

RELATIONSHIPS AMONG LIVING
SQUIRRELS OF THE SCIURINAE

JOSEPH CURTIS MOORE

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CONTENTS

INTRODUCTION	159
The Problem.	159
Taxonomic History	160
Acknowledgments	160
Methods	161
Scope	161
Orientation of the Skull	162
Measurements	164
Catalogued Specimens	166
DEFINITIONS, DIAGNOSES, AND RELATIONSHIPS	167
Tribe Ratufini	167
Tribe Protoxerini	168
Tribe Funambulini	170
Tribe Callosciurini	173
Tribe Sciurini	177
Tribe Marmotini	180
Tribe Tamiasciurini.	182
Tribe Xerini	184
PYGMY SQUIRREL CONVERGENCE	186
ORIGIN OF THE NEOTROPICAL PYGMY GENUS	191
SKULL CHARACTER DIFFERENTIATION IN SCIURINE GENERA	192
Ecological Niche Definitions	192
Tree Squirrel Conservatism	194
Succession in Ground Squirrels	195
CLASSIFICATION OF THE SCIURINAE	198
Key to the Tribes and Subtribes of the Sciurinae	199
SUMMARY	201
Conclusion	201
APPENDIX	202
BIBLIOGRAPHY	205

INTRODUCTION

THE PROBLEM

AS DARLINGTON (1957, p. 325) has recently pointed out, the squirrel family Sciuridae is one of just five families of terrestrial mammals that are now native to, and widely distributed in, Africa, Eurasia, North America, and South America. Furthermore, of these five families the squirrel family is the most diversified, having by Simpson's (1945) account 42 existing genera, compared to the 29 in the Mustelidae, 12 in the Canidae, nine in the Leporidae, and three in the Felidae. Surely it is also the most numerous in individuals. Moreover, if one may delete the flying squirrel subfamily Petauristinae, which inhabits only two continents anyhow, the remaining and zoogeographically far more important subfamily Sciurinae is composed of squirrels whose activity is diurnal. Abundance and diurnal activity have placed the Sciurinae among the easiest of mammals to collect with a gun, and many students of birds as well as of mammals have collected them. Consequently there are splendidly representative study collections of sciurine squirrels in the museums of the world.

Despite the potential importance of this subfamily to small-scale zoogeography and its potential relevance to the understanding of mechanisms of evolution, however, such studies in the Sciurinae may have been delayed because of the difficulties encountered in any attempt to classify the members of the Sciurinae by skull characters. For the tree squirrels in particular, no one has been able to report any satisfactory skull characters that distinguish, even at the generic level, the tree squirrels of the Palearctic and Nearctic regions (*Sciurus*) from *Callosciurus* and others of the Indo-Malayan region, or *Heliosciurus* and others of the Ethiopian region, or *Guerlinguetus* and others from the Neotropical region. Yet the tree squirrel genera *Callosciurus*, *Heliosciurus*, and also *Tamiasciurus* of the Nearctic region have been declared to differ from *Sciurus*, and from one another, at the subfamily level (Pocock, 1923) on the basis of genital characters. Furthermore, Simpson (1945) has accepted Pocock's sub-

families as tribes in his classification of the mammals.

The fossil genera that Simpson (1945) admitted to the five above-mentioned, widespread, terrestrial, mammalian families in his classification are: 56 in the Canidae, 47 in the Mustelidae, 30 in the Felidae, 15 in the Leporidae, but in the Sciuridae, none. On the condition of knowledge of the fossil squirrels Simpson (1945, p. 202) commented: "Fossil squirrels have been often reported, but they have not recently been revised or studied in detail, and many of the identifications seem highly uncertain. . . . The fossil evidence so far gathered does not at all assist in our understanding of the divergence of the innumerable living species or in classifying these."

The problem is, Would an assiduous search for taxonomic characters of the skull in existing genera of the Sciurinae yield evidence of their relationships satisfactory for a more firm classification of the existing Sciurinae?

While doing some revisionary work restricted to Indo-Malayan Sciuridae, the writer found a character of the skull that characterized most of the Indo-Malayan squirrel tribe Callosciurini and distinguished them from the North Temperate Zone squirrels of the tribe Sciurini. The auditory bullae of the Callosciurini each had a single, bony, transverse baffle or partial septum, whereas the bullae of the more northern Sciurini each had two such septa. Further investigation revealed that the Indo-Malayan giant squirrel *Ratufa* had no transbullar septa, and that the Nearctic red squirrel, *Tamiasciurus*, had three. Here seemed to be evidence of especially precise skull character support for three of the tribes of the Sciurinae which had previously been characterized only by genital characters, and a suggestion of the existence of a previously unrecognized tribe. The writer proceeded at once to test this character on the Sciurinae. Variability in the number of transbullar septa in the tree squirrels of Africa and South America, however, necessitated the discovery of other skull characters, and the desirability of proposing a suprageneric clas-

sification of categories characterized by as many skull characters as possible turned the investigation to an open search of the scope of the problem as stated above.

A report on an early stage of this study was read before the Society of Systematic Zool-

ogists at the Indianapolis meeting of the American Association for the Advancement of Science on December 28, 1957, and a summary of the maturing study was reported before the 1958 meeting of the American Society of Mammalogists in June at Tucson, Arizona.

TAXONOMIC HISTORY

Trouessart (1880, pp. 290–293, 315) published a classification of the Sciuridae consisting of five genera, but under *Sciurus* he attempted to characterize 17 subgenera, about half of the names of which survive today as genera. Flower and Lydekker (1891) provided a classification of Sciuridae consisting of 10 living genera divided into two subfamilies, the Sciurinae and the Arctomyinae. Two years later Forsyth Major published the results of his study of the teeth and skulls, and a better classification of 10 genera divided into three subfamilies: Sciurinae for ordinary squirrels, Pteromyinae for flying squirrels, and Nannosciurinae for pygmy squirrels. Miller and Gidley (1918) retained these three subfamilies. Thomas (1915) reported the os penis or baculum to have taxonomic characters useful at the generic level in Sciuridae and proposed to separate the Indo-Malayan tree squirrel from the Holarctic genus *Sciurus* as *Callosciurus* (and partly also *Tomeutes*), because they have a separate blade on the baculum. Pocock (1923) followed Thomas with a study of the baculum and glans penis in the Sciuridae and proposed to distinguish six subfamilies within the Sciuridae based on genital characters and to regard the flying squirrels as a family, Petauristidae.

The six subfamilies included 30 genera. Pocock's treatment of the North American red squirrel, *Tamiasciurus*, as a monotypic subfamily because of its attenuated glans penis and apparent absence of a baculum received enthusiastic endorsement from Mossman, Lawlah, and Bradley (1932) when they reported that the male genital tract of *Tamiasciurus* differed trenchantly from that of other Nearctic squirrel genera. Nevertheless, Chasen (1940) continued to use *Sciurus* instead of *Callosciurus*; Ellerman (1940) used *Callosciurus* with explicit reluctance; and other students of mammals were slow to admit the general validity of Pocock's investigation, until Simpson (1945) accepted it as the best available evidence of natural relationships. Simpson scaled Pocock's subfamilies of Sciuridae down to tribes of Sciurinae and admitted to them 30 genera.

The classifications of the Sciurinae by Flower and Lydekker (1891), Forsyth Major (1893), and Thomas (1897), of the Asiatic genera by Thomas (1908), of the African genera by Thomas (1909), of the American genera by J. A. Allen (1915), and of the North and Central American genera by Miller (1924) and Howell (1938) are listed and discussed by Ellerman (1940, pp. 261–269).

ACKNOWLEDGMENTS

The author is indebted to Dr. Harold E. Anthony of the American Museum of Natural History for the invitation to take up the revisionary work on the Indo-Malayan Sciuridae that G. H. H. Tate had begun as a review, for providing a substantial fellowship to support this work, and for encouraging the digression of more than a year's duration which has resulted in the present paper.

The revisionary work and the presently re-

ported digression from it have been supported by grants from the National Institutes of Health, RG-5327, and the National Science Foundation, G 4447, for which the writer is very grateful.

Important loans of study material were generously provided by Dr. David H. Johnson of the United States National Museum, Washington, D.C.; Mr. Philip Hershkovitz of the Chicago Natural History Museum,

Chicago, Illinois; Miss Barbara Lawrence of the Museum of Comparative Zoölogy, Cambridge, Massachusetts; Dr. Peter Crowcroft of the British Museum (Natural History), London, England; Dr. Georg H. W. Stein, of the Zoologisches Museum Humboldt-Universität, Berlin, Germany; and Dr. W. H. Burt of the Museum of Zoology, University of Michigan, Ann Arbor, Michigan.

Dr. George Gaylord Simpson considerably read the manuscript and asked several helpful questions. Mr. Philip Hershkovitz tested the

treatment of South American squirrels, in an earlier draft, on Chicago Natural History Museum collections, and offered criticisms which helped the writer to reach the present arrangement of some of the South American forms. Dr. Karl F. Koopman read and criticized the manuscript. Dr. Richard G. Van Gelder reviewed the manuscript in a painstaking effort to make it physically error-free. The writer is grateful for this professional helpfulness and acknowledges full responsibility for any error that remains.

METHODS

Presence or absence in the auditory bulla of one or more transverse bony septa is the taxonomically important character the discovery of which inspired the present work. In figure 1 the ventral view of a squirrel skull (A) is provided to indicate the orientation of the auditory bullae, which are stippled. B through G are separate left bullae, each oriented as is the left bulla of the skull. B possesses no transbullar septum, C has but a single transverse septum, D possesses two transverse septa, E has three transverse septa, F has many transverse septa, and G has a honeycomb of septa. In the Sciurinae the range in the number of transbullar septa is from none to three. The possession of many transbullar septa per bulla and a honeycomb of septa has been found only in the flying squirrels, Petauristinae, which are also under study. The auditory bullae shown on the skull (fig. 1A) illustrate the character that distinguishes the genus *Sundasciurus*, wherein the single transverse septum forks very broadly, and the tines of the fork separate off a distinctive chamber of the bulla.

It should be noted that figure 1 shows only the exterior of the bullae and that the septa, although shown with solid lines, are actually internal bony baffles across the chamber of the bulla. There is usually a palpable manifestation of the number and extent of these septa, and translucent bullae show the septa externally as opaque lines. Except in the cases of very translucent bullae, examination was made through the meatus visually or by careful probing. Admitting a strong light through the meatus showed the septa externally as opaque lines in bullae that were at first thought to be impenetrable to light. An in-

dication of the frequency of occurrence of various numbers of transbullar septa per bulla in the various genera is presented in table 1.

In the present study when a character was discovered which it was thought might have diagnostic value for a given taxon, its incidence was checked in the whole series of that taxon available in the Museum, but for comparison with other taxa a synoptic series was used. In enumerating the skull characters of each taxon, the writer has tried to state them, when possible, so that a student can identify a squirrel skull as to tribe, subtribe (if any), and sometimes genus, without recourse to comparative material. These characters are usually listed in the order of the taxonomically most important to the least. Diagnoses of each taxon were prepared with a painstaking use of the synoptic series and occasional checking against large series.

Simpson (1945) and Wood (1955) have been followed regarding the use of the category Sciuridae to include all squirrels and that of Sciurinae as constituting those squirrels without gliding membranes. Simpson (1945) has been followed in the form of the classification. The little-used categories of tribe and subtribe are employed here, not with any idea that other students of mammals will wish to burden handbook classifications with such categories, but as a tool of classification to show natural categories that, as clearly shown in the present paper, do exist.

SCOPE

The present paper treats suprageneric classification of the living Sciurinae. When it was necessary in the prosecution of this work

for the writer to determine for his own satisfaction what skull characters distinguished certain genera, and where this resulted in an apparently new and useful generic or sub-generic diagnosis, it is included as such. However, to provide decisions on what taxa are valid genera and subgenera throughout the Sciurinae was not necessary to accomplish the present work and is outside its scope. The genera and subgenera of the Callosciurina are expected to be diagnosed in a future paper. The others that have not received formal decisions as to rank are in the Funambulini and the Xerini. Decisions that have been reached in the Marmotini result from my following Bryant (1945) in the *Spermophilina* and White (1953) in the *Tamiasina* rather than from a careful empirical assessment.

ORIENTATION OF THE SKULL

In many of the characters of the skull used in the present paper, one structure is said to be farther anterior than another. Particularly if the difference is slight or the two structures

are rather far apart vertically, one finds the orientation of the skull extremely important. To be precise and consistent in this, all such decisions were made while the skull was viewed with its occlusal plane held horizontal or level. As the maxillary tooth row often turns strongly outward posteriorly, raising the outer row of cusps, lowering the inner row of cusps, and thus twisting the actual occlusal plane, the occlusal plane as used here for orienting the skull is the level plane on which the two maxillary tooth rows would rest if the skull could be rested upon it supported only by these teeth. This is determined by holding the skull up in lateral view and sighting across the bottoms of the two maxillary tooth rows.

Proödonty, orthodonty, and opisthodonty are terms, of course, pertaining to the upper incisors. Held in lateral view and oriented as stated in the above paragraph, a skull is, in this paper, considered to have orthodont incisors if a line from the cutting tip to the highest visible point on the front of the tooth appears perpendicular to the occlusal plane.

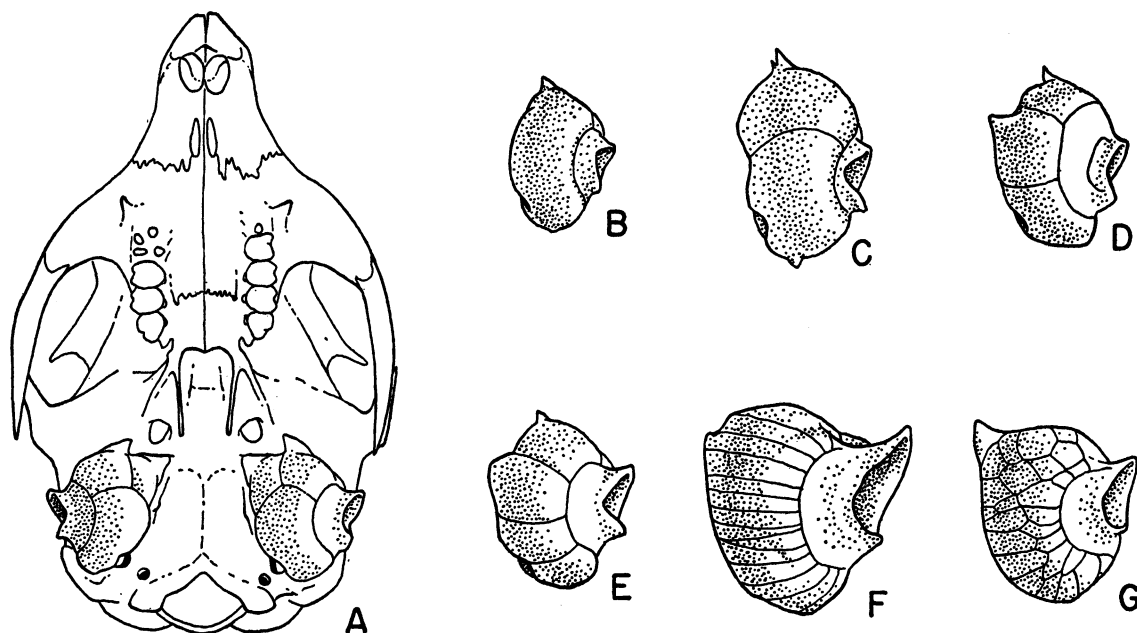


FIG. 1. Auditory bullae of squirrels that exemplify the numbers of transbullar septa. A. Complete skull of *Sundasciurus tenuis* (A.M.N.H. No. 135034). Others are all left bullae oriented as is the corresponding one of *S. tenuis*. B. *Prosciurillus leucomus* (A.M.N.H. No. 152931), no septum. C. *Callosciurus prevosti* (A.M.N.H. No. 102709), one septum. D. *Sciurus vulgaris* (A.M.N.H. No. 92145), two septa. E. *Tamiasciurus hudsonicus* (A.M.N.H. No. 834), three septa. F. *Troglodytes xanthipes* (A.M.N.H. No. 111355), many septa. G. *Petinomys hageni* (A.M.N.H. No. 103150), a honeycomb of septa.

TABLE 1

INCIDENCE OF VARIOUS NUMBERS OF TRANSBULLAR SEPTA IN SAMPLES OF THE GENERA, AND
SOME SUBGENERA, OF THE SCIURINAE

(A septum is counted as a whole one if it extends at least halfway across the bullar
chamber from, or to, the margin of the tympanum, or tympanic annulus.)

	Pairs of Transbullar Septa								
	0	$\frac{1}{2}$	1	$1\frac{1}{2}$	2	$2\frac{1}{2}$	3	$3\frac{1}{2}$	4
Xerini									
<i>Xerus</i>	—	—	1	—	—	—	40	—	—
<i>Atlantoxerus</i> ^a	—	—	—	—	—	—	4	1	—
<i>Spermophilopsis</i>	—	—	—	—	1	—	10	—	—
Tamiasciurini									
<i>Tamiasciurus</i>	—	—	—	—	3	5	128	1	1
<i>Sciurotamias</i>	—	—	—	—	—	—	30	—	—
Marmotini									
<i>Marmota</i>	—	—	9	—	40	—	3	—	—
<i>Spermophilus</i>	—	—	4	12	293	7	—	—	—
<i>Ammospermophilus</i>	—	—	—	—	54	2	—	—	—
<i>Cynomys</i>	—	1	10	18	107	1	—	—	—
<i>Tamias</i>	—	—	1	3	179	5	2	—	—
<i>Eutamias</i>	—	—	1	1	328	4	—	—	—
Sciurina									
<i>Sciurus</i>	—	—	32	33	558	23	8	—	—
<i>Tenes</i>	—	—	—	3	5	6	12	1	—
<i>Reithrosciurus</i>	—	—	—	—	2	—	—	—	—
<i>Guerlinguetus</i>	—	—	28	6	10	—	—	—	—
Microsciurina									
<i>Microsciurus</i>	5	2	18	1	8	—	—	—	—
<i>Leptosciurus</i>	—	—	3	2	26	—	—	—	—
<i>Simosciurus</i>	—	—	10	2	13	—	—	—	—
<i>Syntheosciurus</i> (including <i>Mesosciurus</i>)	—	2	19	11	20	—	—	—	—
Sciurillina									
<i>Sciurillus</i>	—	—	29	—	—	—	—	—	—
Callosciurina									
<i>Callosciurus</i>	3	5	724	15	9	1	—	—	—
<i>Sundasciurus</i>	2	2	64	—	—	—	—	—	—
<i>Aletesciurus</i>	9	4	42	4	—	—	—	—	—
<i>Dremomys</i>	1	1	59	—	—	—	—	—	—
<i>Lariscus</i> (including <i>Menetes</i>)	—	—	124	3	2	—	—	—	—
<i>Nannosciurus</i>	1	—	32	—	—	—	—	—	—
<i>Glyphotes</i>	—	—	9	—	—	—	—	—	—
<i>Rhinosciurus</i>	—	—	11	—	—	—	—	—	—
Hyosciurina									
<i>Hyosciurus</i>	6	—	—	—	—	—	—	—	—
<i>Rubrisciurus</i>	12	3	1	1	—	—	—	—	—
<i>Prosciurillus</i>	70	9	47	2	—	—	—	—	—
<i>Exilisciurus</i>	50	—	1	—	—	—	—	—	—
Funambulini									
<i>Funambulus</i>	—	—	20	3	8	—	—	—	—
<i>Paraxerus</i>	—	—	48	2	39	1	—	—	—
<i>Funisciurus</i>	—	—	118	—	—	—	—	—	—
<i>Myosciurus</i>	—	—	—	—	4	—	—	—	—
Protoxerini									
<i>Protoxerus</i>	—	—	52	—	—	—	—	—	—
<i>Epixerus</i>	—	1	1	—	1	—	—	—	—
<i>Heliosciurus</i>	15	8	47	5	8	1	—	—	—
Ratufini									
<i>Ratufa</i>	196	—	2	—	—	—	—	—	—

^a One further specimen of *Atlantoxerus* had six septa in one bulla and four in the other.

