	A	x	x	x
Sciurus niger (92)	—	—	A	—	—	—	—	—
Sciurus carolinensis (203)	x	x	A	x	x	—	—	—
Sciurus griseus (9)	—	x	A	x	—	—	—	—
Neotropical Region								
Sciurus aureogaster (1)	—	x	—	—	—	—	—	—
Syntheosciurus granatensis (?)	—	A	—	—	—	—	—	—
Sciurillus pusillus (2)	—	x	—	—	—	—	—	—
Ethiopian Region								
Protoxerus stangeri (1)	—	x	—	—	—	—	—	—
Heliosciurus species (3)	x	x	x	—	—	—	—	—
Paraxerus species (5)	x	x	—	—	—	—	—	—
Funisciurus pyrrhopus (?)	—	x	—	—	—	—	—	—
Oriental Region								
Funambulus pennanti (10)	—	x	A	x	—	—	—	—
Callosciurus caniceps (14)	x	A	x	x	x	—	—	—
Callosciurus notatus (25)	x	A	x	x	—	—	—	—
Callosciurus nigrovitattus (23)	x	A	x	x	—	—	—	—
Sundasciurus tenuis (4)	—	x	x	x	—	—	—	—
Sundasciurus lowi (4)	—	x	x	—	—	—	—	—

In one of the three subtribes of the Marmotini, the giant ground squirrels (chucks and marmots or whistlers), the Marmotina, adequate data for a comparison of brood size among the several species have not been found. For the species *monax* in New York, Hamilton (1934, p. 112) reports a range of from two to six and an average of 4.07 in 31 sets of embryos and 18 counts of placental scars. Howell (1915, p. 12) records exceptional litters of seven, eight, and nine for *monax*. For the rock-chuck or yellow-bellied marmot (species *flaviventris*), Couch (1930, p. 4) writes, "Examination of large numbers of pregnant females gave the number of young as varying from 3 to 6, with an average between 4 and 5." Howell (1915, p. 12) claims that the range of the size of the brood in *flaviventris* is three to eight, and Schooley's (1934, p. 479) average of 6.2 embryos in 44 specimens of *flaviventris* agrees with the numbers given by Howell. For the northern species *caligata*, Taylor and Shaw (1927, p. 90) state that the broods in Mt. Rainier National Park "are two to four in number." No data are given, and one must assume that this information was obtained from field observations of litters of young that were old enough to have emerged from their dens. Data thus obtained probably should not be compared with embryo counts.

In the chipmunk subtribe Tamiina, some data for at least seven species are available (given in table 7 with the most northern species within the genus at the top). For four of the seven species the data are from California and Nevada and are consequently subject to altitudinal interference with any latitudinal climatic cline that might otherwise be observed. Nevertheless, broods of larger size are evident in the two species of *Eutamias* that have ranges extending farthest to the north.

For the Spermophilina, the subtribe that gives the tribe Marmotini its great climatic range, much more data are available. Table 8 presents data on brood size for the Nearctic ground-squirrel subtribe Spermophilina, arranged with the most northern species within each genus at the top. The latitudes that were used in tables 7 and 8 were determined from the maps of each species in Hall and Kelson (1959).

The broods of the only Arctic species of the large genus *Spermophilus*, as table 8 shows, are large but not so large as those of four well-sampled species with less northern ranges: *franklini*, *tridecemlineatus*, *townsendi*, and *beecheyi*. The sample of *columbianus* is very small, but the samples of *richardsoni* and *lateralis* are at least large enough for one to inquire with some justice whether the indicated small sizes of the broods reflect some local or temporary condition affecting the sample or some specialization of the species. The three species farthest south are ones on which data are few, but those that are available indicate a tendency towards smaller broods near or in the tropics. In the very southernmost part of the range, of the southern species *variegatus*, it may be significant that Villa (1942, p. 557) reported, "The fe-