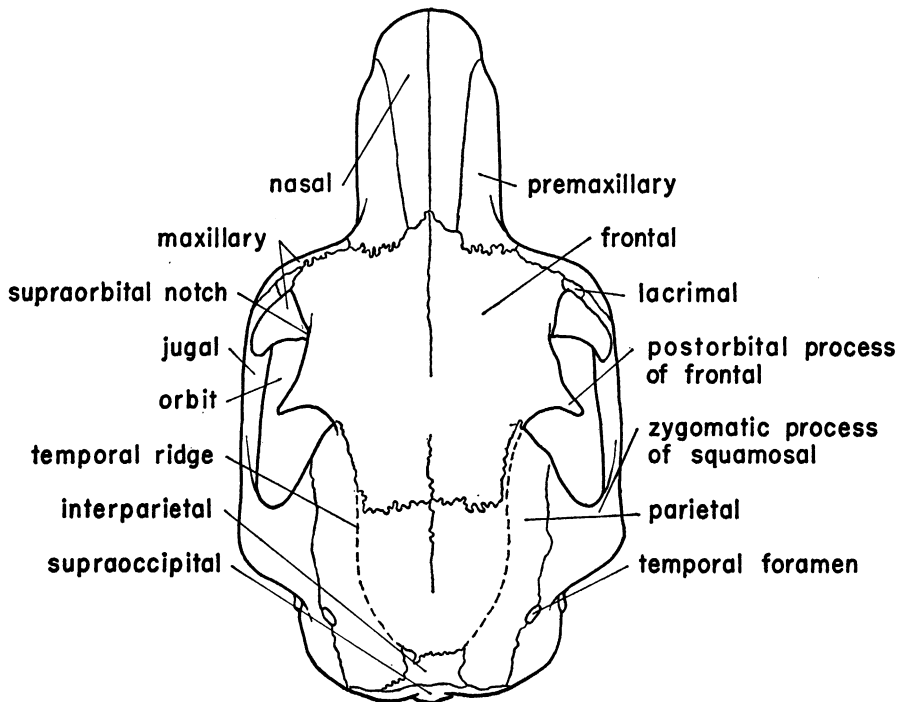


FIG. 2. Dorsal aspect of the skull of a squirrel, *Reithrosciurus macrotis*, identifying features used in characterizing taxa of the Sciurinae. If the adjective is used alone, bone is ordinarily implied, i.e., "nasal" [bone].

If the posterior angle of this line to the occlusal plane is visibly less than 90 degrees, the teeth are proödont. If the angle exceeds 90 degrees the teeth are opisthodont.

Names of foramina are those used by John Eric Hill (1935). When two foramina pierce the squamosal bone in the postglenoid area, the anterior one is, in this paper, considered the postglenoid foramen, the posterior one the subsquamosal. In taxa in which only one regularly occurs, evidence as to which it is was sought in those occasional specimens that have the other showing in a vestigial (or incipient) condition. Occasionally, in the *Marmotini* the temporal foramen has evidently migrated from the squamosoparietal suture to the postglenoid area. This was determined by the facts that it makes a third foramen in the postglenoid area, leaves no foramen in the suture, and can in occasional individuals be found only halfway in its migration.

MEASUREMENTS

Measurements, with the use of sliding, dial calipers with parallel jaws, have been made in the present study as defined below:

OCCIPITONASAL LENGTH: The greatest length of skull from the anteriormost tip of the nasals to the posteriormost point on the supraoccipital.

ORBITONASAL LENGTH: The distance from the anterior edge of the right orbit, taken in the notch of the lacrimal bone, to the anterior tip of the right nasal bone.

ORBITAL LENGTH: The greatest inside distance from the anterior edge of the orbit, in the notch of the lacrimal bone, to the posterior extremity of the orbit on the edge of the zygomatic process of the squamosal. This might correctly be said to measure the greatest length of the combined orbit and temporal fossa. However, the temporal fossa is often so reduced in squirrels that it is here a convenience, as employed by Ellerman (1949, p. 5), to disregard it.

ORBITAL WIDTH: The greatest inside measurement, approximately at right angles to the line of the orbital length, from the frontal to the jugal.

INTERORBITAL BREADTH: The least distance across the frontals between the rims of the orbits, excluding the reducing effect of the supraorbital notches.

POSTORBITAL CONSTRICTION: The least breadth of the skull immediately posterior to the postorbital processes of the frontals.

LENGTH OF MAXILLARY TOOTH ROW: The

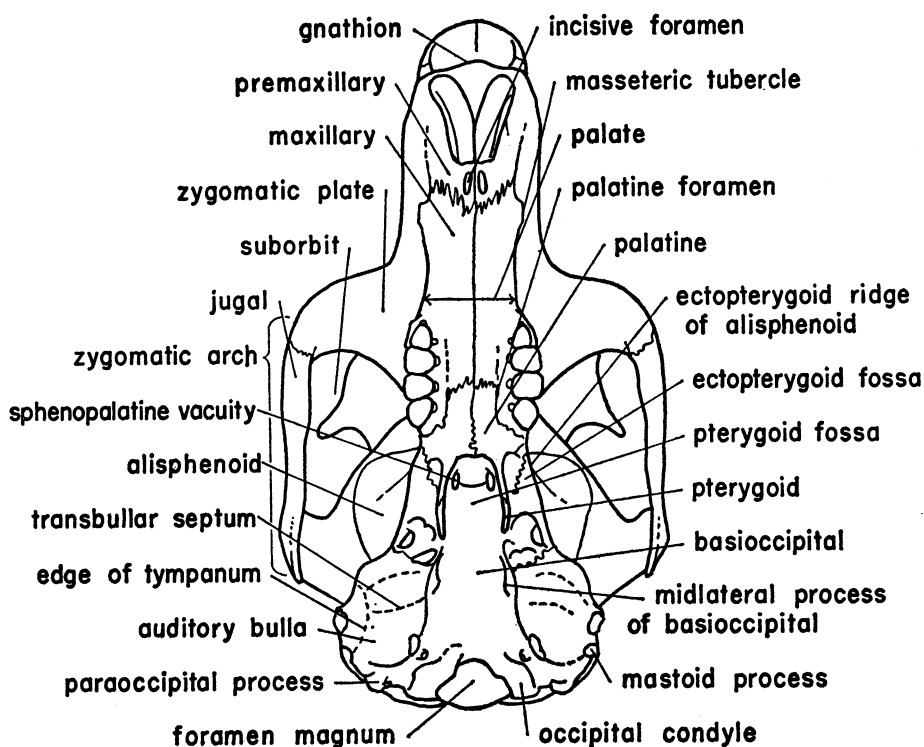


FIG. 3. Ventral aspect of the skull of a squirrel, *Reithrosciurus macrotis*, identifying features used in characterizing taxa of the Sciurinae. Note that in this genus the palatines intrude upon the pterygoid fossa far posterior to the end of the tooth row.

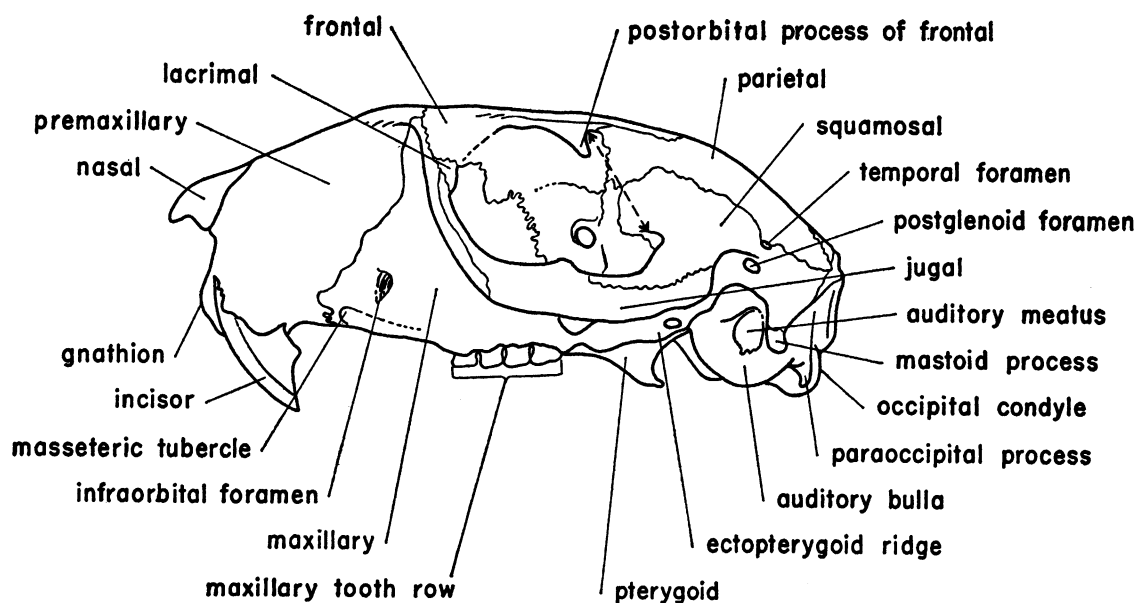


FIG. 4. Lateral aspect of the skull of a squirrel, *Reithrosciurus macrotis*, identifying features used in characterizing taxa of the Sciurinae. Note that the incisor (tooth) is extremely opisthodont. The maxillary teeth, left to right, are the fourth premolar and the first, second, and third molars. Dashed line with arrows is that along which "height of squamosal" is observed.

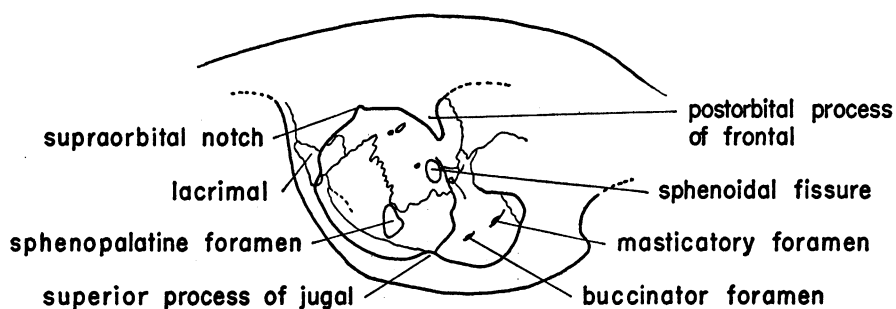


FIG. 5. View into the orbit from an angle slightly above that of figure 4, to show the important foramina which in that drawing are hidden behind the jugal. The separation of the buccinator and masticatory foramina is unusual in the Sciurinae but characterizes several important genera.

greatest length of the row of right upper cheek teeth, omitting the third premolar, if present. This is a measurement of the teeth, not of the alveoli.

LENGTH OF INFRAORBITAL CANAL: The least distance from the anterior margin of the suborbit to the lateral lip of the infraorbital foramen.

The reader must note that, in seeking the characters that distinguish between any two taxa in the section on characterizations, he must look in the diagnoses of both taxa. The diagnosis of the Marmotini shows the characters that the Marmotini possess that distinguish them, for example, from the Protoxerini, but other characters that also distinguish the two tribes are possessed by the Protoxerini and will be found in the diagnosis of that tribe.

CATALOGUED SPECIMENS

References to individual specimens by their catalogue numbers are preceded by initials that represent the institutions in which the specimens are catalogued, as follows:

- A.M.N.H., the American Museum of Natural History
- B.M., British Museum (Natural History), London
- C.N.H.M., Chicago Natural History Museum
- M.C.Z., Museum of Comparative Zoölogy at Harvard College, Cambridge, Massachusetts
- U.M.M.Z., Museum of Zoology, University of Michigan, Ann Arbor
- U.S.N.M., United States National Museum, Washington
- Z.M.H.U., Zoologisches Museum Humboldt-Universität, Berlin

DEFINITIONS, DIAGNOSES, AND RELATIONSHIPS

THE TERMS "definition" and "diagnosis" are used here as distinguished by Simpson (1943, p. 152): "definition," to describe the observed characters and limits of a taxon, "diagnosis," to state the observed differences between the taxa.

Because the tribes Sciurini and Callosciurini can be satisfactorily defined only by characters of their bacula, and not yet by characters of the skull, and because the definitions and diagnoses presented here are constructed of skull characters, the several constituent subtribes of the Sciurini and Callosciurini are treated instead of those two tribes. The characteristic ending "ina" is depended upon to distinguish these subtribes from the tribes.

TRIBE RATUFINI

INDO-MALAYAN GIANT SQUIRRELS

The genus *Ratufa* constitutes this tribe and has the following significant characters:

1. No transbullar septum crosses the chamber of the auditory bulla.

2. In lateral aspect the lateral lip of the infraorbital foramen is vertical or inclined forward at the top, and the upper part of it reaches the maxillary-premaxillary suture.

3. The postglenoid foramen is single, round, and obsolescent, and no subsquamosal foramen pierces the squamosal.

4. The squamoso-alisphenoid suture lies about halfway between the posterior margin of the base of the zygomatic process of the squamosal and the third molar, and this suture lies at about right angles to a line connecting these points.

5. The palatines are very short, the pterygoid fossa extending forward to the third molar and sometimes almost to the second molar.

6. The postorbital constriction is less than 0.80 of the interorbital breadth (without the orbital notches).

7. In fully adult individuals the sagittal suture and frontoparietal suture ankylose completely, so that there remain no visible sutures on the dorsal surface of the skull from the anterior edge of the frontals to the posterior edge of the parietals.

8. The long orbit is about 0.73 to 0.88 of the great interorbital breadth.

9. The interorbital breadth is great, for the width of the orbit is only about 0.50 (0.44 to 0.58) of it.

DIAGNOSIS OF THE TRIBE RATUFINI

The Ratufini are distinguished from the other tribes and subtribes of Sciurinae by the above enumerated characters as follows: from the Hyosciurina by 2, 4, 5, 6, and 7; from the Protoxerini by 1, 2, 4, 5, 6, 7, 8, and 9; from the Funambulini by 1, 4, 5, 6, 7, 8, and 9; from the Callosciurina by 1, 4, 6, and 7; from the Sciurillina by 1, 3, 4, 5, 6, 7, and 9; from the Sciurina by 1, 2, 3, 4, 5, 6, and 7; from the Microsciurina by 1, 2, 4, 5, 6, and 7; from the Marmotini by 1, 2, 3, 4, 5, 8, and 9; from the Tamiasciurini by 1, 2, 3, 4, 5, 6, 7, 8, and 9; and from the Xerini by 1, 2, 3, 4, 5, 6, 7, 8, and 9.

The order of taxonomic importance of the above characters is evidently 4, 1, 5, 6, 7, 8, 2, 9, 3.

RELATIONSHIPS OF THE TRIBE RATUFINI

Although the differences between *Ratufa* and *Rubrisciurus* are numerous and striking, certainly indicating long separation with divergent development, which justify classifying them in separate tribes, there are important characters which show remarkably strong similarities. These are the absence of transbullar septa, a likeness of the infraorbital foramen and masseteric tubercle, and the intrusion of the pterygoid fossa into the palatal area between the maxillary tooth rows. That *Ratufa* has fewer important similarities to the other members of the Hyosciurina is to be expected, because the evolutionary development of *Hyosciurus* and *Exilisciurus* has been for such specialized habits that one could not expect the retention of so many structural similarities as in *Rubrisciurus*, which is rather like *Ratufa* in bodily size and proportions if not also habits.

The pushed-up character of the rostrum of *Ratufa* might seem to be an important characteristic of the Ratufini, but it also occurs in *Heliosciurus* (Protoxerini), *Sciurotamias*

(*Tamiasciurini*), *Marmota* and *Tamias* (*Marmotini*), and *Simosciurus* (*Microsciurina*).

Similarities of *Ratufa* to the Protoxerini that may indicate relationship are several but trivial, and here quite as well as in the relationship of *Ratufa* to the Hyosciurina the differences are very great. The similarities to the Protoxerini are the rather large relative size of the sphenopalatine foramen, opisthodonty, the absence of the third upper premolar, and the absence of a blade on the baculum. However, *Ratufa* also shares with the sun squirrel genus of the Protoxerini, *Heliosciurus*, a character that is rare in this subfamily, namely, the complete ankylosis in adults of the frontoparietal suture.

TRIBE PROTOXERINI

AFRICAN GIANT SQUIRRELS AND THE SUN SQUIRREL

This tribe consists of the genera *Protoxerus*, *Epixerus*, and *Heliosciurus*, which are endemics of the Ethiopian region. This tribe possesses the following taxonomic skull characters:

1. The supraorbital notch is closed on the margin of the orbit and persists as a foramen piercing the frontal.
2. The length of the canal of the infraorbital foramen is no more than half of that of the maxillary tooth row.
3. The sphenopalatine foramen is large, occasionally quite as large as the sphenoid fissure.
4. In lateral aspect the lip of the infraorbital foramen is concave.
5. There is no third upper premolar.

DIAGNOSIS OF THE TRIBE PROTOXERINI

The Protoxerini differ from the other tribes and subtribes of the Sciurinae by the above characters, as follows: from the *Ratufini* by 1, 2, and 4; from the *Hyosciurina* by 1, 3, and 5; from the *Funambulini* by 1, 3, and 5; from the *Callosciurina* by 1 and 5; from the *Sciurillina* by 1, 2, 3, 4, and 5; from the *Sciurina* by 1; from the *Microsciurina* by 1 and 2; from the *Marmotini* by 3; from the *Tamiasciurini* by 1 and 2; and from the *Xerini* by 1, 2, and 3.

GENUS PROTOXERUS

AFRICAN GIANT SQUIRREL

DIAGNOSIS: 1. The sutures bounding the combined interparietals, and separating the parietals at the midline, ankylose completely and disappear before adulthood. 2. The auditory bulla is substantially longer than the maxillary tooth row. 3. The buccinator and masticatory foramina form a single, though elongate aperture. 4. The nasal is shorter (in midsagittal length) than the least interorbital breadth. 5. The temporal ridges form a sagittal crest in adults. 6. The anteromesial tip of the nasal bone is produced to a rather sharp point (about 45° to 55°). 7. The infraorbital foramen is an oval, open fenestra through the zygomatic plate rather than a laterally compressed canal.