TABLE 7

SIZE OF BROOD IN RELATION TO CLIMATE (LATITUDE) IN NEARCTIC TAMIINA

Name	Latitude	Brood Size Mean	Brood Size Range	Sample	Authority
Eutamias					
minimus	33°–64°	5.5	4–7	41	Criddle, 1943, p. 82
amoenus	38°–55°	6.1	4–8	17	Tevis, 1955, p. 75
townsendi	37°–50°	4.2	2–5	9	Tevis, 1955, p. 75; Hall, 1946, p. 345
quadrimaculatus	37°–41°	4.4	2–6	12	Tevis, 1955, p. 75; Hall, 1946, p. 346
quadrivittatus	34°–41°	3.7	2–5	6	Hooper, 1941, p. 24; Hall, 1946, p. 341
speciosus	34°–40°	4.3	3–6	9	Hall, 1946, p. 344; Tevis, 1955, p. 75
Tamias					
striatus	30°–51°	5.0	2–7	41	Condrin, 1936, p. 233

TABLE 8

SIZE OF BROOD IN RELATION TO CLIMATE (LATITUDE) IN NEARCTIC SPERMOPHILINA

Name	Latitude	Brood Size Mean	Brood Size Range	Sample Reported	Authority
Spermophilus					
undulatus	55°–70°	7.5	5–12	13	Macpherson and Manning, 1959, p. 44
columbianus	49°–57°	4.6	2–7	5	Shaw, 1925, p. 109
richardsoni	40°–55°	6.1	—	33	Howell, 1938, p. 10
franklini	37°–55°	8.0	4–11	26	Sowls, 1948, p. 119
lateralis	33°–54°	5.5	3–8	43	Tevis, 1955, p. 75
tridecemlineatus	27°–55°	8.1	4–12	269	Criddle, 1939, p. 3
townsendi	37°–48°	9.4	5–15	146	Alcorn, 1940, p. 164
beldingi	35°–45°	8±	4–12	—	Howell, 1938, p. 12
beecheyi	30°–47°	7.7	5–12	40	Linsdale, 1946, p. 337
tereticaudatus	27°–35°	9.0	6–12	6	Howell, 1938, p. 31
spilosoma	20°–42°	5.6	3–8	14	Baker, 1956, p. 206; Bailey, "1931" (1932)[a]
variegatus	18°–41°	5.3	4–7	3	Bailey, 1931, p. 99; Hooper, 1941, p. 23
annulatus	18°–22°	4.0	—	1	Hooper, 1955, p. 8
Cynomys					
leucurus	38°–45°	5.5	2–10	67	Stockard, 1929, p. 475
ludovicianus	28°–49°	5.0	2–10	48	Wade, 1928, p. 150
gunnisoni	33°–38°	—	3–4	11	Scheffer, 1947, p. 404; Hooper, 1941, p. 24
Ammospermophilus					
leucurus	24°–43°	7.8	5–11	10	Hall, 1946, p. 317
harrisi	28°–37°	6	—	1	Bailey, 1931, p. 99

[a] Data also added from other sources.

males obtained the 12th of August were pregnant, each one with three embryos of advanced development."

In the prairie-dog genus *Cynomys* the available data indicate a north-to-south diminishing trend in the size of the brood. In the genus *Ammospermophilus* the species *leucurus* would, both by latitude of range and size of broods, fit in among the *tridecemlineatus* to *tereticaudatus* groups of species of *Spermophilus*.

It should be said that there is some strong evidence that the size of the brood may vary appreciably within some species. Linsdale (1946, p. 337) cites a number of reports of such a variation in the species *beecheyi*, and Alcorn (1940, p. 164) records an impressive example of a difference in one species (*townsendi*) in the average annual size of broods for two consecutive years. On the other hand Criddle (1939, p. 3) reports, from 25 years of recording counts of embryos in *tridecemlineatus* in Manitoba, that a careful study of his records shows no notable variation from one year to the next and that the average is "practically the same throughout the 25 years." Tables 5 and 7 make it obvious that we are only at the beginning of real knowledge of this matter, and Criddle's work, although already 20 years old, apparently still provides the most data available on any single species, from a study of by far the longest duration. Where variations in the average size of broods can be found in good samples from consecutive years, their extent and apparent causes seem to the present writer to be eminently worthy of investigation. The presently available information suggests that the variation within a species is not of a magnitude comparable to differences observed between north temperate and tropical squirrels and would not invalidate such comparisons as are attempted in the present paper.

Between the sizes of broods, as shown in table 8, and the number of pairs of functional mammae, as shown in table 5, some correlation may be seen in those species of *Spermophilus* for which most data were found. Of the four species in which some (or all) individuals

possess six pairs of functional mammae, each has an average size of brood reported as 7.5 or higher. In contrast, the species of *Spermophilus* in which the sample contains some or all individuals with only four or three pairs of functional mammae are reported to have average sizes of brood that are low, 5.5 for the only species for which there is a comparably large sample. In the prairie-dog genus *Cynomys*, the species *ludovicianus* which has only four pairs of functional mammae is reported to have a slightly smaller average size of brood than the species *leucurus*, in which pairs of functional mammae number five.

Tropical

The ground squirrels of the tribe Marmotini are almost completely Holarctic. None of this tribe penetrates the tropical regions of the Old World, and only a few species penetrate the edge of the New World tropics: *Spermophilus annulatus*, *adocetus*, *mexicanus*, and *perotensis*, according to Hall and Kelson (1959). Otherwise, there are no ground squirrels in the Neotropical Region, and probably none has ever reached South America.

There are tropical ground squirrels of the tribe Xerini in Africa. Dekeyser (1955, p. 185) says of the ground squirrel *Xerus* [*Euxerus*] *erythropus chadensis* of tropical Africa, which has three pairs of mammae, that it produces three to four young to a brood in French North Africa. Loveridge (1922, p. 63) took a female of *Xerus rutilus saturatus* at Longido on January 31 which "had two fetuses in uterus." This species has but two pairs of mammae. Haagner (1920, p. 89) says of the South African ground squirrel, *Geosciurus capensis*, which also has but two pairs of mammae, "Numbers of these squirrels have been bred in the National Zoological Gardens [Pretoria, South Africa] and the quota of young at a birth apparently varies from two to six—four being the usual number."

In the tropical Oriental Region the terrestrial squirrels have long noses and have, I think, quite apparently evolved directly from tree squirrels of the Oriental tribe Callosciurini, perhaps polyphyletically. In the vicinity of Kuala Lumpur, Malaya, Harrison (1955, p. 458) obtained one record of a pregnant, striped, ground squirrel, *Lariscus insignis*, that was carrying a litter of two; and three pregnant females of the ant-eater squirrel *Rhinosciurus laticaudatus* with one to two embryos (average, 1.3). *Lariscus insignis* has three pairs of mammae; *Rhinosciurus*, apparently only two. Harrison classifies *Callosciurus lowi* ecologically as a ground squirrel. Although this decision by Harrison is apparently based only on his observation that it "frequents the ground rather than the lower tree layer" (with nothing said about where it takes refuge or where it builds its nest; see Moore, 1959, p. 192, for ecological definitions of "tree" squirrel and "ground" squirrel), it is tentatively followed in the present paper. Harrison found four sets of embryos in *C. lowi*, ranging in number from two to three (average, 2.2). *Callosciurus lowi* has three pairs of mammae.

Although these data on the size of the brood of tropical ground squirrels are pitifully scant, what there are suggest that the average number in the brood is as many as four but is generally fewer, whereas the average size of the brood of terrestrial squirrels in north temperate climates (table 9) is only occasionally as low as four. In a gross way at least the data on the size of the brood in ground squirrels suggest a climatic trend which corresponds to the one indicated for the numbers of pairs of functional mammae. These trends are from larger average size of brood and larger numbers of pairs of functional mammae in a north temperate climate to smaller numbers of both in a tropical climate.