GENUS EPIXERUS

AFRICAN GIANT SQUIRREL

DIAGNOSIS: 1. The sutures bounding the interparietal bones, and separating the parietals in the midline, remain prominent in the adult. 2. The auditory bullae are small, only about the length of the maxillary tooth row. 3. The buccinator and masticatory foramina are separate (but not so widely so as in *Heliosciurus*). 4. The nasal bone is longer (along the midsagittal line) than the least distance between the rims of the orbits. 5. There is no sagittal crest. 6. The anteromesial tip of each nasal bone forms a rather blunt point (about 65° to 75°). 7. The infraorbital foramen is a simple, oval opening through the zygomatic plate rather than a laterally compressed canal.

GENUS HELIOSCIURUS

AFRICAN SUN SQUIRREL

DIAGNOSIS: 1. A temporal foramen is present in the squamosoparietal suture dorsal to the postglenoid foramen. 2. The masseteric tubercle projects outward from the surface of the maxillary bone as a prominent process. 3. The buccinator and masticatory foramina are widely separate. 4. The frontoparietal suture is absent in adults.

RELATIONSHIPS OF THE TRIBE PROTOXERINI

The geographic proximity of the genera comprising this tribe to the *Funisciurina* and

the Myosciurina, and the fact that the bacula of none of these three taxa resembled either the *Sciurus* kind of baculum or the *Callosciurus* kind, were reasons enough for Pocock (1923) to classify their constituent genera as members of his subfamily Funambulinae (equals the tribe Funambolini Simpson).

Pocock (1923) points out that the bacula vary greatly in the genera of his Funambulinae, the sun squirrels (*Heliosciurus*) seeming to have no baculum at all, whereas giant squirrels (*Protoxerus*) have fairly large ones, and African squirrels of the Funambolini (genera *Funisciurus* and *Paraxerus*, including *Tamiscus* and *Aethosciurus*) have minute bacula, whereas the Indian striped squirrels (*Funambulus*) have well-developed bacula. The characters of the glans penis as reported by Pocock (1923) also differ widely in the genera of his subfamily Funambulinae. Furthermore, although the number of transbullar septa per auditory bulla tends to be constant in most tribes of the Sciurinae, in both tribes of African tree squirrels there are taxa in which this character is quite variable. *Paraxerus*, for example, seems quite as likely to have two septa as one. While several forms of *Heliosciurus* examined vary between no septa and one per bulla, the 37 examples of *Heliosciurus g. loandicus* vary freely between no septa and two per bulla, with a mode of 12 specimens having one septum in each bulla, and one extreme with two septa in one bulla and three in the other. The available sample of *Funambulus pennanti*, furthermore, shows 14 with one septum per bulla to eight specimens with two septa per bulla.

In view of the above variability in the characters of the transbullar septa as well as the baculum and glans penis, the present writer felt obliged to seek out other characters of the skull which would reveal more satisfactory relationships between the genera of Pocock's Funambulinae. (The removal of *Ratufa* to form a separate tribe is discussed elsewhere.) Despite the presence in the Protoxerini of only three good genera, the variability of characters of the skull in one of them, the sun squirrel genus *Heliosciurus*, is so great that distinctive characters which occur consistently in all three genera are not impressive, even though to the student their

close relationship is. For instance, a prominent skull character that is rare in the Sciuridae generally but apparently constant in *Protoxerus* and *Epixerus*, the oval, window-like, infraorbital foramen, is very closely approached also in *Heliosciurus*, but only in one form that the writer has seen. Other *Heliosciurus* have laterally compressed infraorbital foramina with short canals. Another kind of relationship between these genera is the variation in a character unusual in the Sciuridae, i.e., the separation of the buccinator foramen from the masticatory foramen. In *Heliosciurus* they are widely separated, the most unusual condition. In one of the African giant squirrel genera, *Epixerus*, they are quite separate but much less widely so. In the other African giant squirrel genus, *Protoxerus*, there is a single elongated foramen, completing the sequence. This evidence, in addition to that implicit in the characterization of the tribe, supports the recognition of it as a natural unit.

The evidence utilized in the present study to define and diagnose the taxa of African tree squirrels does not suggest so close a relationship between the Protoxerini and the Funisciurina as may exist. These two taxa, almost alone among tree squirrels, generally possess long orbits. (Only in the case of diminutive forms do they have short orbits, and shortening of the orbit is one of the most constant characters of dwarfing in the Sciurinae.) The interorbital breadth of the Protoxerini and the Funisciurina is generally smaller than is common for tree squirrels. The character 2 for the tribe Protoxerini, short infraorbital canal, is generally possessed also by the Funisciurina. These three characters, partially shared by the Protoxerini and the Funisciurina, differ so strongly from those of other tree squirrels that one can entertain little doubt that the nearest relatives of the Protoxerini are the Funisciurina.

Didier (1953, p. 68) illustrates a squirrel baculum which is supposed to be that of *Heliosciurus gambianus rufobrachium*, but is quite like the baculum of *Sciurus*. As he makes no mention of the disagreement between this and Pocock's (1923, p. 229) description and illustration of the extremely thin penis and apparent absence of a baculum

in *Heliosciurus rufobrachium hardyi*, Pocock's work is accepted as correct.

Long orbits and short interorbital breadth are characteristic features of ground squirrels. It would seem easier for ground squirrels than tree squirrels to have reached the Ethiopian region from the Palearctic during some pluvial period. One needs at least to consider the possibility that tree squirrels may not have crossed the filter barrier separating these two regions, and that Ethiopian tree squirrels evolved from ground squirrel stock which now survives as the Xerini. The long orbits and short interorbital breadths of the Protoxerini and Funisciurina suggest this. The separation of the buccinator foramen from the masticatory foramen in *Heliosciurus* and *Epixerus* of the Protoxerini and *Xerus* and *Atlantoxerus* of the Xerini lends this suggestion further support. Also, the masseteric tubercles of *Heliosciurus* are remarkably like those of the Xerini.

TRIBE FUNAMBULINI

This tribe consists of African tree squirrels of the genera and subgenera *Funisciurus*, *Paraxerus*, *Tamiscus*, and *Aethosciurus*; the African pygmy squirrels, *Myosciurus*; and the Indian striped squirrels, *Funambulus*.

This tribe is linked together by the following skull characters:

1. The dorso-anterior process of the premaxillary bone, which in most squirrels rises to abut evenly with the anterolateral angle of the nasal bone, is entirely lacking, or where only obsolescent (as in some Funisciurina), is substantially overshot by the nasal bone.

2. There are one or two transverse bony septa per auditory bulla.

DIAGNOSIS OF THE TRIBE FUNAMBULINI

The tribe Funambulini is distinguished from the other tribes and subtribes of the Sciurinae by the above enumerated characters, as follows: from the Ratufini by 1 and 2; from the Hyosciurina by 1 and 2; from the Protoxerini by 1; from the Callosciurina by 1; from the Sciurillina by 1; from the Sciurina by 1; from the Microsciurina by 1; from the Tamiasciurini by 1 and 2; from the Marmotini by 1; and from the Xerini by 1 and 2.

SUBTRIBE FUNAMBULINA

INDIAN STRIPED SQUIRRELS

The polytypic genus *Funambulus*, which is restricted to India and Ceylon, constitutes this subtribe.

The taxonomic skull characters of this subtribe are as follows:

1. The sharp anterior edge of the zygoma extends forward onto the rostrum as a sharply defined ridge well beyond the maxillo-premaxillary suture to about halfway between the orbit and the tip of the rostrum.

2. The lateral edge of the nasal bone extends forward, free of the premaxillary bone, so that the anterolateral angle of the nasal is forward of, and not in contact with, the premaxillary bone.

3. There are well-developed midlateral processes of the basioccipital.

DIAGNOSIS OF THE SUBTRIBE FUNAMBULINA

The subtribe Funambulina is distinguished from other Funambulini by the above enumerated characters as follows: from the Funisciurina by 1, 2, and 3; and from the Myosciurina by 3.

RELATIONSHIPS OF THE SUBTRIBE FUNAMBULINA

Prasad (1954, 1957) has studied the genital tract of *Funambulus* and finds it to be of the type having no penial duct which Mossman, Lawlah, and Bradley (1932) had found distinguished the Nearctic red squirrel, *Tamiasciurus*, so trenchantly from several genera of the Sciurini, Marmotini, and Petauristinae. *Tamiasciurus* has enjoyed tribal distinction (Simpson, 1945) on the basis of its peculiar genital tract, without any support yet demonstrated (until the present paper) for differentiation even from *Sciurus* in the characters of the skull. Prasad (1957, p. 21) indicates that parallel evolutionary development of the type of genital tract is more probable than close relationship between *Tamiasciurus* and *Funambulus* and proposes that *Tamiasciurus* and *Funambulus* separately be accorded subfamily rank. However, one might note that the presently constituted subfamily Sciurinae is native to and widely distributed in Africa, Eurasia, North America, and South America. If the Sciurinae can be demonstrated to have

a single division that evidently began long enough ago and has reached a degree of differentiation that warrants making two subfamilies of the one, there should be no great quarrel with having the newly recognized subfamily extend from India to North America to include *Funambulus* and *Tamiasciurus*.

The differences with which Prasad has concerned himself are, of course, great ones. He was unable to say, however, whether or not any (or all) other genera of the large tribe Funambulini Simpson (except *Ratufa*, which is here shown to be quite distinct from the Funambulini), and the equally large tribe Callosciurini, have the type of male genital tract that has no penial duct. To contemplate the erecting of separate subfamilies for the genera *Tamiasciurus* and *Funambulus* because they differ importantly from *Ratufa*, *Sciurus*, *Tamias*, *Marmota*, *Citellus*, *Glaucomys*, *Petaurista*, and possibly *Heliosciurus* is a bit extreme. These are samples of only two of the 12 genera of Petauristinae that Simpson (1945) provisionally accepts, and samples of only three of the eight tribes of Sciurinae recognized in the present paper.

If a large group that includes, for example, something like the Callosciurini, Funambulini, and Tamiasciurini as recognized here does eventually prove to have the type of male genital tract with no penial duct, then a case will exist for the recognition of this group as a distinct subfamily. If future work establishes that only *Tamiasciurus* and *Funambulus* have this type, such a distinction may not be justified. Otherwise, *Hyosciurus* and *Reithrosciurus* each may deserve subfamily distinction on the trenchant peculiarities of their skull characters. Or two tree squirrels, *Protoxerus* and *Epixerus*, and the ground squirrels *Eutamias* and *Tamias* may as well be taken to constitute a separate superfamily because each has the infraorbital foramen oval and fenestroid instead of laterally compressed to form a canal as in the other Sciuridae. This latter character of the infraorbital foramen is a classically important one, still accepted as the distinguishing feature (Wood, 1955, p. 172) of the superfamily Sciuroidea. The four genera mentioned are here regarded as constituting two separately occurring exceptions, and their exceptional

character is regarded as of no special significance in the classification. To acknowledge it even separately by erecting, for example, two new subfamilies would mask the natural relationships they otherwise display.

The geographical and skull character evidence available indicates that *Funambulus* is most closely related to *Funisciurus*, *Paraxerus*, and *Myosciurus*, although subtribally distinguished from them. As far as is known, these genera may also have male genital tracts of the type without a penial duct. Until the genital tracts of these Funambulini are known, to regard the genus *Funambulus* even as tribally distinct would be to obscure the relationships shown here, and these relationships are based on characters which are known for all tribes of the Sciurinae.

SUBTRIBE FUNISCIURINA

This subtribe consists of African squirrels of the genera and subgenera *Funisciurus*, *Paraxerus*, *Tamiscus*, and *Aethosciurus* (but not *Aethosciurus ruwenzori*, which belongs in *Heliosciurus*).

This subtribe possesses taxonomic skull characters as follows:

1. The sharp anterolateral edge of the zygomatic arch continues forward as a sharp ridge onto the rostrum but stops well short of the premaxillary bone and rises no higher than the lower edge of the lacrimal bone.

2. The anterolateral corner of the nasal bone overshoots the nasal process of the premaxilla, so that the latter makes an indentation in the lateral margin of the nasal.

DIAGNOSIS OF THE SUBTRIBE FUNISCIURINA

The subtribe Funisciurina differs from other squirrels of the tribe Funisciurini by the above enumerated characters as follows: from the Funambulina by 1; and from the Myosciurina by 2.

RELATIONSHIPS OF THE SUBTRIBE FUNISCIURINA

By its character 1, the subtribe Funisciurina further shows its remoteness of relationship to the geographically associated Protoxerini as well as to all other Sciurinae. The distinction from the Protoxerini is further em-

phasized by the following taxonomic skull characters of the Funisciurina: (1) The sphenopalatine foramen is very much smaller than the sphenoid fissure. (2) The mid-lateral processes of the basioccipital are obsolescent. (3) The upper incisors are frequently proödont and rarely opisthodont. The discussion of the Protoxerini deals with other aspects of these relationships.

SUBTRIBE MYOSCIURINA

AFRICAN PYGMY SQUIRRELS

This subtribe is constituted by the single, tropical, West African genus *Myosciurus*.

The taxonomic skull characters are:

1. It has two transbullar septa.
2. It has no postglenoid foramen piercing the squamosal.
3. There is no ectopterygoid ridge of the alisphenoid.
4. There is no masseteric tubercle.
5. The infraorbital foramen has a canal which may range from about one-fourth to one-third of the length of the maxillary tooth row.
6. There are no third premolars.
7. The occlusal surfaces of the maxillary tooth row are excessively tilted laterally away from the horizontal (to the extent of 75° in the upper third molar).
8. From the lateral view, the area of the rostrum on which part of the masseter originates, considerably exceeds the area remaining forward of it.
9. There is a wide and extremely short interparietal bone which remains distinct in the adult.

DIAGNOSIS OF THE SUBTRIBE MYOSCIURINA

This very distinctive subtribe is distinguishable from other squirrels of the Funambulini by the above enumerated characters, as follows: from the Funisciurina by 2, 3, 4, 6, 7, 8, and 9; from the Funambulina by 1, 2, 3, 4, 5, 6, 7, 8, and 9.

RELATIONSHIPS OF THE SUBTRIBE MYOSCIURINA

The thesis that the Myosciurina are, despite their great peculiarity, most closely related to the Funisciurina has some support additional to that implicit in the diagnoses.

Although *Myosciurus* is the only African squirrel that has two transbullar septa per bulla in the whole sample (four) examined, one genus of the Funisciurina, *Paraxerus*, apparently has two septa per bulla quite as often as one (39 to 38 in a sample of 78). In the Funisciurina only one foramen pierces the squamosal in the postglenoid region (apparently the postglenoid foramen), whereas other African squirrel tribes (and the Sciurini and the Marmotini) regularly or incipiently (or obsolescently?) have a second one, the subsquamosal foramen. *Myosciurus*, having none, is nearer the Funisciurina. This may invoke the thought that the absence of the postglenoid foramina possibly results here from the specialization of diminutive size, as it also characterizes the South American pygmy squirrel. However, the postglenoid foramen is well developed in the two genera of East Indian pygmy squirrels.

Of course, two transbullar septa may suggest relationship to the Sciurini, which may be thought to be strengthened by the fact that *Myosciurus* shares a character with *Reithrosciurus*, the Guerlinguetina, and the Microsciurina, namely, the retention in adults of sutures bounding the interparietals. However, Oldfield Thomas (1915, p. 386) evidently found the baculum of *Myosciurus* to be not of the sciurine type. Furthermore, the Sciurini and the tribes closely related to them have proportionally long infraorbital canals (least distance between suborbit and infraorbital foramen), whereas *Myosciurus* has an extraordinarily short one. This character not only distinguishes the African pygmy squirrels sharply from the Sciurini but relates them closely to the Funisciurina and also the Protoxerini, for the tree squirrels in the Ethiopian region exhibit a strong tendency as a whole to short infraorbital canals.

The short infraorbital canal could associate *Myosciurus* with the Protoxerini about as easily as with the Funambulini, and such a suggestion is somewhat reënforced by the concave shape of the infraorbital foramen in lateral view and the absence of a third upper premolar. Believed by the writer to outweigh these, however, are tribal character 1 of the Funambulini, subtribal character 1 of the Funisciurina (which the Myosciurina share), and the two additional characters described

in the first paragraph of this discussion.

The high squamosal of *Myosciurus* and its possession of open sutures around the interparietal may at first be thought to link it with the Xerini. However, a high squamosal characterizes the other pygmy squirrel genera, *Sciurillus*, *Exilisciurus*, and (to a somewhat lesser extent) *Nannosciurus*, and is therefore suspected of being a product of dwarfing. Also the short infraorbital foramen fits no better with the Xerini than with the Sciurini.

TRIBE CALLOSCIURINI

SUBTRIBE CALLOSCIURINA

INDO-MALAYAN TREE, GROUND, AND PYGMY SQUIRRELS

The subtribe Callosciurina consists of the Indo-Malayan genera and subgenera *Callosciurus*, *Tamiops*, *Sundasciurus*, *Glyphotes*, *Lariscus*, *Paralariscus*, *Menetes*, *Dremomys*, *Nannosciurus*, and *Rhinosciurus*.

This subtribe has the following taxonomic skull characters:

1. The auditory bulla has a single transbullar septum.

2. A single, rather large and round foramen, probably the subsquamosal, pierces the squamosal bone in the postglenoid area.

3. The ventral portion of the lateral lip of the infraorbital foramen stands away from the surface of the rostrum, forming a projecting angle on which the masseteric tubercle is a mildly roughened area which is only slightly thickened and barely, if at all, elevated.

4. From the anterior edge of the zygomatic process of the squamosal a ridge extends across the squamosal to or onto the alisphenoid, and this ridge is thick.

5. The supraorbital notch is obsolescent (generally absent but occasionally occurring as a very shallow, broad indentation of the frontal).

6. The upper incisor teeth are generally proödont and only occasionally orthodont.

DIAGNOSIS OF THE SUBTRIBE CALLOSCIURINA

This Indo-Malayan subtribe is distinguishable from the other tribes of the Sciurinae as follows: from the Hyosciurina by 1; from the Ratufini by 1, 2, and 6; from the Protoxerini by 3, 4, and 5; from the Funambulini by 4;

from the Sciurillina by 2 and 3; from the Sciurina by 1 and 2; from the Microsciurina by 4 and 5; from the Marmotini by 1, 2, and 5; from the Tamiasciurini by 1, 2, 4, and 5; and from the Xerini by 1, 2, 3, 5, and 6.

GENUS NANNOSCIURUS

BLACK-EARED PYGMY SQUIRREL

DIAGNOSIS: 1. The rostrum constitutes a disproportionately large part of the skull, the orbitonasal length being half of the occipitonasal length. 2. The lip of the intraorbital foramen is convex in lateral aspect, and the top of the opening is its most posterior part. 3. The infraorbital foramen opens at the maxillo-premaxillary suture. 4. The canal of the infraorbital foramen is substantially longer than the maxillary tooth row. 5. The plane of the zygomatic plate is about 90 degrees from the occlusal plane. 6. The length and width of the orbit are about the same. 7. The interparietal bone in adults is outlined by open sutures.