The diurnal squirrel subfamily is not alone in having larger broods in a temperate climate than in a tropical one. Lack (1954, p. 37), in his book on "The natural regulation of animal numbers," states the case for birds: "In general there is a marked increase in average clutch-size from the tropics outward toward the poles. This holds both in different populations of the same species and in different species in the same genus, and the trend is found not only in passerine and related orders, but also in owls, hawks, herons, gulls, rails, grebes, gallinaceous birds and some waders . . . In many song-birds the average clutch in central Europe is more than twice that of the same or a closely related species in the tropics. The proportionate increase between central Europe and the arctic is much smaller."

TABLE 9

CLIMATE AND SIZE OF BROOD IN GROUND SQUIRRELS

(A indicates average; x shows range; figures in parentheses are sample size; authorities are given in text.)

	Brood Size														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Nearctic Region															
Spermophilus lateralis (43)	—	—	x	x	x	Ax	x	x	—	—	—	—	—	—	—
tridecemlineatus (269)	—	—	—	x	x	x	x	xA	x	x	x	x	—	—	—
townsendi (146)	—	—	—	—	x	x	x	x	xA	x	x	x	x	x	x
beecheyi (40)	—	—	—	—	x	x	x	Ax	x	x	x	x	—	—	—
Cynomys leucurus (67)	—	x	x	x	x	x	Ax	x	x	x	x	—	—	—	—
Cynomys ludovicianus (48)	—	x	x	x	x	A	x	x	x	x	x	—	—	—	—
Eutamias minimus (41)	—	—	—	x	x	Ax	x	—	—	—	—	—	—	—	—
Ethiopian Region															
Xerus erythropus (?)	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—
Xerus rutilus (1)	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—
Xerus capensis (?)	—	x	x	A	x	x	—	—	—	—	—	—	—	—	—
Oriental Region															
Lariscus insignis (1)	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—
Rhinosciurus laticaudatus (3)	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—

To interpret this trend Lack (*loc. cit.*) continues: "A widespread phenomenon such as this requires a general explanation. In Central Europe the summer day is about half as long again as in the tropics. Hence, other things being equal, a parent bird should be able to raise more young simultaneously [having more hours per day to gather food for the larger brood]. As the adult must spend some time in rest and sleep, an increase in daylength from 12 to 18 hours is probably much more effective than an increase from 18 to 24 hours. That is probably why the average clutch shows a much greater increase between the tropics and central Europe than between central Europe and the arctic." It should be said that Lack's explanation is predicated on the thesis that the average size of the brood in animals that feed their young is inherited and is adapted by natural selection to the greatest size for which the parent will, on the average, have the ability to find adequate food.

The information presented here on the Sciurinae suggests that the north-to-south trend in the size of the brood that is reported by Lack as broadly applicable in those members of the Class Aves with altricial young will be found, when more quantitative information becomes available, to obtain broadly among members of the Class Mammalia that have altricial young. Other mammals may present, as do the Sciurinae, a corresponding morphological trend in secondary sex characters that is not available in birds.[1]

[1] While the present paper was in press, a pioneer attempt was published by Lord (1960) to determine from data in the literature whether litter size increases with latitude generally in North American mammals. He found evidence of greater litter size in higher latitudes in six groups: *Sylvilagus; Microtus; Peromyscus; Sciurus* and *Tamiasciurus* combined; *Tamias* and *Eutamias* combined; and *Sorex, Microsorex, Notiosorex,* and *Blarina* combined. But among the more fossorial and hibernating *Spermophilus, Geomys,* and *Thomomys,* and among carnivores, he found generally equivocal or negative evidence.

LATITUDE AND ANNUAL PRODUCTION OF YOUNG

THE NUMBER OF BROODS of young produced per year may have an important bearing on the relative rates of evolution in the different species. The available information is extremely scant, but what comes readily to hand at least suggests, for instance, a great difference between the tree squirrels of a boreal climate and the subtropical Indian squirrel *Funambulus pennanti*. How accurate the available information is and whether it applies, as a sort of latitudinal cline, in other squirrels remains to be discovered. Regrettably, the following information serves better to show how scarce is knowledge of this sort than to reveal definite relationships.

TREE SQUIRRELS

Layne (1954, p. 248) indicates that the number of litters raised by a single adult female of the boreal tree squirrel *Tamiasciurus hudsonicus* averages fewer than two, and that its annual product would hence average perhaps considerably fewer than 10.

Individual adult females of the tree squirrels *Sciurus carolinensis* and *S. niger* of the deciduous forests of the temperate climate are not known to raise more than two broods of young a year, hence would on the average produce fewer than six young a year (Brown and Yeager, 1945, p. 488; Shorten, 1951, p. 457). The most satisfactory evidence that individuals of either one of these species produces two broods of young per year is that of Baumgartner (1940, p. 4), who found that, of 40 tagged females of *Sciurus niger rufiventer* in Ohio, which were presumably recaptured and reëxamined sufficiently often, 33 definitely produced two litters in one year and seven definitely produced but one brood in one year.

One individual of the tree squirrel *Funambulus pennanti*, adapted to the arid areas of subtropical India, observed during two and a half years by Banerji (1955, 1957) bore 10 litters of young, one about every three months, or an average period of 88.4 days. The nine gestation periods that were recorded ranged from 40 to 43 days and averaged 42. The annual production of young by this squirrel averaged 11.2.

The Neotropical tree squirrel *Sciurus deppei* of eastern Mexico and Central America is said to "breed throughout the year" (Hall and Kelson, 1959, p. 381). Such a statement does not reveal how many broods a year an individual may bear, of course, for, if the species breeds aseasonally, individuals could be confined to one brood a year and the species could still produce young in every month. If Lack's (1954) principle regarding what limits the number of young applies here, and it evidently should, then it seems much more likely that individuals of this species produce more than one brood of young per year. Because there is an alternation of rainy and dry seasons, there should be an annual peak of food abundance with which a seasonal peak in the production of young might be expected to coincide. Dalquest (1953, p. 89) says the food of *deppei* "includes many forest fruits." If the adult individuals of *deppei* regularly produce three or four broods of young a year, in terms of annual production they would, at the rate cited above of four (two to eight) young per litter, be the most prolific tree squirrels known. Other things being equal, such reproductive capacity would theoretically give them an advantage in the rapid evolution of adaptive characteristics.

In the vicinity of Kuala Lumpur, Malaya, the tropical climate is virtually seasonless, and there J. L. Harrison (1955, p. 456) appears to have found at least 6 per cent of all females of *Callosciurus notatus* and *C. nigrovittatus* pregnant in each three-month period of the year. Pregnancies rose, however, to peaks of 29 per cent and 20 per cent, respectively, in these two species for the April–June period. Harrison does not give dates, even by three-month periods, for the other five squirrel species for which he had (fewer) pregnancy records. He shows (1955, p. 453) that males of *C. nigrovittatus* are taken with sperm in the epididymes at any time of year, but that males without sperm are three times as numerous in January–March and July–September as in the intervening three-month periods. His data (Harrison, 1955, p. 454) on the average weight of testes show a strong peak for *C. nigrovittatus* in the April–

June quarter and a weak peak in October–December, but for *C. notatus* the testes average heaviest in the July–September period with a build-up towards a peak showing in April–June. In 126 mature females of *Callosciurus notatus*, Harrison (1955, p. 456) reports 25 (about 20 per cent) as having embryos large enough to be detected by inspection, by which it is assumed that he means inspection of the reproductive tract with the unaided eye. Because Harrison's (1955) data were obtained during all months of the year and over a period of five years (1948–1952) in an area where there is virtually no seasonal variation in climate, it seems fair to infer that mature female *individuals* of this species are in this condition of pregnancy 20 per cent of the time, which would be 73 days of a year. If these assumptions are correct, and if the proportion of the unknown gestation period for this species during which pregnancy would be detected by Harrison's methods can be estimated as about 25 days, these data would indicate an average of three broods of young a year. Further, if the gestation period of *C. notatus* is similar to that of *Funambulus pennanti* (42 days) and the time required for rearing the young is about the same for the two species, then four litters a year in *notatus* would be theoretically possible, and producing only three of a possible four would give the peak in pregnancies that is remarked upon above.