GENUS RHINOSCIURUS

ANT-EATING SQUIRREL

DIAGNOSIS: 1. The upper incisors are dwarfed (diameters about 1.0 mm. by 1.5 mm.). 2. The skull is attenuated (diastema about 0.84 to 0.94 of the mastoid breadth). 3. The diameter of the third upper premolar is about two-thirds of that of the fourth upper premolar. 4. The canal of the infraorbital foramen is less than half of the length of the maxillary tooth row. 5. The third upper premolar reaches farther forward than the infraorbital foramen. 6. The occiput has a very strong median keel and two fairly prominent lateral ones. 7. The superior process of the jugal is obsolescent. 8. The greatest length of the nasals approximates the mastoid breadth.

KEY TO THE GENERA AND SUBGENERA OF THE SUBTRIBE CALLOSCIURINA

1. Sutures bounding interparietal bone do not ankylose and disappear in adults; top of infraorbital foramen in contact with maxillo-premaxillary suture
genus *Nannosciurus*
- Sutures bounding interparietal ankylose completely; infraorbital foramen not in contact with maxillo-premaxillary suture2
2. Occiput has pronounced median keel and two

- fairly prominent lateral ones; infraorbital canal length less than half of that of maxillary tooth row genus *Rhinosciurus*
Occiput not prominently keeled; length of infraorbital canal more than half of that of maxillary tooth row 3
3. Incisors broad; lower ones with anterior faces flat or concave genus *Glyphotes*
Incisors not especially broad; lower ones with anterior faces convex 4
4. Transbullar septum broadly forked medially (genus *Sundasciurus*) 5
Transbullar septum without fork 6
5. Sagittal crest present in adults; skull longer than 45 mm. subgenus *Aletesciurus*
No sagittal crest; skull shorter than 45 mm. subgenus *Sundasciurus*
6. Least interorbital breadth exceeds greatest length of nasal (genus *Callosciurus*) . . . 7
Least interorbital breadth is less than greatest length of nasal 8
7. Orbital length is less than 13 mm.
. subgenus *Tamiops*
Orbital length exceeds 13 mm.
. subgenus *Callosciurus*
8. Upper cheek tooth with largest occlusal area is the fourth premolar; occlusal surfaces of unworn cheek teeth are of mild relief (genus *Lariscus*) 9
Upper cheek tooth with largest occlusal area is the first or second molar; surfaces of unworn cheek teeth have strong relief . . 10
9. Orbital length exceeds 0.80 of orbitonasal length subgenus *Paralariscus*
Orbital length is less than 0.80 of orbitonasal length subgenus *Lariscus*
10. Each molariform tooth has a central valley so deep that it persists encircled by enamel long after other occlusal features have been planed away; ectopterygoid ridge of alisphenoid less than 1 mm. high and very slight genus *Menetes*
Occlusal relief not great enough for exceptional persistence of central valley; ectopterygoid ridge at least 1 mm. high genus *Dremomys*

RELATIONSHIPS OF THE SUBTRIBE CALLOSCIURINA

This large and varied but rather closely localized subtribe of squirrels seems most closely related to the Hyosciurina. The evidence for this, in addition to what may be derived from the diagnoses, lies principally in characters of the bacula (Pocock, 1923) and geographic considerations.

One is tempted, of course, to suspect a

common origin for several genera of long-nosed squirrels, *Rhinosciurus*, *Hyosciurus*, *Lariscus*, *Dremomys*, and *Menetes*. Indeed, Zahn (1942) boldly recognized *Dremomys* as a subgenus of *Rhinosciurus*, and *Hyosciurus heinrichi* as a mere species of *Rhinosciurus*. The evidence presented in the diagnoses of the Hyosciurina, the Callosciurina, and *Rhinosciurus* should adequately demonstrate the relationships recognized in the present work, but further evidence has been assembled, for publication elsewhere, which more completely dispels belief in the congeneric relationship of *Rhinosciurus laticaudatus* and *Hyosciurus heinrichi*.

It should, perhaps, be noted that Didier (1952, p. 16) has illustrated a baculum of *Menetes berdmorei* without the separate blade which it must have to belong to the Callosciurini. However, he expresses no concern with this, and, because Pocock (1923, p. 221) illustrates the baculum of *Menetes berdmorei* with a separate dorsal blade, Pocock's work is accepted as correct.

SUBTRIBE HYOSCIURINA

The pig squirrel, *Hyosciurus*, the tree squirrel *Prosciurillus*, and the large red squirrel *Rubrisciurus*, all of Celebes, and the patternless pygmy squirrels, *Exilisciurus*, of Borneo and the Philippines constitute the subtribe Hyosciurina.

This subtribe is composed of exceedingly diverse units which have in common rather few taxonomic skull characters, as follows:

1. There is more frequently no transbullar septum across the auditory bulla.
2. A large, single, postglenoid foramen pierces the squamosal.
3. The orbital length is less than 0.90 of the interorbital breadth.
4. The orbital length is less than 0.65 of the orbitonasal length.
5. The sphenopalatine foramen is less than half of the area of the sphenoidal fissure.

DIAGNOSIS OF THE SUBTRIBE HYOSCIURINA

The Hyosciurina are distinguished from other Sciurinae by the above enumerated characters, as follows: from the Ratufini by 2, 3, 4, and 5; from the Protoxerini by 3, 4, and 5; from the Funambulini by 1; from the Callosciurina by 1; from the Sciurillina by 1

and 2; from the Sciurina by 1, 2, 4, and 5; from the Microsciurina by 1, 3, and 4; from the Marmotini by 1, 2, 3, and 4; from the Tamiasciurini by 2, 3, and 4; and from the Xerini by 1, 2, 3, and 4.

RELATIONSHIPS OF THE SUBTRIBE HYOSCIURINA

Although apparently related to the Ratu-fini by significant skull characters as stated in the discussion of the relationships of *Ratufa*, the Hyosciurina are, nevertheless, considered to be more closely related to the Callosciurina. The single postglenoid foramen, the short orbital length, the rather considerable interorbital breadth, the rather long to extremely long rostrum, the rather small sphenopalatine foramen, the slightly constructed masseteric tubercle, the heavy zygomatic ridge across the anterior surface of the squamosal, and the strong tendency to proödonty constitute an abundance of similarities to the Callosciurina, some of them surely important, which support the concept of close relationship. The presence of a separate blade on the baculum (Pocock, 1923, p. 223) of *Exilisciurus exilis*, *E. whiteheadi*, and *Prosciurillus murinus* strengthens this concept.

It should be noted that the Celebesian genus *Prosciurillus* is in fact not identifiable as belonging to the Hyosciurina or to the Callosciurina, because in the one character that best distinguishes the two tribes, *Prosciurillus* is quite variable. In the sample examined, 70 individuals of *Prosciurillus* are like the Hyosciurina in having no septa, and 47 have one in each bulla as do the Callosciurina. Each of the three species of *Prosciurillus* varied in this same respect: *leucomus* 45 to 20, *abstrusus* 9 to 12, and *murinus* 16 to 15. Although the general proportions of *Prosciurillus* skulls may seem close to those of generalized tree squirrels of the Callosciurina, such a similarity would hardly be better justification for placing *Prosciurillus* in the Callosciurina than the geographic range is for placing it in the Hyosciurina.

That the distinction between the Hyosciurina and the Callosciurina depends on a single character is attributable in part to the fact that three of the genera composing the Hyosciurina are so divergent.

GENUS *PROSCIURILLUS*

CELEBESIAN TREE SQUIRREL

DIAGNOSIS: 1. The posteriormost edge of the suborbit is (in lateral view) directly beneath, or anterior to, the postorbital process of the frontal. 2. The anterior extension of the suborbit approximates or exceeds that of the orbit. 3. The frontal bones extend a quarter of their length forward of the orbits.

GENUS *HYOSCIURUS*

PIG SQUIRREL

DIAGNOSIS: 1. The upper incisors are orthodont. 2. The orbitonasal length is about twice the interorbital breadth. 3. The gnathion protrudes beyond the incisor more than the anteroposterior width of the incisor. 4. The nasal projects beyond the incisor more than twice the anteroposterior width of the incisor. 5. The ectopterygoid ridge of the alisphenoid is obsolescent.

RELATIONSHIPS: Ellerman (1949, p. 14) noted the important difference between *Hyo-sciurus* and *Rhinosciurus* and quite rightly inferred that they acquired their specializations of extremely long noses separately. Zahn (1942, p. 116) took an extreme position in regarding them as a single genus. (See above under Relationships of the Subtribe Callosciurina.)

GENUS *EXILISCIURUS*

PATTERNLESS PYGMY SQUIRRELS

DIAGNOSIS: 1. The interorbital breadth equals the length of the frontals. 2. The width of the orbit about equals the length of the orbit. 3. A bony ridge extends ventromedially across the face of the alisphenoid from the base of the zygomatic process of the squamosal. 4. The line of junction of the zygomatic plate with the rostrum is 90 degrees from the occlusal plane. 5. The midlateral processes of the basioccipital are obsolescent. 6. The occipitonasal length is less than 30 mm. 7. The interparietal bone in adults is outlined by open sutures.

RELATIONSHIPS: The present writer (1958) has earlier provided evidence of a generic distinction between the patterned pygmy squirrels, *Nannosciurus melanotis*, and the patternless pygmy squirrels, *Exilisciurus exilis* and others, of the East Indies. That evidence, as shown in the classification offered

here, is thought actually to indicate a distinction sufficiently great that neither genus is believed to have evolved directly from the other. They are classified in separate subtribes, *Exilisciurus* in the Hyosciurina and *Nannosciurus* in the Callosciurina.

Because all the evidence for this generic and subtribal distinction need not be shown above in definitions of the taxa involved, perhaps the details should be recorded here. In a sample of 14 *Exilisciurus exilis* from Borneo, 13 have no transbullar septa; of 10 *E. surrutilus* from Mindanao (Chicago Natural History Museum material), none has transbullar septa; of eight *E. concinnus* from Basilan Island (five in the Museum of Comparative Zoölogy, three in the United States National Museum), none has transbullar septa; and of 20 *E. whiteheadi* from Mt. Kinabalu, Borneo (19 in the United States National Museum, one in the Chicago Natural History Museum) none has transbullar septa. Thus the sample of *Exilisciurus* shows a ratio of 50 without transbullar septa to one with. (The one with transbullar septa has one septum in each bulla.) In the other tribe, of the available sample of 33 *Nannosciurus melanotis*, 32 have a transbullar septum in each bulla and one has none.

In the diagnosis of *Exilisciurus* (Moore, 1958) five other skull characters are offered that distinguish that genus from *Nannosciurus*: 1. The lateral lip of the infraorbital foramen does not stand out from the wall of the rostrum and serves as a masseteric tubercle. 2. The maxillary tooth rows converge posteriorly. 3. The upper fourth premolar is smaller than the upper third molar. 4. The second upper molar characteristically has the largest occlusal surface of the maxillary cheek teeth. 5. Projections of the premaxillary do not commonly intrude posteriorly into the maxillary on each side of the incisive foramina for a distance exceeding or approximating the length of the foramina. To these another distinguishing character may now be added: 6. The lateral lip of the infraorbital foramen does not connect at the top with the maxillo-premaxillary suture.

This distinction of the East Indian pygmy squirrels as genera of two separate tribes, and the implication that they have evolved separately as pygmy squirrels, certainly are con-

trary to a belief in a common subfamily or other natural taxon for the pygmy squirrel genera of the three tropical faunal regions of the world. (See also Pygmy Squirrel Convergence, below.)

GENUS *RUBRISCIURUS*

CELEBESIAN GIANT SQUIRREL

DIAGNOSIS: 1. There are trenchant supra-orbital notches. 2. There is a long, high, sagittal crest. 3. The temporal ridges are relatively short and straight. 4. The zygoma is extremely wide at the superior process of the jugal, its greatest width being about one-quarter of its greatest length. 5. In side view the lip of the infraorbital foramen is strongly convex. 6. The postorbital process of the frontal is well anterior to the posterior margin of the suborbit. 7. The pterygoid fossa extends anterior to the posterior extremities of the tooth rows. 8. Less than one-quarter of the length of the frontals is forward of the orbits. 9. The upper cheek tooth rows (crowns) are parallel, not convergent posteriorly.

RELATIONSHIPS: Some special discussion is called for here. The evidence connecting this genus, in particular, with the Ratufini is discussed in the consideration of the characters of *Ratufa*. However, characters suggesting relationship of *Rubrisciurus* to *Sundaesciurus* (*Aletesciurus*) *hippurus* should at least be mentioned. In addition to having skull characters similar to those of *Rubrisciurus*, *Aletesciurus* is the only one of 10 living genera and subgenera of Bornean Sciurinae that has emigrated to colonize successfully the two parts of the Philippine Islands nearest Borneo: the Palawan group of islands to the north and Mindanao to the northeast. Such colonization suggests that some of its ancestors may, more readily than other forms, have crossed the water gap to Celebes in some way and survived and evolved as *Rubrisciurus*.

The similarities of *Aletesciurus* to *Rubrisciurus* include an impressive general likeness of the dorsal profile, strongly proödont upper incisors, and characters 2 and 5 of the Hyosciurina described above (5 does not characterize *Aletesciurus* but occurs in it not infrequently). *Aletesciurus hippurus*, more frequently than any other species of the

Callosciurina, exhibits the occasional absence of the transbullar septa.

On the other hand, the Y-shaped transbullar septum of *Aletesciurus* is not even incipient in *Rubrisciurus*, and the above characters 1, 3, 4, and 7 are foreign to *Aletesciurus*. The weight of evidence seems against very close relationship and suggests that it is best to explain the occurrence of the similarities between *Rubrisciurus* and *Aletesciurus* as convergent selection for characters long present in the gene pool of the Sciurinae.

TRIBE SCIURINI

SUBTRIBE SCIURINA

TYPICAL TREE SQUIRRELS

This subtribe consists of the genera *Sciurus* (including *Neosciurus*, *Echinosciurus*, *Hesperosciurus*, *Baiosciurus*, *Otosciurus*, and *Tenes*), *Reithrosciurus*, and *Guerlinguetus* (including *Hadrosociurus* and *Urosociurus*).

The Sciurina are distinguished by the following skull character:

1. The squamosal bone extends up the cranium no more than about halfway from the posterior edge of the suborbit to the base of the postorbital process of the frontal (fig. 4).

DIAGNOSIS OF THE SUBTRIBE SCIURINA

The subtribe is distinguishable from all other members of the Sciurinae by the above character (possibly excepting *Rupestes*).

GENUS GUERLINGUETUS

BRAZILIAN TREE SQUIRREL

DIAGNOSIS: 1. The sutures bounding the interparietals do not ankylose fully but remain distinct in the adult. 2. Only one foramen regularly pierces the squamosal in the postglenoid region, apparently the postglenoid foramen (the subsquamosal foramen being obsolescent.)

SUBGENUS GUERLINGUETUS

DIAGNOSIS: 1. The sphenopalatine foramen is generally a little larger than the sphenoidal fissure. 2. The orbit is of about medium length.

SUBGENUS HADROSCIURUS

DIAGNOSIS: 1. The sphenopalatine foramen is generally about twice as large as the

sphenoidal fissure. 2. The orbit is proportionally long.

GENUS REITHROSCIURUS

BORNEAN TASSEL-EARED SQUIRREL

DIAGNOSIS: 1. The most arched part of the dorsal profile of the skull is at the frontonasal sutures. 2. The masseteric tubercle extends forward a tooth row length from the fourth premolar. 3. The buccinator foramen and masticatory foramen are widely separated. 4. The extremely opisthodont upper incisors are compressed, so that the width of one is less than half of its depth (2.5 mm. to 6.0 mm.). 5. The anterior surface of the upper incisor is sculptured with fine longitudinal striations. 6. The length of nasal bone substantially exceeds the length of the orbit. 7. The area of the side of the rostrum upon which part of the masseter originates greatly exceeds the area remaining forward of it. 8. The length of the infraorbital canal exceeds that of the maxillary tooth row.

GENUS SCIURUS

HOLARCTIC TREE SQUIRREL

DIAGNOSIS: 1. There are two or three transbullar septa in each auditory bulla. 2. Both the postglenoid and the subsquamosal foramina ordinarily pierce the squamosal bone in the postglenoid region as functional foramina.

SUBGENUS SCIURUS

HOLARCTIC TREE SQUIRREL

DIAGNOSIS: The transbullar septa are two in each auditory bulla (see table 1).

SUBGENUS TENES

PERSIAN SQUIRREL

DIAGNOSIS: 1. The transbullar septa (see table 1) are most often three in each auditory bulla. 2. The dorsal process of the jugal is high and pointed. 3. The masseteric tubercle is more prominent than in *Sciurus*.

RELATIONSHIPS OF THE SUBTRIBE SCIURINA

It is clear now that Pocock's Sciurinae (= Sciurini Simpson, 1945), based on a single character, the *Sciurus* type of baculum, should include the squirrels here constituting the subtribal units Sciurina, Sciurillina (An-

thony and Tate, 1935, p. 3), and *Microsciurina*. It is believed that this common possession of the *Sciurus* type of baculum indicates a natural relationship and remains the sole means of characterizing the tribe Sciurini. However, equally natural relationship is seen in the lesser distribution of another exclusive character, an easily observed, trenchant feature of the skull which characterizes the genera *Sciurus*, *Reithrosciurus*, and *Guerlinguetus*. This is the low squamosal, character 1 of the subtribe Sciurina, as shown above. It distinguishes these genera from all other squirrels and for this reason is accepted as the basis for delimiting the subtribe.

Reithrosciurus, of course, shows much specialized development, and one would be tempted to show this in its classification, if it did not have the characters that appear quite reasonably (on a sample of two) to place it here. Some forms of *Hadroskiurus* strongly resemble *Reithrosciurus* in the diminution of the maxillary tooth row and concurrent projection of the masseteric tubercle a tooth row length forward of the tooth row. Strong opisthodonty helps to show that *Reithrosciurus* is not closely related to the Callosciurini, which surround it in the Indo-Malayan region (and isolate it by about 2000 miles from its nearest tribal relative), for proödonty is a strong general characteristic of the Callosciurini. The separation of the buccinator and masticatory foramina seen in *Reithrosciurus* is fairly rare in the Sciurinae, occurring otherwise only in *Epixerus* and *Helioskiurus* and in *Xerus* and *Atlantoxerus* (not *Spermophilopsis*). It characterizes five Old World genera of squirrels, then, of three different tribes.

The transbullar septa of the Persian squirrel *Tenes* are structurally feeble than those of other squirrels that have three septa in each bulla and also are much more variable. In a sample of 24 skulls, 13 have three septa in each bulla, and four have no more than two in each bulla. One of the 13 skulls has four septa in one bulla; one of the four skulls has a single septum in one bulla. However, because Ognev (1940, p. 425) shows that *Tenes* has a *Sciurus* type of baculum, and because its squamosal is very low, *Tenes* is confidently placed in the Sciurini rather than the Tamiasciurini.

Recognizing *Hadroskiurus* as a subgenus instead of a genus is a matter of conservatism rather than conviction. No skull character other than size, or something immediately related to size, has distinguished it well from *Guerlinguetus* for me in this study, which has, however, been primarily concerned with suprageneric categories.