Harrison (1955, p. 456) also obtained 23 records of pregnancy from a collection of 125 mature females of *C. nigrovittatus*. The remarks in the preceding paragraph on *C. notatus*, therefore, apply rather well to *C. nigrovittatus*. His data on *C. caniceps* were fewer (14 pregnancies in 55 mature females), and the ratio is higher.

In the Ethiopian sun-squirrel species *Heliosciurus gambianus*, Verheyen (1951, p. 155) states that there are two broods of young per year.

GROUND SQUIRRELS

Of the Nearctic Ground squirrels that are listed in table 7, the data made available by the authorities indicated there, or by Asdell (1946), show that from north to south in the species of *Spermophilus* from *undulatus* through *beecheyi*, each has but one brood of young a year, but the still more southern *tereticaudatus* and *spilosoma* have two broods a year. In *variegatus* two broods a year is considered probable, but for *annulatus* there is no information. In the prairie-dog genus *Cynomys* all three of the species listed in table 7 are reported to have but one brood of young a year. If the three prairie-dog species were ranked among those of *Spermophilus* on the north-to-south scale, they would all fit in above those with two broods (i.e., above *tereticaudatus*). *Ammospermophilus leucurus*, the antelope ground squirrel, is known to have two broods of young a year, and its north-to-south range places it between the lowest of the others with a single brood and *S. tereticaudatus*. Thus, in the data at hand there appears to be an abrupt change from one brood a year in all the northern species to more than one brood a year in the southern species.

In the tropical ground squirrels of the Ethiopian Region, Powell (*in* Shortridge, 1934, p. 312), says of *Geosciurus capensis*, "They breed twice a year; the young begin to breed at six months."

SUMMARY

THE DISCOVERY IS REPORTED of a third line of evidence which separates the large tribe of Oriental tree squirrels Callosciurini from the Holarctic members of the tribe Sciurini and also associates the widely disjunct Bornean tassel-eared squirrel *Reithrosciurus* with the Holarctic Sciurini. The third line of evidence is the number of pairs of functional mammae, which are four in the Holarctic Sciurini but only two or three in the Callosciurini. Data in the new line of evidence are presented for samples of 34 of the 37 genera of the subfamily Sciurinae of diurnal squirrels. Their significance to the interrelationships of the eight tribes and their constituent subtribes and genera and occasionally lower categories is evaluated.

In general the new line of evidence is equivocal or supports the latest classification of the subfamily Sciurinae. It also suggests some minor refinements. For example, within the large Oriental squirrel subgenus *Callosciurus* a previously unsuspected division of the species is discovered that separates grossly the Malaysian from the Indo-Chinese species. The species of the Indo-Chinese Subregion have two pairs of mammae; those of the Malaysian Subregion, generally three.

In addition to being of systematic value in its geographic variation, the number of pairs of functional mammae is shown to vary with latitude. The number of pairs generally decreases from boreal and temperate climates to tropical.

Data from the literature on the size of the brood are presented which reveal that it is correlated with a reduction in mammae from temperate to tropical climates. In the tree squirrels as a whole and in the ground squirrels as a whole, there seems to be a strong trend of larger towards smaller broods from the north temperate climates to tropical climates. This trend corresponds with the decrease in the size of the clutch in birds from the north temperate to tropical climates, but in squirrels the trend seems also to be correlated with a meristic morphological difference—the number of pairs of mammae.

No clear answer is at hand for an important question concerning evolution: Do the squirrels of the temperate climate with more mammae and larger broods actually produce more young per year? A definite north-to-south increase of broods from one to two broods per year is found in Nearctic ground squirrels. Data from *Funambulus pennanti* in India and three species of *Callosciurus* in Malaya hint that the females of tropical species may rear three or four broods in a single year, instead of one or two as do their relatives in more northern latitudes.

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