A general character, the reach of the squamosal bone up the side of the cranium towards the base of the postorbital process of the frontal, is shown to be a highly important tribal character in the Sciurinae. At one extreme it distinguishes the Sciurina from all other tribes, and at the other extreme it distinguishes the tribe Xerini and the genera *Sciurillus*, *Exilisciurus*, and *Myosciurus*.

The failure of the suture bounding the interparietals to ankylose completely and disappear is not an exclusive character of *Guerlinguetus*, of course, for it also distinguishes *Microsciurus*, *Atlantoxerus*, *Spermophilopsis*, and *Myosciurus*. Its occurrence in *Microsciurus*, however, calls attention to the close relationship between *Microsciurus* and the Neotropical member of the Sciurina, the genus *Guerlinguetus*. However, the regular presence of this character in two of the three genera of the Xerini and in the Myosciurina does not indicate close relationship between the Sciurini and the Myosciurina or the Xerini.

SUBTRIBE MICROSCIURINA

This subtribe is made up of Neotropical tree squirrels of the genera and subgenera *Microsciurus*, *Leptoskiurus*, *Simosciurus*, *Syntheosciurus*, and *Mesoskiurus*.

The taxonomic skull characters of the subtribe are as follows:

1. In lateral aspect the lip of the infraorbital foramen is concave and the lower limb of this crescent shape characteristically extends about as far forward as the posterior one extends upward.

2. The masseteric tubercle protrudes laterodorsally as a minute process constituting the anterior tip of the lip of the infraorbital foramen.

3. The number of transbullar septa varies between one and two per bulla.

4. The squamosal bone extends up the side of the cranium more than halfway from the

posterior margin of the suborbit to the base of the postorbital process of the frontal.

DIAGNOSIS OF THE SUBTRIBE MICROSCIURINA

The Microsciurina are distinguishable from the other Sciurinae by the above enumerated characters, as follows: from the Hyosciurina by 1, 2, and 3; from the Ratufini by 1, 2, and 3; from the Protoxerini by 1 and 2; from the Funambulini by 1 and 2; from the Callosciurina by 1 and 2; from the Sciurillina by 1 and 2; from the Sciurina by 4; from the Marmotini by 1 and 2; from the Tamiasciurini by 3; and from the Xerini by 1, 2, and 3.

GENUS MICROSCIURUS

DIAGNOSIS: The sutures bounding the interparietal bone do not ankylose completely in the adult, but remain quite distinct.

SUBGENUS MICROSCIURUS

DIAGNOSIS: 1. The orbit is exceedingly short (the postorbital process of the frontal is generally over the base of the zygomatic process of the squamosal). 2. The upper incisors are proödont. 3. The postglenoid foramen pierces the squamosal bone, but the subsquamosal foramen is absent or obsolescent. 4. There is one pair of transbullar septa. 5. The upper third premolars are present.

SUBGENUS LEPTOSCIURUS

DIAGNOSIS: 1. There are generally two pairs of transbullar septa. 2. There are no third upper premolars. 3. The postglenoid foramen is present, but the subsquamosal foramen is obsolescent. 4. The orbital length is rather short.

SUBGENUS SIMOSCIURUS

DIAGNOSIS: 1. The orbit is long. 2. The upper incisors are opisthodont. 3. There are no third upper premolars. 4. The transbullar septa occur as one or two pairs with equal frequency. 5. The pairs of postglenoid foramina are one or two with about equal frequency.

GENUS SYNTHEOSCIURUS

DIAGNOSIS: The sutures that outline the interparietal bones ankylose so completely in adults that the sutures do not show.

SUBGENUS SYNTHEOSCIURUS

DIAGNOSIS: (As known from the type of *poasensis* and three examples of *brochus*). 1. The upper incisors are proödont. 2. There is a pair of third upper premolars. 3. The fourth upper premolar equals the third upper molar in occlusal surface. 4. The sphenopalatine vacuities are present and large.

SUBGENUS MESOSCIURUS

DIAGNOSIS: 1. The upper incisors are orthodont or mildly opisthodont. 2. There are no third upper premolars. 3. The fourth upper premolars are less in occlusal area than the third upper molars. 4. The sphenopalatine vacuities are obsolescent.

RELATIONSHIPS OF THE SUBTRIBE MICROSCIURINA

The Microsciurina show their close relationship to the Sciurina in several significant characters: 1. The characters of the infra-orbital foramen and masseteric tubercle are closely alike. 2. *Microsciurus* and *Simosciurus*, particularly, show close relationship to *Guerlinguetus* of the Sciurina in that the sutures bounding the interparietal are not ankylosed in adults. 3. Didier (1955) provided illustrations of the bacula of several named forms of Microsciurina: *Microsciurus (florentiae)*, p. 425), *Leptosciurus (pucherani)*, p. 422), and *Mesosciurus (granatensis)*, p. 417, and *pyrrhinus*, p. 424). These show very close similarity to the bacula that he illustrated of certain South American Sciurina: *Hadrosiurus (igniventris)*, p. 418; *pyrrhonotus*, p. 418; and *tricolor*, p. 421) and *Guerlinguetus (ingrami)*, p. 420; *ignitis*, p. 423; and *aestuans*, Didier, 1952, p. 10). An illustration of the baculum of *Sciurillus* by Anthony and Tate (1935, p. 3) shows strongly the general shape of the *Sciurus* type despite the otherwise great specialization of *Sciurillus*. The character of the bacula in these illustrations is accepted as evidence of close relationship of the Microsciurina and the Sciurillina to the Sciurina, an affinity suggested, of course, by their geographic proximity. The character of the baculum and geographic proximity, however, suggest closer relationship between the Microsciurina, the Sciurina, and the Sciurillina than would be assumed from the large number of skull characters that differentiates the Sciurillina from the other two.

SUBTRIBE **SCIURILLINA**

NEOTROPICAL PYGMY SQUIRREL

This South American monotypic subtribe is constituted by the genus *Sciurillus*.

The taxonomic skull characters of the Sciurillina are:

1. The auditory bulla has a single bony transbullar septum.
2. The postglenoid area of the squamosal is not pierced by a foramen.
3. There is no masseteric tubercle.
4. The length of the canal of the infraorbital foramen equals or exceeds that of the maxillary tooth row.
5. The lateral lip of the infraorbital foramen, in lateral aspect, slants forward and upward to the premaxillary bone.
6. The anterior ends of the nasals are squarely truncated instead of converging forward.
7. A foramen opens from the (dorsal) base of the posterior end of each wing of the pterygoids.
8. The length and breadth of the orbit are about equal.
9. The width (or length) of orbit is only about half of the interorbital breadth.
10. No frontoparietal suture is seen in the skulls of adults.
11. A greater area of the side of the rostrum is maxilla than premaxilla.
12. The jugal is slender and lacks a superior process.

DIAGNOSIS OF THE SUBTRIBE
SCIURILLINA

This pygmy squirrel subtribe is distinguishable from the other Sciurinae by the above enumerated characters, as follows: from the Ratufini by 1, 2, 3, 4, 6, 7, 8, 9, 11, and 12; from the Hyosciurina by 1, 2, 5, 7, 10, 11, and 12; from the Protoxerini by 2, 3, 4, 5, 6, 7, 8, 9, and 11; from the Funambulini by 2, 4, 5, 7, 9, 10, and 11; from the Callosciurina by 2, 3, 5, 7, 10, and 11; from the Sciurina by 1, 2, 3, 5, 6, 7, 8, 9, 10, and 11; from the Microsciurina by 2, 3, 4, 5, 6, 7, 8, 9, 10, and 11; from the Marmotini by 1, 2, 3, 5, 6, 7, 8, 9, and 11; from the Tamiasciurini by 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, and 11; and from the Xerini by 1, 2, 3, 4, 5, 7, 8, 9, 10, and 11.

RELATIONSHIPS OF THE SUBTRIBE
SCIURILLINA

Although evidently related to the Sciurina and Microsciurina by the character of its baculum (Anthony and Tate, 1935, p. 3), *Sciurillus* is one of the most distinctive genera of squirrels in the world. The above diagnosis shows that the Sciurillina differ from no other tribe of squirrels by fewer than six skull characters. In this measure of divergence (which is admittedly skewed by monotypy) they are approached only by the Ratufini. The factors that distinguish *Sciurillus* from the African and East Indian pygmy squirrels are discussed below under Pygmy Squirrel Convergence.

TRIBE **MARMOTINI**

TYPICAL GROUND SQUIRRELS

This tribe consists of Palearctic and Nearctic ground-dwelling squirrels of the genera *Marmota*, *Cynomys*, *Spermophilus*, *Ammospermophilus*, *Eutamias*, and *Tamias*.

The Marmotini possess in common the following taxonomic skull characters:

1. There are two transbullar septa per auditory bulla.
2. The orbital length is at least 1.15 of the interorbital breadth.
3. There is no temporal foramen in the squamosoparietal suture.
4. The sphenopalatine foramen has less than half of the area of the sphenoidal fissure (except in *Spermophilus citellus*).
5. The supraorbital notches are generally open and generally trenchant.

DIAGNOSIS OF THE TRIBE MARMOTINI

The Marmotini are distinguished from other tribes and subtribes of the Sciurinae by the above enumerated characters as follows: from the Ratufini by 1, 2, 3, 4, and 5; from the Hyosciurina by 1, 2, and 3; from the Protoxerini by 3, 4, and 5; from the Funambulini by 3; from the Callosciurina by 1, 2, 3, and 5; from the Sciurillina by 1 and 2; from the Sciurina by 2, 3, and 4; from the Microsciurina by 2 and 3; from the Tamiasciurini by 1 and 3; and from the Xerini by 1 and 3.

RELATIONSHIPS OF THE TRIBE MARMOTINI

The Marmotini are an exceedingly numerous and diverse group, well deserving more

intimate study than Howell (1938) was able to give them concerning evidences of supra-specific relationships, evidence of speciation, and evidences of intercontinental migration. The subtribes Tamiina and Marmotina stand sharply apart in the integrated diversity of the Marmotini, as shown by the skull character diagnoses. The extent to which their bacula and baubella diverge from those of the *Spermophilina* does not, however, seem greater in the collective illustrations published by Pocock (1923, p. 235), Howell (1938, pl. 13), Wade and Gilbert (1940, pp. 55, 58, 60), Didier (1952, pp. 20-21; 1953, p. 71), White (1953b, p. 629), and Layne (1954, p. 360), than the diversity present within the *Spermophilina* alone. White (1953a, p. 560) nevertheless tentatively assigned *Eutamias* to the *Callosciurini* because of the extent to which its baculum differs from the bacula of the other Marmotini and, except for having no separate blade, resembles those of *Callosciurini*. I do not believe, however, that he would insist on this against the evidence made available in the present report, which associates *Eutamias* with *Tamias* in the Marmotini and distinguishes it from the *Callosciurini* by five diagnostic skull characters.

The Marmotini show similarities to the Xerini in the long orbit, narrow interorbital breadth, relatively small sphenopalatine foramen, generally trenchant supraorbital notches, and the sharp, projecting anterior edge of the zygoma which virtually makes a fossa of the zygomatic plate. These similarities are largely ones of large, dorsally oriented eyes associated with ground-dwelling habits and may result from convergence. In addition the Tamiina share opisthodonty with the Xerini.

The Marmotini share a few characters with *Sciurus* which may suggest relationship: (1) two transbullar septa in each bulla; (2) generally two foramina in the postglenoid area; and (3) generally trenchant supraorbital notches.

One genus of somewhat uncertain relationships, of which the male genital tract characters and baculum are not known, exhibits general skull characters that suggest possible relationship to the Tamiina but is here believed to result from convergent selection

because of habitat similarities. This is *Sciurotamias*, the relationships of which are discussed in the *Tamiasciurini*.

SUBTRIBE TAMIINA

CHIPMUNKS

This tribe consists of two closely related genera, Holarctic *Eutamias* and Nearctic *Tamias*.

The taxonomic skull characters of the chipmunks are as follows:

1. The infraorbital foramen is oval in shape, and opens fenestra-like and directly through the zygomatic plate rather than passing the plate as a canal and then opening well forward of the plate.
2. The masseteric tubercles lie ventrad and slightly mesiad of the infraorbital foramina instead of laterad.
3. The frontoparietal suture is not ankylosed even in adults.
4. The least distance from the suborbit to the infraorbital foramen only approximates the length of the incisive foramen.
5. The angle of the zygomatic plate with the occlusal plane of the maxillary tooth rows is only about 45 degrees.
6. The suborbit extends anteriorly at least as far as the anterior face of the first upper molar but often as far forward as midway in the fourth upper premolar.
7. The upper incisors are opisthodont.
8. The temporal ridges do not meet to form a sagittal crest.

DIAGNOSIS OF THE SUBTRIBE TAMIINA

The chipmunk subtribe is distinguishable from the subtribe Marmotina by the above enumerated characters, as follows: 1, 2, 3, 4, 5, 6, 7, and 8; and from the *Spermophilina* by 1, 2, 3, 4, and 5.

SUBTRIBE SPERMOPHILINA

HOLARCTIC GROUND SQUIRRELS

The subtribe consists of the Holarctic genus *Spermophilus* and the Nearctic genera *Ammospermophilus* and *Cynomys*.

The taxonomic skull characters of this subtribe are:

1. The highest point on the skull above the occlusal plane is on the frontal bone above the orbits, not on the nasal.
2. The least distance from the suborbit to

the infraorbital foramen notably exceeds the length of the incisive foramen.

3. The infraorbital foramen passes through the zygomatic plate as a somewhat laterally compressed canal, and opens forward of the plate.

DIAGNOSIS OF THE SUBTRIBE SPERMOPHILINA

The *Spermophilina* are distinguishable from the *Marmotina* by the character 1 above, and from the *Tamiina* by 2 and 3.

SUBTRIBE MARMOTINA

MARMOTS, ROCK CHUCKS, AND WOODCHUCKS

The taxonomic skull characters of this subtribe are:

1. The greatest width of the rostrum at the ends of the masseteric fossae approximates the greatest width of the parietal bones.

2. The least interorbital breadth is one and one-half times the least postorbital constriction.

3. The greatest breadth of both nasals approximates the orbital width.

4. The fourth upper premolar equals or exceeds the first upper molar in occlusal area.

5. The point of greatest elevation above the occlusal plane is on the rostrum.

6. The paroccipital processes extend ventrad well beyond the auditory bullae.

7. The nasals extend posteriorly beyond the anterior edges of the orbits, often to the supraorbital notches.

DIAGNOSIS OF THE SUBTRIBE MARMOTINA

The *Marmotina* are distinguishable from the *Spermophilina* by the above enumerated characters 1, 2, 3, 4, 5, 6, and 7; and from the *Tamiina* by 1, 2, 3, 4, 6, and 7.

RELATIONSHIPS OF THE SUBTRIBE MARMOTINA

Bryant (1945) has demonstrated that the distinction of the genus *Marmota* from the other Holarctic ground squirrels is somewhat greater than generic. Five of the above characters are adapted from ones offered in Bryant's (1945, p. 373) classification. The *Marmotina* and the *Tamiina* are more closely related to the *Spermophilina* than to each other. The *Spermophilina* are an amorphous group with no skull characters of their own

found to distinguish them from both the other ground squirrel subtribes.

TRIBE TAMIASCIURINI

NEARCTIC RED SQUIRREL AND MONTANE CHINESE ROCK SQUIRREL

The *Tamiasciurini* consist of only two genera, *Tamiasciurus* of the coniferous forests of North America and *Sciurotamias* of the mountains of China.

This tribe possesses the following taxonomic skull characters:

1. Each auditory bulla has three transbullar septa.

2. The postglenoid region of the squamosal is pierced by both the postglenoid and the subsquamosal foramina.

3. The supraorbital notches of the frontals are open and usually trenchant.

DIAGNOSIS OF THE TRIBE TAMIASCIURINI

The *Tamiasciurini* are distinguished from other tribes of the *Sciurinae* by the above enumerated characters, as follows: from the *Ratufini* by 1, 2, and 3; from the *Hyosciurina* by 1 and 2; from the *Protoxerini* by 1 and 3; from the *Funambulini* by 1 and 2; from the *Callosciurina* by 1, 2, and 3; from the *Sciurilina* by 1, 2, and 3; from the *Sciurina* by 1; from the *Microsciurina* by 1; from the *Marmotini* by 1; and from the *Xerini* by 2.

GENUS TAMIASCIURUS

NEARCTIC RED SQUIRREL

DIAGNOSIS: 1. The sphenopalatine foramen substantially exceeds the area of the sphenoidal fissure. 2. The sharp anterior edge of the zygomatic arch does not extend onto the premaxillary bone.

GENUS SCIUROTAMIAS

MONTANE CHINESE ROCK SQUIRRELS

DIAGNOSIS: 1. There are two dorsal processes on the zygomatic arch, one on the jugal and one on the zygomatic process of the squamosal. 2. The ectopterygoid ridge of the alisphenoid is obsolescent. 3. The upper incisors are rather strongly opisthodont. 4. The sphenopalatine foramen is substantially less than half of the area of the sphenoidal fissure. 5. The arch of the dorsal profile of the skull is very flat.

SUBGENUS RUPESTES

DIAGNOSIS: (This is a rare rock squirrel, known from but four localities in Yunnan and Sikang, China. The one skull available to the writer, U.S.N.M. No. 255138, exhibits the upper fourth premolars not fully erupted, and the cheek teeth entirely unworn, hence is very likely subadult, and its occiput and auditory bullae are missing. Nevertheless, the following characters that it possesses are indicative of very strong subgeneric distinction from *Sciurotamias davidianus*, to which it is certainly, nevertheless, most closely related.)

1. The squamosal is low, measured as in figure 4.
2. The zygomatic plate ascends to a point only halfway in the height of the rostrum.
3. The superior process of the jugal is posterior to the midlength of the orbit and is high.
4. The temporal ridges are trenchant.
5. The postorbital process of the frontal is very short (less than 1 mm. in this specimen).
6. There are no upper third premolars.

These six characters distinguish *Sciurotamias (Rupes) forresti* from *Sciurotamias (Sciurotamias) davidianus*, and from *Tamiasciurus* as well.

RELATIONSHIPS OF THE TRIBE
TAMIASCIURINI

Tullberg (1899) noted that the Nearctic red squirrel had a long, tapering glans penis without a baculum. This was verified and figured by Pocock (1923, p. 213). Mossman, Lawlah, and Bradley (1932) found further that the male genital tract of *Tamiasciurus* differed markedly from the tracts of other Nearctic squirrel genera, and they considered this fact to be strong support for classifying *Tamiasciurus* as a distinct subfamily as Pocock (1923) had done. No skull characters had been shown to distinguish *Tamiasciurus* from *Sciurus*, however, and many authors persisted in regarding *Tamiasciurus* as perhaps a subgenus of *Sciurus*, until Howell's (1938) classification of North American Sciuridae or even until Pocock's baculum-based classification of squirrels was accepted in Simpson's (1945) classification of the mammals, with *Tamiasciurus* recognized as tribally distinct. Even then, Bryant (1945, p. 383) concluded: "As determined by a study of the osteological and myological features, *Tamiasciurus* . . . is not generically

distinct from *Sciurus*." He pointed out that too little work had been done on genital tracts for their taxonomic value to be adequately assessed, but gave *Tamiasciurus* generic rank because of the peculiarities of its genital tract. The present study reports for the first time two trenchant characters of the skull that support tribal distinction: *Tamiasciurus* is the only squirrel genus in the Western Hemisphere that has three transbullar septa, and unlike *Sciurus* it has a high squamosal.

To what other squirrels *Tamiasciurus* is most closely related remains a mystery, but, as regular possession of three transbullar septa in each auditory bulla is almost as rare among Eurasian squirrels as among New World ones, the presently available evidence points to *Sciurotamias*, the montane rock squirrel of China. This squirrel has three transbullar septa in each bulla, and a few other less important skull characters permit the union of these two genera in a single tribe. Skull character differences between these two genera show them to be otherwise quite strongly divergent, however, and it is felt that *Sciurotamias* may only tentatively be classified in the Tamiasciurini because the nature of its baculum and genital tract remains unknown.

It has recently been shown by Layne (1952) that *Tamiasciurus hudsonicus loquax* does in fact possess a rudimentary baculum, averaging 0.26 mm. in length. This does not perceptibly lessen the here-established justification of tribal rank for *Tamiasciurus*. After describing and comparing the baubella or os clitoridis of Nearctic Sciuridae, Layne (1954, p. 365) noted that *Tamiasciurus* was the only genus in which the baubellum was found to be greatly reduced and frequently lacking, and he (p. 363) concludes, I think rightly: "The reduced development of the os genitale in this genus probably represents an advanced degree of specialization in which these structures are in the process of being eliminated."

Because having three transbullar septa per bulla also characterizes the tribe Xerini, one wonders, naturally, whether it indicates close relationship between the Xerini and the Tamiasciurini. It can be said that *Sciurotamias*, the montane rock squirrel of China, is intermediate between *Tamiasciurus*, the

Nearctic tree squirrel, and the Afro-Asian ground squirrels of the Xerini, both geographically and in habit and habitat. Furthermore, the skull of *Sciurotamias* has the general appearance of that of a ground squirrel, and it shares two only moderately important skull characters with the Xerini: 1. The upper incisors are rather strongly opisthodont. 2. The sphenopalatine foramen is substantially less than half of the area of the sphenoidal fissure.

One other bit of evidence remains to be mentioned. On examining a skull of the Persian squirrel *Tenes*, one might thrill at the discovery of three transbullar septa per bulla in a tree squirrel the skull of which is indeed very like that of *Tamiasciurus*. However, the number of septa is quite variable in *Tenes*, and *Tenes* has that unique skull character of the Sciurini, a low squamosal. Finally, the baculum of *Tenes* has been shown to be quite like that of *Sciurus*, so the possibility of close relationship between *Tamiasciurus* and *Tenes* is considered rather remote.

The subgenus *Rupestes* appears to have such trenchant skull characters that, if the sample were only slightly larger and fully adult, *Rupestes* would be accepted by the writer as a genus.

TRIBE XERINI

The Ethiopian and Palearctic ground squirrels of the genera *Xerus*, *Atlantoxerus*, and *Spermophilopsis* constitute this tribe.

The Xerini possess the following taxonomic skull characters:

1. The squamosal bone extends up to the base of the postorbital process of the frontal.
2. There are three transbullar septa in each auditory bulla.
3. The length of the lacrimomaxillary contact greatly exceeds that of the lacrimojugal on the dorsolateral surface of the skull.
4. The bony palate extends posteriorly beyond the ends of the maxillary tooth rows a distance equaling or exceeding the antero-posterior width of the third molar. (Frequently half of the length of the palatine bone is posterior to the third molar.)
5. The upper incisors are opisthodont.
6. The ventral portion of the lip of the infraorbital foramen forms a thick, prominent, masseteric tubercle.

7. The sharp, blade-like anterior edge of the zygoma overhangs the zygomatic plate so far as to make a deep fossa of it.

DIAGNOSIS OF THE TRIBE XERINI

The tribe Xerini may be distinguished from the other tribes of the Sciurinae by the above enumerated characters, as follows: from the Hyosciurina by 2, 3, 5, 6, and 7; from the Callosciurina by 1, 2, 3, 4, 5, 6, and 7; from the Ratufini by 1, 2, 3, 4, 6, and 7; from the Protoxerini by 1, 2, 3, 4, and 7; from the Funambulini by 1, 2, 3, 4, and 7; from the Sciurina by 1, 2, and 3; from the Sciurillina by 2, 3, 4, 5, 6, and 7; from the Microsciurina by 1, 2, 3, 4, 5, 6, and 7; from the Marmotini by 1, 2, 3, and 4; and from the Tamiasciurini by 1, 3, 6, and 7.

RELATIONSHIPS OF THE TRIBE XERINI

Where to place the curious prairie-dog-like *Spermophilopsis leptodactylus* in the classification of the Sciuridae has been a problem. Pocock (1923) omitted it altogether from his classification, and Frechkop (1932, no. 19) did not consider it in his evidence for making a separate family for the African ground squirrels. Ellerman (1940, p. 272) included *Spermophilopsis* with *Xerus* and *Atlantoxerus* as genera in what he called "E section." Ognev (1940, p. 432) gave *Spermophilopsis* separate subfamily status. Most recently Simpson (1945, p. 79) recorded it as *incertae sedis* in his tribe Xerini.

The above characterization of the tribe Xerini shows seven taxonomic skull characters in which *Spermophilopsis* consorts with the Xerini. The diagnosis of the Xerini shows that the most important four of these distinguish the Xerini (hence *Spermophilopsis*) from the Marmotini, and the diagnosis of the tribe Marmotini shows one further distinguishing skull character. If these five are not enough, it may be added that the following skull characters also distinguish *Spermophilopsis* from the Marmotini: 1. The lacrimal bone, as exposed on the dorsolateral surface of the skull, is very large, and its greatest width is greater than twice the distance that separates the lacrimal from the premaxillary. 2. The sutures separating the interparietal bones from the parietals do not become completely closed by ankylosis but remain

evident in adults. (The first is almost an exclusive character of the Xerini, but *Atlantoxerus* curiously does not share it. The second character *Spermophilopsis* shares with *Atlantoxerus* but with no other ground squirrels.)

On the other hand, only one nice character associates *Spermophilopsis* with the Marmotini: 3. The buccinator and masticatory foramina are confluent in *Spermophilopsis*, as in the Marmotini, but widely separated in all the other Xerini. The preponderance of skull character evidence allocates *Spermophilopsis* to the Xerini.

The relationships of *Spermophilopsis* to the other genera and subgenera of the tribe Xerini are worth noting. It shares three characters with *Atlantoxerus* which distinguish these two genera from the rest of the tribe: 4. The outline of the posterior aspect of the occiput is a simple arch in these two, but is straight-sided with a low arched top in the others. 2. The sutures delimiting the interparietals are not ankylosed in adults and still show rather clearly. 5. On the dorsolateral surface of the skull the jugal meets the lacrimal as a short wedge between it and the maxillary, rather than ending bluntly truncated against the lacrimal. In possessing the latter condition *Xerus* is unique among the Sciurinae.

These are outstanding taxonomic characters and indicate, perhaps surprisingly, that *Atlantoxerus* is more closely related to

Spermophilopsis than to *Xerus*. However, because each of these two genera shares one important character with *Xerus* and not with the other, it seems unsuitable to place *Atlantoxerus* and *Spermophilopsis* in a subtribe separate from *Xerus*.

It may further be noted that in a superficial way the skull of *Atlantoxerus getulus* most nearly resembles that of *Xerus rutilus*, and that the skull of *Spermophilopsis* most closely resembles that of *Geosciurus*. However, in view of the evidence of relationship found in what are believed to be more conservative skull characters, and discussed above, these superficial resemblances probably represent convergence.

The genera or subgenera *Geosciurus* and *Euxerus* are treated provisionally as subgenera here, although they seem to be quite as strongly differentiated for subgenera as the genera *Xerus*, *Atlantoxerus*, and *Spermophilopsis* are for genera. Certainly if Didier's (1952, p. 18) illustrations of a baculum of *Xerus erythropus erythropus* are correct, and if the characters shown are reasonably constant for *Euxerus*, then there is a good case for raising *Euxerus* to generic level. However, Pocock's (1923, p. 16) illustrations and descriptions of the bacula of *Euxerus erythropus* differ greatly from Didier's and resemble those of *Xerus* and *Geosciurus* much more closely. Because Didier (1952) seems unconcerned about this, Pocock's work is accepted as correct.

PYGMY SQUIRREL CONVERGENCE

FORSYTH MAJOR (1893) divided the squirrels into three subfamilies, as follows: tree and ground squirrels, the Sciurinae; flying squirrels, the Pteromyinae; and pygmy squirrels, the Nannosciurinae. Miller and Gidley (1918) accepted this classification and considered the subfamily Nannosciurinae to include the pygmy squirrels of the East Indies, *Nannosciurus*; the West African pygmy squirrels, *Myosciurus*; and the South American pygmy squirrels, *Sciurillus*. (See fig. 6.) Thomas (1915, pp. 385-386), however, had reported that *Nannosciurus* had a compound baculum whereas *Myosciurus* had a simple one, and that, "Consequently the separation of the Nannosciurinae as a subfamily set over against other squirrels is flatly contradicted." Pocock (1923, p. 212) echoed, "... the subfamily Nannosciurinae must be abolished as composed of heterogeneous elements, alike only in convergent characters." Anthony and Tate (1935, p. 3) figured the baculum of *Sciurillus*, showing it to be of still a third kind, which is that by which Pocock had characterized the Sciurini, thus completing the evidence from bacula that these three far-flung genera of pygmy squirrels are less closely related to one another than to the tree squirrels with which each is geographically associated.

The skull character similarities between the several genera of pygmy squirrels are very striking, however, and, in spite of the evidence from the bacula, Ellerman (1940, p. 269) retained the earlier grouping of the pygmy squirrel genera by placing them in what he termed a "*Nannosciurus* Section: Pygmy Squirrels with highly abnormal cranial characters; the Nannosciurinae of Miller and Gidley, and Forsyth Major."

Neither the similarities nor the differences between skull characters of these genera have been adequately considered, nor has the subject been treated previously in any detail by a student who had examples of all the pygmy squirrel genera before him.¹ Anthony and

Tate (1935, p. 4) listed skull characters in which the pygmy squirrels *Sciurillus* of Brazil and *Nannosciurus* [*melanotis*] are alike and which differentiate them from tree squirrels such as *Sciurus vulgaris*, *carolinensis*, and others. Nine of these are here restated so that they characterize also the species *Myosciurus minutus*, *Exilisciurus exilis*, *E. whiteheadi*, *E. concinnus*, and *E. surrutilus*: 1. The interorbital breadth is about equal to the length of the frontal. 2. The long axis of the orbit is shortened until the orbit appears circular. 3. The zygomatic process of the squamosal is shifted forward until the base of it is beneath the postorbital process of the frontal. 4. Broader contact of the maxilla with the frontal separates the lacrimal very widely from the frontal process of the premaxilla. 5. The greater part of the lacrimal is extruded into the margin of the orbit. 6. Viewed from the side, the area of the rostrum from which the infraorbital part of the masseter originates exceeds the area remaining forward of it. 7. From, and continuous with, the anterior edge of the zygomatic process of the squamosal, a protrusive bony ridge extends across the face of the inflated alisphenoid. 8. The upper incisors are strongly proödont. 9. The coronoid process of the mandible is substantially reduced.

To the above similarities between pygmy squirrels of different continents three items pertaining to *Myosciurus* of Africa and *Nannosciurus* of Malaysia may be added from Forsyth Major (1893, p. 190), with modification, even though he had no *Sciurillus*: 10. The junction of the zygomatic plate with the rostrum is virtually at a right angle to the occlusal plane. 11. The center of the orbit is posterior to the midlength of the skull. 12. The occlusal surfaces of the upper molar teeth present only three complete transverse ridges instead of four; the third

simus, and two species of *Microsciurus*. These 22 include some treatment of the first 10 of the "similarities" listed in the present paper and the first five of the six "differences" cited here from the literature. None of the nine skull character differences between pygmy squirrel genera reported as original in the present paper were recognized by Hill, but he reaches the same major conclusion about relationships of pygmy squirrels.

¹ While the present paper was in press, Hill (1959) published a table for comparison of 22 characters in *Myosciurus*, *Sciurillus*, and *Nannosciurus* (but omitting any representative of what is now *Exilisciurus*), with *Callosciurus notatus*, *Prosciurillus leucomus*, *Glyphotes*

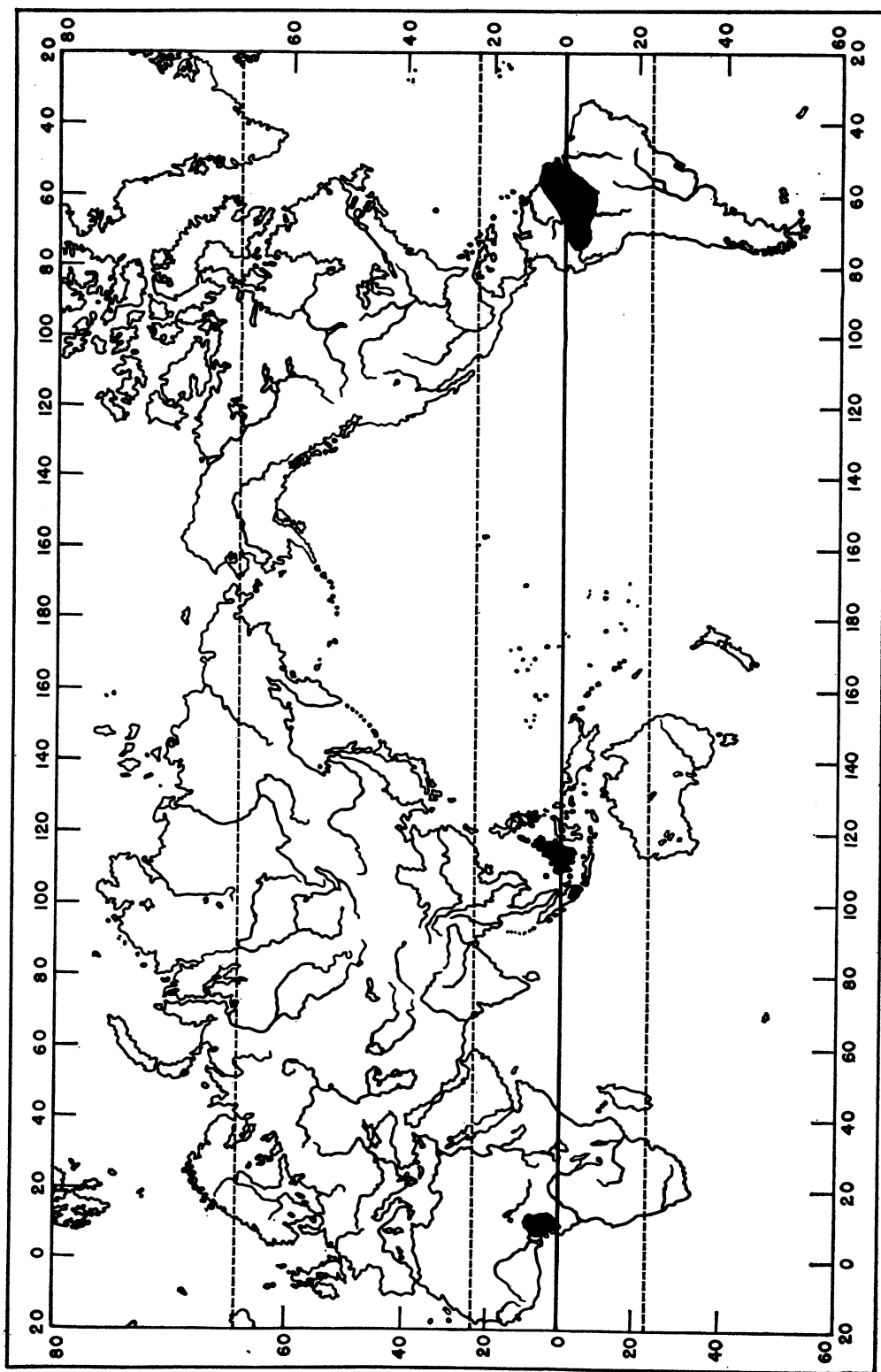


FIG. 6. The distribution of the pygmy squirrels: left to right on the map, African *Myosciurus*, combined East Indian ranges of *Nannosciurus* and *Exilisciurus*, and South American *Sciurillus*. The ranges of *Myosciurus* and *Sciurillus* are only approximations.

from anterior is reduced sometimes to little more than a minute cusp.

Differences in skull characters between genera of pygmy squirrels have received less attention. Anthony and Tate (1935, p. 5) list four differences between *Sciurillus* and *Nannosciurus* which are applied here to *Exilisciurus* and *Myosciurus* as well: 1. *Sciurillus* has well-developed paroccipital processes, whereas these are varyingly obsolescent in the other three genera. 2. *Sciurillus* has a well-developed median spinous projection of the palate into the pterygoid fossa. This is uncommon in *Nannosciurus*, perhaps absent in *Myosciurus*, but frequent in *Exilisciurus*. 3. The ectopterygoid fossa is in *Sciurillus* almost as deep as the pterygoid fossa in *Sciurillus*, but is noticeably less deep in *Nannosciurus* and part of *Exilisciurus*. (*Myosciurus* has no ectopterygoid fossa.) 4. *Sciurillus* has a slender jugal with no superior process, but in the other genera the jugal is broadened and has a superior process.

Ellerman (1940, p. 313) contributed the further observations that in *Myosciurus* the absence of an ectopterygoid ridge of the alisphenoid (hence no ectopterygoid fossa) and an "abnormal" infraorbital foramen distinguishes this genus from the other pygmy squirrels. This comment may be improved for use here as follows: 5. *Myosciurus* has no ectopterygoid ridge of the alisphenoid, although this is well developed in the other pygmy genera. 6. The length of the infraorbital canal exceeds the length of the maxillary tooth row in *Sciurillus* and closely approaches it in *Nannosciurus* and *Exilisciurus*, but in *Myosciurus* the canal is only about one-quarter or one-third of the length of the tooth row.

To these the present writer adds: 7. *Myosciurus* is characterized by two transbullar septa in each auditory bulla, whereas *Nannosciurus* and *Sciurillus* are distinguished by one, and *Exilisciurus* by the absence of any. 8. In *Exilisciurus* and *Nannosciurus* a single large foramen pierces the squamosal in the postglenoid area, but in the other two genera none does. 9. In *Nannosciurus* there is a well-developed muscle attachment area on the slightly projecting lateral lip of the infraorbital foramen which constitutes a masseteric tubercle. In *Exili-*

sciurus the attachment area is dissociated from the foramen but lies just ventrad of it as a slightly roughened circular area which may be slightly elevated, sunken, or neither. In the other two there is not even a vestige of a masseteric tubercle. 10. Only in *Sciurillus* do the sutures bounding the interparietal ankylose completely. In the others open sutures outline this bone. 11. Only in *Sciurillus* does the frontoparietal suture ankylose completely. 12. The upper extremity of the lip of the infraorbital foramen connects with the maxillo-premaxillary suture in *Sciurillus* and *Nannosciurus* but does not in other pygmy squirrels. 13. The upper end of the lateral lip of the infraorbital foramen (in lateral view) slants forward in *Sciurillus* but not in the others. 14. In *Sciurillus* the maxilla provides a substantially greater area of the lateral surface of the rostrum than does the premaxilla, which is not true in the others. 15. In *Myosciurus* the occlusal surface of the upper third molar is at an angle of 70 degrees to 80 degrees from the occlusal plane (as defined here). In *Nannosciurus* and *Exilisciurus* this may often reach 45 degrees. In *Sciurillus* the teeth are oriented more as those of ordinary tree squirrels.

The above 15 differences in skull characters are, except for 2 and 3, trenchant, consistent ones and recognized to be of generic importance here. All but the first three are found in one or more other genera of the Sciurinae to be of value as generic characters. Numbers 7 and 8 are even so important as to characterize polytypic tribes. *Sciurillus*, it may now be observed, is distinguishable from all the other pygmy squirrels by 1, 4, 10, 11, 13, and 14. *Myosciurus* is distinguishable from all the others by 5, 6, 7, and 15. *Nannosciurus* is so distinguishable only by 9. *Exilisciurus* is so distinguishable solely by 7. *Exilisciurus* may be the least specialized, but is also the only pygmy genus that is known to be polytypic.

Having established that, in addition to the differences of the baculum among the pygmy squirrel genera, there are differences in the number of transbullar septa and many other previously unnoted but taxonomically important differences of the skull, perhaps one needs to reexamine the list of similarities of the skull between these genera which have been or could be supposed to unite them as a

geographically scattered but related unit and distinguish them from other potential relatives which are geographically near.

Of the similarities listed, 1 is found in *Glyphotes simus* and several species of *Callosciurus* that are geographically associated with the Malaysian pygmy genera, and in some forms of *Microsciurus* that occur geographically close to *Sciurillus*. Numbers 2 and 3 occur in the East Indies in *Hyosciurus* and *Prosciurillus* of Celebes and are approximated in *Glyphotes simus* of Borneo and *Sundasciurus fraterculus* of the Mentawi Islands. They also occur in *Microsciurus similis* of South America and are closely approached in *Paraxerus alexandri* of Africa and *Funambulus sublineatus* of peninsular India.

Prosciurillus. Number 12 applies as well to *Glyphotes simus* as it does to *Sciurillus*. Many, if not all, of these characters which have been assumed to characterize and distinguish the widely separated pygmy squirrels are here shown to occur in tree squirrels of the same geographic areas that the pygmy genera occupy. It seems, therefore, quite possible that *Myosciurus* could have been produced locally by the same African stock that produced *Paraxerus alexandri* and *Funambulus sublineatus*. It seems equally possible that *Sciurillus* derives from ancestral stock which produced the Sciurini including *Microsciurus* of South America. And it seems possible that *Nannosciurus* and *Exilisciurus* derive from stock that produced

TABLE 2

THE OCCURRENCE (X) AND INCIPIENCE (/) OF THE TWELVE ALLEGEDLY PYGMY SQUIRREL SKULL CHARACTERS IN DIMINUTIVE TREE SQUIRRELS

	1	2	3	4	5	6	7	8	9	10	11	12
<i>Glyphotes simus</i>	x	/	/	x	—	—	/	x	—	/	—	x
<i>Sundasciurus fraterculus</i>	—	—	—	—	—	—	/	x	—	/	—	—
<i>Prosciurillus murinus</i>	—	x	x	—	—	x	x	x	—	x	x	—
<i>Tamiops rodolphei</i>	—	—	—	—	—	x	—	x	—	/	—	—
<i>Funambulus sublineatus</i>	—	/	/	—	—	x	—	x	x	—	—	—
<i>Paraxerus alexandri</i>	—	/	/	—	x	—	—	x	—	—	—	—
<i>Microsciurus similis</i>	x	x	x	/	—	—	—	x	x	/	—	—

Number 4 is also associated with strong specialization for broad frontals in species of *Callosciurus* and in *Prosciurillus leucomus* and *Glyphotes simus* in the East Indies. It is approached in *Microsciurus similis* in South America. Number 5 is common in the Funisciurina. Number 6 applies as well to *Prosciurillus murinus*, *Tamiops rodolphei*, and *Funambulus sublineatus* as it does to *Myosciurus*. Number 7 is present in *Prosciurillus* and is definitely incipient in *Glyphotes simus* and *Sundasciurus fraterculus*. Number 8 is common throughout the Callosciurini, is strongly developed in small Microsciurini, and occurs in several small Funisciurina. Number 9 characterizes *Funambulus*, *Xerus*, and *Microsciurus*. Number 10 occurs in *Prosciurillus murinus* and is approached by *Microsciurus similis*, *Sundasciurus fraterculus*, *Glyphotes simus*, and *Tamiops rodolphei*. Number 11 applies to

the tree squirrels of the Malaysian subregion. Thus, we have indications that each of the genera of pygmy squirrels could have been produced by ancestors of its own geographic neighbors.

The occurrence or incipience of supposedly pygmy squirrel characters in other species of small squirrels inhabiting tropical jungles seems rather striking. This is shown succinctly in table 2. There it is evident that every one of the 12 skull characters that are thought to distinguish the pygmy squirrel genera as a group occurs in fact in some tree squirrel genus in a diminutive species. On the average each of these 12 skull characters occurs or is incipient in diminutive species of three tree squirrel genera, a fact that strongly suggests that these 12 characters are selected for by forces that evolve dwarf squirrels from the existing stocks of tree squirrels. Suggestion of such selection seems to be strength-

ened by the fact that, while *Glyphotes simus* is by its peculiar incisors obviously specialized for a quite different niche from that of the pygmy genera, in attaining dwarf size it has acquired four, and appears to be acquiring four more, of these supposedly pygmy squirrel characters.

The evidence from the bacula and from the number of transbullar septa indicates that pygmy squirrels must be most closely related to geographically close tree squirrel relatives. The evidence from the skull characters, which have been supposed to differentiate the pygmy squirrels as a taxonomic unit, reveals that these characters could have been produced by the local ancestral stocks. It may be inferred from study of the skulls of diminutive species of tree squirrel genera that the 12 skull characters that appear to unite the pygmy genera are results of dwarfing. Further evidence from the study of skull

characters shows that many previously unnoticed, trenchant differences between the pygmy genera exist. The conclusion is, therefore, inescapable that pygmy squirrels are not a natural group.

Such a conclusion connotes that the name "pygmy squirrel" is quite arbitrary in meaning (defined so in the section on ecological classification). Although virtually nothing is known of the ecological niches of pygmy squirrel genera, it now appears quite probable from morphology that the species *Sundasciurus fraterculus*, *Prosciurillus murinus*, and perhaps *Funambulus sublineatus* and others that occupy jungle habitats similar to those of the pygmy squirrel genera, particularly those that have been geographically isolated from invasion by the pygmy genera (but also *Microsciurus similis* which has not), are in fact incipient pygmy squirrels.

ORIGIN OF THE NEOTROPICAL PYGMY GENUS

Sciurillus IS IN ITS SKULL CHARACTERS (see table 3) one of the most highly specialized genera in the whole Sciurinae. This raises an interesting question. No squirrels are known to have occurred in South America before the late Pliocene, when the rise of an isthmus provided them direct access to it from North America. Can so highly specialized a genus as *Sciurillus* have originated no longer ago than the very late Pliocene? A possibility surely exists that *Sciurillus* could have differentiated to a considerable extent before reaching South America. If it is assumed that pygmy size was an adaptation for a tropical niche in the Pliocene, as it evidently is now, it seems possible that *Sciurillus* could have become generically differentiated earlier in the Pliocene on the southern tip of North America in a tropical habitat presumably available there. Such a stock, already well differentiated, may even have reached South America by rafting before the Isthmus formed, for the fossil fauna of northern South America is only poorly known as yet (Fields, 1957), and so small and scarce a form

would rarely be found fossil. Climatic and vegetational changes in the Pleistocene could have eliminated *Sciurillus* from its range north of the Isthmus, but restriction to its present range possibly results from rather recent competition and replacement in some parts of its niche by species of *Microsciurus*. It certainly is unlikely that the ancestors of *Sciurillus* rafted very early to South America as an unspecialized tree squirrel and became specialized on that continent before the rise of the Isthmus. In that circumstance both generalized and specialized squirrels that are more distinctively relatives of *Sciurillus* should be occupying other squirrel niches or showing up more readily as fossils. The probability seems greatest to the present writer that *Sciurillus* may constitute one indirect bit of the evidence for which Darlington (1957) asks, of differentiation of a tropical fauna on the southern extension of the North American continent prior to the rise of the isthmian connection with South America.

SKULL CHARACTER DIFFERENTIATION IN SCIURINE GENERA

IT HAS BECOME EVIDENT during the course of this investigation that the various genera that may be ecologically classified as tree squirrels possess few distinguishing skull characters, but that squirrel genera that have evolved towards great size or diminutive size generally have a greater number of distinguishing characters of the skull. While the tree squirrel genera *Callosciurus*, *Sciurus*, and *Tamiasciurus*, for example, even though they be accepted as tribally different, could not until the present study be distinguished by skull characters even at the generic level, ground squirrel genera most closely related to each of these genera could be quite easily distinguished by skull characters. The pygmy squirrels most closely related to *Sciurus*, and *Callosciurus*, differ from one another in many skull characters. Giant squirrel genera, whatever their relationships, differ abundantly from one another in skull characters. One might ask whether the squirrels that are thought or known to have more specialized habits are actually more differentiated than tree squirrels by these morphological criteria.

Table 3 lists the genera of the Sciurinae. In the body of that table are numerical references to the above-described skull characters of each genus and those of its tribe and subtribe that distinguish the genus from at least 30 of the other 36 genera of the Sciurinae. The characters that serve only for more limited distinction are omitted. In any instance in which a character is single, as enumerated in its formal description but for the purposes of table 3 actually constitutes two characters, its number is recorded twice (e.g., in *Funisciurus*). The numbers that are in parentheses are, for the Callosciurina, from the key to the genera of that subtribe; for the Xerini, those of characters that are delineated in the discussion of the relationships of that tribe. An x for a genus signifies a generic character not formally defined in the present paper: for *Dremomys*, it is an elongate rostrum; for *Funisciurus*, it is the peculiar enamel pattern of the cheek teeth; for *Cynomys*, it is that the cheek teeth are much wider than long. In a few instances in the formal diagnoses a character is listed for one

genus to distinguish it conveniently from two others of its tribe, when it is in fact the contrasting condition in the two other genera that is more unusual in the Sciurinae as a whole. As the latter condition is not listed and delineated, the number of the described condition is bracketed in table 3 to indicate the contrasting condition and is listed opposite the genus or genera possessing the contrasting condition.

Such a tabulation as this is somewhat rough because, first, the genera have certainly not been searched equally for skull characters, and, second, the definitions and diagnoses do not include every character noticed that would distinguish it from 0.83 of the other genera. The purpose of the diagnosis of a subtribe is obviously to distinguish it from other subtribes within the tribe, and characters that would be pertinent in table 3 may have been overlooked because they did not serve the purpose at hand. Nevertheless, it is believed that the differences between occupants of the several ecological niches are roughly correct.

ECOLOGICAL NICHE DEFINITIONS

The following criteria were used in the classification of the genera ecologically as tree, ground, pygmy, and giant squirrels. Tree squirrels are those that nest above the ground in trees, take refuge primarily in trees when fleeing enemies, and obtain a substantial portion of their food from the fruits, buds, and other material of trees. Ground squirrels are those that nest in burrows in the ground, take refuge in burrows usually when fleeing enemies, and feed principally on low-growing plants. Pygmy squirrels are those forms extremely specialized for diminutive size that are included in the genera *Nannosciurus*, *Exilisciurus*, *Myosciurus*, and *Sciurillus*. (This arbitrary definition is employed because the ecology of pygmy squirrels remains almost entirely unknown.) Giant (tree) squirrels are tree squirrels of great size the ecological niche of which appears to be limited rather closely to the upper levels of tropical primary jungle. The long-nosed ground squirrels of southeastern Asia

TABLE 3
DEGREE OF DIFFERENTIATION IN RELATION TO ECOLOGICAL NICHES OF THE GENERA OF THE
SCIURINAE^a

	Tribal	Characters of the Skull Subtribal	Generic	Totals
TREE SQUIRRELS				
<i>Tamiasciurus</i>	1	—	2	2
<i>Sciurus</i>	—	1	—	1
<i>Tenes</i>	—	1	—	1
<i>Guerlinguetus</i>	—	1	—	1
<i>Microsciurus</i>	—	—	—	—
<i>Syntheosius</i>	—	—	—	—
<i>Heliosciurus</i>	1, 2	—	3, 4	4
<i>Funisciurus</i>	1	1, 1	x	4
<i>Paraxerus</i>	1	1, 1	—	3
<i>Funambulus</i>	1	—	—	1
<i>Callosciurus</i>	—	—	—	—
<i>Sundasciurus</i>	—	—	(1)	1
<i>Glyphotes</i>	—	—	(1, 2)	2
<i>Prosciurillus</i>	—	—	2	1
GIANT SQUIRRELS				
<i>Reithrosciurus</i>	—	1	2, 3, 4, 6, 7, 8	7
<i>Protoxerus</i>	1, 2	—	7, [1]	4
<i>Epixerus</i>	1, 2	—	3, 7, [1]	5
<i>Rubrisciurus</i>	—	1	3, 4, 5	4
<i>Ratufa</i>	1, 2, 2, 4, 5, 6, 7	—	—	7
PYGMY SQUIRRELS				
<i>Sciurillus</i>	—	2, 3, 4, 5, 6, 7, 8, 9, 10, 11	—	10
<i>Myosciurus</i>	1	2, 3, 4, 5, 7, 8	—	7
<i>Nannosciurus</i>	—	—	2, 3, 4, 5, 6	5
<i>Exilisciurus</i>	—	1	1, 2, 3, 5, 6	6
GROUND SQUIRRELS				
<i>Xerus</i>	1, 2, 3, 4, 6	—	(1, 3, [4, 5])	9
<i>Atlantoxerus</i>	1, 2, 3, 4, 6	—	(3)	6
<i>Spermophilopsis</i>	1, 2, 3, 4, 6	—	(1, 3)	7
<i>Sciurotamias</i>	1	—	1, 2	3
<i>Spermophilus</i>	3	[3]	—	2
<i>Ammospermophilus</i>	3	[3]	—	2
<i>Cynomys</i>	3	[3]	x	3
<i>Eutamias</i>	3	1, 2, 4	—	4
<i>Tamias</i>	3	1, 2, 4	—	4
<i>Marmota</i>	3	[3], 1, 2, 3, 4	—	6
LONG-NOSED SQUIRRELS				
<i>Dremomys</i>	—	—	—	—
<i>Lariscus</i>	—	—	(1)	1
<i>Menetes</i>	—	—	(1)	1
<i>Rhinosciurus</i>	—	—	1, 2, 3, 4, 5, 6, 8	7
<i>Hyosciurus</i>	—	1	2, 3, 4, 5	5

^a For the significance of the numbers and symbols in the body of the table, see text (p. 192).

and the East Indies constitute a surprisingly ill-differentiated, widespread, dominant group. Very little is known of their ecology, but it seems to differ basically from the primarily open-land but also forest-edge and scrub habitat of the Xerini, Spermophilina, and Marmotina. The habitat of the long-nosed squirrels seems to be primarily forest floor but also forest edge and scrub.

The relict, giant, Bornean squirrel *Reithrosciurus*, with two septa, is evidently adapted to living on the ground in primary jungle (Banks, 1949, p. 64). Its claws are more slender and less abruptly curved than those of *Ratufa*, although these two squirrels are about the same size, but they are not so straight as those with which *Marmota* burrows. Nor are its great ear tufts and enormous bush of a tail likely appendages of a burrowing animal. Perhaps it nests in tree hollows, forages on the ground, and escapes enemies because of its large size and speed and, to a lesser extent than in some tree squirrels, by climbing trees. Banks (*loc. cit.*) states that it feeds on fallen fruit and the bark of trees. The latter would be particularly interesting, for its extremely opisthodont, somewhat compressed incisors strongly suggest some specialized feeding habit.

Marmota occupies a distinctive niche which might be called the giant, ground squirrel one, but, as *Marmota* is alone in this category, it would seem unnecessary fragmentation to treat it as a special category in table 3.

Another case is exemplified by the long-nosed, terrestrial, insectivorous squirrel *Rhinosciurus*. The incisor teeth in *Rhinosciurus* are strongly modified for forceps-like grasping. The cheek teeth are somewhat simplified (as is the case in other ant-eating mammals) and may wear away entirely during the animal's active life, as though it also ingests a great deal of grit with its food. These factors, together with the enormously elongated rostrum, recommend the recognition of a special niche, for the occupation of which *Rhinosciurus* could be called the ant-eating squirrel. The pig squirrel, *Hyosciurus*, surely should be placed in this category, although nothing is yet known of its food habits. While the teeth of *Hyosciurus* show no such modification, its claws are highly developed for digging, and the rostrum, as is

that of *Rhinosciurus*, is extraordinarily produced.

TREE SQUIRREL CONSERVATISM

The skull character data provided in table 3 show comparatively little differentiation in the tree squirrels of ordinary size in any part of the world and from whatever tribal stock. Genera of the giant squirrel, pygmy squirrel, and ground squirrel niches appear to exhibit more differentiation in characters of the skull.

Tree squirrels, because of their diurnal activity and the boldness that they no doubt derive in part from being easily able to attain safety up a tree while still in plain sight of a presumed enemy, are the most familiar members of the squirrel family to man. This historical familiarity, specifically of *Sciurus vulgaris*, has resulted in an overwhelming primacy of the tree squirrel name *Sciurus* in nomenclature of the squirrel subfamily Sciurinae. Some familiarity with the nomenclature of this group might lead one subconsciously to expect that tree squirrels as an ecological type antedate and have given rise to the phyla of squirrels occupying other ecological niches. The absurdity of an *a priori* opinion on squirrel phylogeny so tainted is obvious. The niche or role of a tree squirrel is a fairly specialized way of life among rodents as a whole, however basic it may in fact be within the limits of the squirrel family. The large, generally somewhat distichous, bushy tail, the adaptive development of the claws and limbs, the habit of arboreal nesting, and the feeding principally upon tree products constitute considerable specialization.

Tree squirrels include more genera than do any other squirrel niche, and they also have a somewhat greater world range than even the combined groups of ground squirrels, for tree squirrels reach Central America and South America and have greater ranges in the Palearctic and Nearctic regions (see range maps in Palmer, 1954; Ognev, 1940; and van den Brink, 1955). The nearly worldwide availability of the tree squirrel niche and occupation of it on four continents by the Sciurinae have provided tree squirrels more than usual opportunity for evolutionary divergence through geographic separa-

tion. That such geographic separation, and sufficient divergence to insure reproductive isolation, must have taken place long ago is indicated by the findings of Pocock (1923) and supported strongly by those of the present paper, yet table 3 shows that tree squirrel genera, after the present search for skull characters, are remarkably devoid of differentiation in characters of the skull. This conservatism in tree squirrels suggests that the tree squirrel niche must be extremely exacting in anatomical requirements. It implies further that the selection in this severely conservative role must also be extremely similar in various parts of the world. The similarities between ordinary tree squirrels of tribally separate stocks, and the scarcity of important skull character differences between them shown in table 3, appear to constitute a polytypic example of extreme conservatism and imply that tree squirrels were well adapted to their niche very early.

SUCCESSION IN GROUND SQUIRRELS

From table 3 it appears that, quite in contrast to the tree squirrels, the Xerini have no genera at all that are conservative in skull characters. Furthermore, if one considers the disjunct range of the Xerini, as shown in figure 7, one may in the age and area concept of Simpson (1940, p. 144) interpret the Xerini as in the contracting phase of their evolution. The other ground squirrel tribe, the Marmotini, has, however, genera that are shown in table 3 to be very conservative in their skull characters. (The *Spermophilina* were less intensively searched for generic skull characters in the present study than were other phyla, but I think that they are probably as conservative as they are represented in the table.) The geographic range of the Marmotini, particularly of the *Spermophilina*, as shown in figure 7, and the *Tamiina* as shown by Palmer (1954) and Ognev (1940), suggests that they are still in the expanding phase of evolution. *Sciurotamias*, a montane rock squirrel of China, which is here placed tentatively in the *Tamiasciurini* but may be to the Xerini what the chipmunks are to the *Spermophilina*, shows rather little skull character differentiation in table 3, but its geographic range, given in figure 7, is small and isolated from the range of any close relatives.

In accordance with the age and area concept of Simpson (1940, p. 144) these characteristics of the ranges of the various ground squirrels suggest that the Xerini are in the contracting phase of their evolution and that *Sciurotamias* may be in a contracting or a shrinking phase, but that the Marmotini are in the expanding phase of their evolution or at the peak of it. Together with the observed variance in differentiation of the skull, these observations suggest that the Marmotini are succeeding the Xerini and *Sciurotamias*. There is a close general resemblance between the skulls of the Marmotini and those of the Xerini which also suggests that the Xerini may have given rise to the Marmotini.

Although the long-nosed squirrels are the terrestrial squirrels of the Indo-Malayan region, there is no resemblance between their skulls and those of the Marmotini or the Xerini that would suggest close relationship. Except for the transbullar septa, however, a case might possibly be made for the relationship of the long-nosed squirrels to *Sciurotamias*, especially through *Menetes*. The occurrence of separate blades on the known bacula of long-nosed squirrels, and the characteristic single pair of transbullar septa, both indicate that the long-nosed squirrels belong properly to the *Callosciurina*, except for *Hyosciurus*, of course, which has no septa and belongs in the contribal *Hyosciurina*. As pointed out in the niche definitions, what is known of the habitat of long-nosed squirrels seems to be basically different from that of ground squirrels, and reinforces the morphological evidence that these Indo-Malayan squirrels, though terrestrial, occupy a different niche from that of ground squirrels as well as enjoy only a distant relationship to them.

The conservatism of three of the genera of long-nosed squirrels in skull characters, as shown in table 3, is remarkable. Their ranges, although not shown here, have been mapped for a separate report and seem generally to indicate that these squirrels are in the expanding phase of their evolution. The range of *Dremomys* may overlap that of *Marmota* in Nepal, Sikkim, and Szechwan, and does overlap that of *Sciurotamias* in Szechwan. Mr. T. Donald Carter tells me that at the places

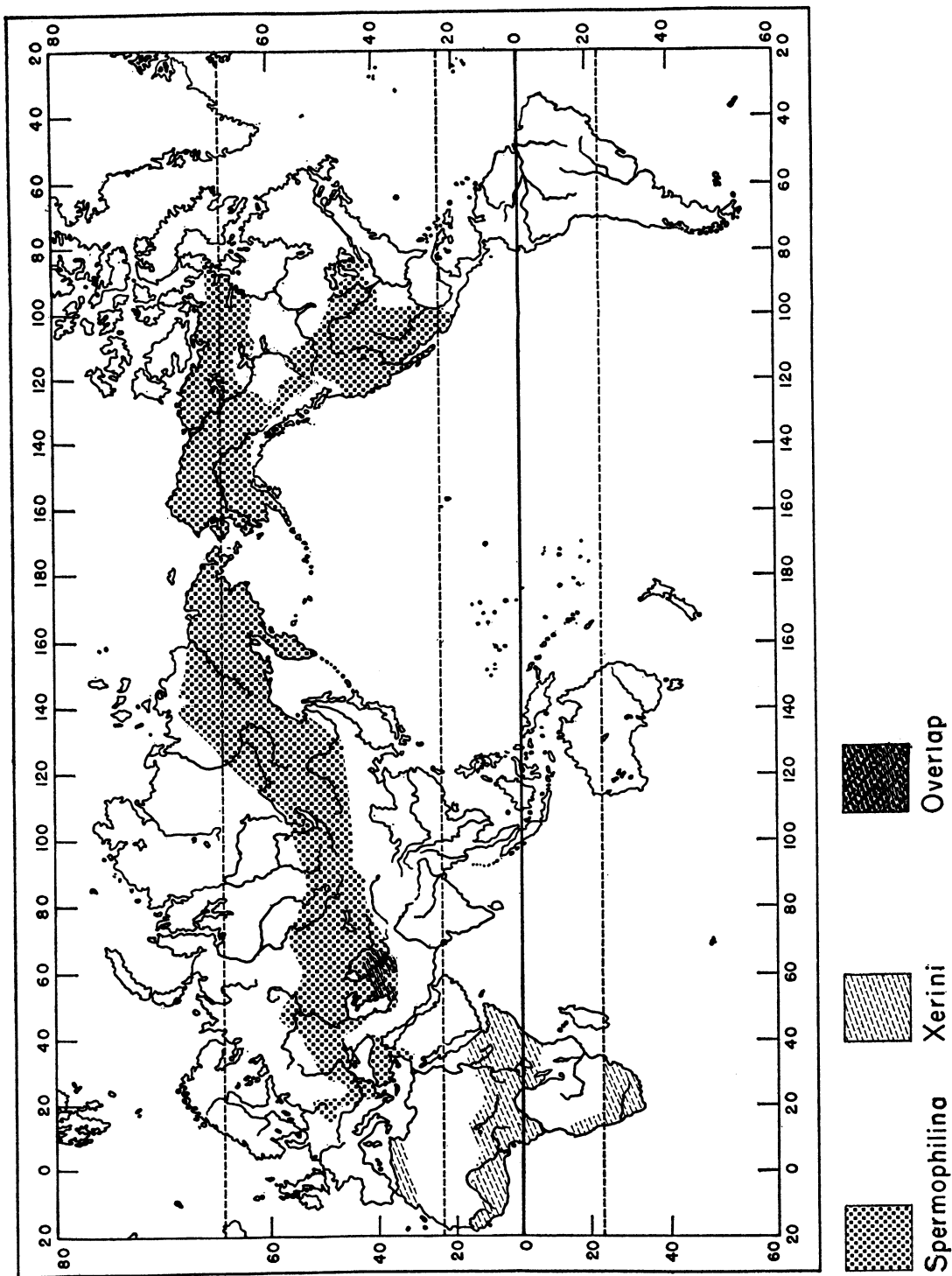


FIG. 7. The ranges of the Spermophilina and the Xerini, contrasting the disjunct, apparently relictual ranges of the xerine genera with the wide sweep of the more dominant ground squirrel group. In the Xerini the range of *Spermophilopsis* is shown to be engulfed by that of the Spermophilina (data from Ognev, 1940); *Atlantoxerus* is isolated in north Africa; the subgenus *Geosciurus* seems somewhat isolated in South Africa; and the subgenera *Xerus* and *Euxerus* are broadly sympatric across middle Africa.

where he collected both genera near Wenchwan in Szechwan, China, *Dremomys* were observed running about over down timber in coniferous forest, whereas *Sciurotamias* lived as a ground squirrel in the occasional grassy, boulder-strewn level spots along the bed of a generally precipitous mountain stream. Otherwise the ranges of long-nosed squirrels are well removed from those of ground squirrels.

In summary, it seems certain that the

Marmotini are replacing the Xerini as the dominant ground squirrel phylum. It is uncertain whether the Marmotini arose from the Xerini or from the dominant tree squirrel phylum that has two septa, but the latter is thought the more probable. It seems quite certain that the terrestrial long-nosed squirrels of the Indo-Chinese and Malaysian subregions are not closely related to either ground squirrel tribe but originated from the basic stock of the Callosciurini.

CLASSIFICATION OF THE SCIURINAE

IN THE FOLLOWING CLASSIFICATION the names of Pocock's (1923) six subfamilies remain as tribes (Simpson, 1945), but two more tribes are admitted, both of them salvaged from Pocock's heterogeneous subfamily Funambulinae (=Funambolini Simpson, 1945). Pocock's Sciurinae and Callosciurinae (=Sciurini Burmeister, 1854, and Callosciurini Simpson, 1945) appear to be clearly differentiated natural groups on the characters of their bacula and are retained here as tribes on that basis alone. The largest natural groups distinguishable within these two tribes by characters of the skull can consequently be recognized only as subtribes, even though on degree of differentiation they may merit tribal rank, which means that the subtribal categories under the Sciurini and the Callosciurini are of somewhat greater importance than are those, for example, under the Marmotini.

The order of the tribes in the following classification is approximately that of those having no septa to those with three transbullar septa per auditory bulla, which is apparently the order of increasing complexity.

Family Sciuridae Gray, 1821, p. 304. Squirrels.

Subfamily Sciurinae Baird, 1857, p. 240. Squirrels with no gliding membranes.

Tribe Ratufini, new form. Indo-Malayan giant squirrels.

Ratufa Gray, 1867.

Tribe Protoxerini, new form. African giant and sun squirrels.

Protoxerus Major, 1893. (Including *Allosciurus* Conisbee, 1953, for *Myrsilus* Thomas, 1909, preoccupied.) African giant squirrel.

Epixerus Thomas, 1909. African giant squirrel.

Heliosciurus Trouessart, 1880. Sun squirrel.

Tribe Funambolini Simpson, 1945, p. 79 (=Funambulinae Pocock, 1923). Indian and African tree and pygmy squirrels.

Subtribe Funambulina, new form. Indian striped squirrel.

Funambulus Lesson, 1832. Indian striped squirrel.

Subtribe Funisciurina, new form.

Funisciurus Trouessart, 1880.

Paraxerus Major, 1893. (Includes *Aethosciurus* Thomas, 1916; *Tamiscus* Thomas, 1918.)

Subtribe Myosciurina, new form.

Myosciurus Thomas, 1909. African pygmy squirrel.

Tribe Callosciurini Simpson, 1945, p. 79 (=Callosciurinae Pocock, 1923). Oriental squirrels.

Subtribe Callosciurina, new form.

Callosciurus Gray, 1867. (Includes *Tomentes* Thomas, 1915; *Tamioops* Allen, 1901.)

Sundasciurus Moore, 1958. (Includes *Aletesciurus* Moore, 1958.)

Glyphotes Thomas, 1898. Sculptor squirrel.

Nannosciurus Trouessart, 1880. Black-eared pygmy squirrel.

Dremomys Heude, 1898. (Includes *Zetis* Thomas, 1908.)

Lariscus Thomas and Wroughton, 1909 (= *Laria* Gray, 1867, nec Scopoli, 1763). (Includes *Paralariscus* Ellerman, 1947.) Malaysian striped ground squirrel.

Menetes Thomas, 1908. Siamese ground squirrel.

Rhinosciurus Gray, 1843. Ant-eating squirrel.

Subtribe Hyosciurina, new form.

Hyosciurus Archbold and Tate, 1935, p. 1. Pig squirrel.

Prosciurillus Ellerman, 1947. Celebesian tree squirrel.

Rubrisciurus Ellerman, in Laurie and Hill, 1954, p. 94. Celebesian giant squirrel.

Exilisciurus Moore, 1958. East Indian patternless pygmy squirrel.

Tribe Sciurini Burmeister, 1854, p. 145. Holarctic and Neotropical tree and pygmy squirrels, and *Reithrosciurus*.

Subtribe Sciurina, new form.

Reithrosciurus Gray, 1867. Bornean tassel-eared squirrel.

Sciurus Linnaeus, 1758. (Includes *Neosciurus* Trouessart, 1880; *Echinosciurus* Trouessart, 1880; *Hesperosciurus* Nelson, 1899; *Baiosciurus* Nelson, 1899; *Otosciurus* Nelson, 1899; *Tenes* Thomas, 1909, p. 468, footnote.) Holarctic tree squirrel.

Guerlinguetus Gray, 1821. (Includes *Hadrosociurus* Allen, 1915; *Urosociurus* Allen, 1915.)

- Subtribe Microsciurina, new form
Microsciurus Allen, 1895. (Includes *Lep-
 tosciurus* Allen, 1915; *Simosciurus*
 Allen, 1915.)
Syntheosciurus Bangs, 1902. (Includes
Mesosciurus Allen, 1915.)
- Subtribe Sciurillina, new form.
Sciurillus Thomas, 1914. Neotropical
 pygmy squirrel.
- Tribe Marmotini Simpson, 1945, p. 79
 (= Marmotinae Pocock, 1923). Hol-
 arctic ground squirrels.
- Subtribe Tamiina, new form. Chipmunks.
Tamias Illiger, 1811. Eastern Nearctic
 chipmunk.
Eutamias Trouessart, 1880. (Includes
Neotamias Howell, 1929.) Holarctic
 chipmunk.
- Subtribe Sperophilina, new form.
Spermophilus Cuvier, 1825. (Includes
Otospermophilus Brandt, 1844; *Ic-
 tidomys* Allen, 1877; *Xerospermophilus*
 Merriam, 1892; *Callospermophilus*
 Merriam, 1897; *Poliocitellus* Howell,
 1938.) Holarctic ground squirrel.
Ammospermophilus Merriam, 1892. An-
 telope ground squirrel.
Cynomys Rafinesque, 1817. Prairie dog.
- Subtribe Marmotina, new form.
Marmota Frisch, 1775 (= *Arctomys*
 Schreber, 1780). (Includes *Marmotops*
 Pocock, 1922.) Chuck.
- Tribe Tamiasciurini Simpson, 1945, p. 78
 (= Tamiasciurinae Pocock, 1923).
Tamiasciurus Trouessart, 1880. Nearctic
 red squirrel.
Sciurotamias Miller, 1901. (Includes
Rupestes Thomas, 1922.) Montane
 Chinese rock squirrel.
- Tribe Xerini Simpson, 1945, p. 79 (= Xerinae
 Osborn, 1910, p. 535).
Xerus Hemprich and Ehrenberg, 1832.
 (Includes *Geosciurus* Smith, 1834;
Euxerus Thomas, 1909.) Ethiopian
 ground squirrels.
Atlantoxerus Major, 1893. Barbary
 ground squirrel.
Spermophilopsis Blasius, 1884. Trans-
 caucasian ground squirrel.

KEY TO THE TRIBES AND SUBTRIBES OF THE SCIURINAE

As table 1 shows, some specimens are at variance with the key characters, such as the number of transbullar septa. When it becomes evident that a specimen does not fit the characters of the key, one must, of course,

assume that the specimen is at variance in at least one character and can, by trying the alternatives one by one, still key out the specimen. Certain terms used here are defined in the Introduction or are illustrated in figures 2, 3, 4, and 5.

1. Each auditory bulla has three transbullar septa 2
 Each auditory bulla has fewer than three septa 4
2. The squamosal bone extends up to the base of the postorbital process of the frontal, and the length of the lacrimomaxillary contact greatly exceeds that of the lacrimojugal on the dorsolateral surface of the skull tribe Xerini
 The squamosal does not extend up to the postorbital process, and the lacrimomaxillary contact is shorter than the lacrimojugal contact 3
3. The superior process of the jugal is high and sharply pointed.
 . . . subgenus *Tenes* of subtribe Sciurina
 The superior process of the jugal is low and very blunt tribe Tamiasciurini
4. There are no temporal foramina in the squamosoparietal suture (tribe Marmotini) 5
 One or more temporal foramina are present in the squamosoparietal suture 7
5. The frontoparietal suture ankyloses completely in adults, and the infraorbital foramen opens anterior to the maxillary plate, not through it 6
 The frontoparietal suture remains open in adults, and the infraorbital foramen opens fenestra-like through the maxillary plate subtribe Tamiina
6. The greatest width of the rostrum at the anterior ends of the masseteric fossae approximates the greatest width of both parietal bones subtribe Marmotina
 The greatest width of the rostrum at the ends of the masseteric fossae is notably less than the greatest width of both parietals subtribe Sperophilina
7. The squamosal bone extends up the cranium no more than about halfway from the base of the zygomatic process of the squamosal to the base of the postorbital process of the frontal (as in fig. 4)
 subtribe Sciurina of Sciurini
 The squamosal bone extends notably farther up the cranium than halfway between the bases of these two processes. 8
8. A greater area of the side of the rostrum is maxilla than premaxilla

- subtribe *Sciurillina* of *Sciurini*
 The maxilla provides less of the area of the
 side of the rostrum 9
 9. The auditory bulla has no transbullar septum
 10
 There are one or two septa per auditory bulla
 13
 10. The frontoparietal suture ankyloses com-
 pletely in adults, and the top of the infra-
 orbital foramen is in contact with the
 maxillopremaxillary suture.
 tribe *Ratufini*
 The frontoparietal suture remains open in
 adults, and the infraorbital foramen is not
 in contact with the maxillopremaxillary
 suture 11
 11. The supraorbital notches are trenchant and
 open, and the size is very large (occipito-
 nasal length 63 to 70 mm. in sample of 14)

 genus *Rubrisciurus* of subtribe *Hyosciurina*
 The supraorbital notches otherwise, and the
 size is smaller 12
 12. The suborbit extends no farther posterior than
 the postorbital process of the frontal, and
 a quarter of the length of the parietals is
 forward of the orbits.
 . . . other genera of subtribe *Hyosciurina*
 The suborbit extends posterior to the post-
 orbital process of the frontal, and less than
 a quarter of the length of the parietals lies
 forward of the orbits 13
 13. The supraorbital notch is obsolescent as a
 notch, being closed at the margin of the
 orbit so that it exists as a foramen piercing
 the frontal (and the masseteric fossa ex-
 tends forward on the rostrum to the
 premaxilla) tribe *Protoxerini*
 The supraorbital notch otherwise (or the
 masseteric fossa stops well posterior to the
 maxillopremaxillary suture) 14
 14. There is a dorso-anterior process on the pre-
 maxillary which rises to meet the nasal bone
 at the anterolateral angle of the latter . 17
 Such a process is lacking, or if only obsolescent
 as in some *Funisciurina*, is substantially
 posterior to the anterolateral angle of the
 nasal bone (tribe *Funambulini*) 15
 15. No postglenoid foramen pierces the squamo-
 sal, and there is no masseteric tubercle and
 no ectopterygoid ridge of the alisphenoid
 subtribe *Myosciurina*
 A foramen pierces the postglenoid area of the
 squamosal, and a masseteric tubercle and
 ectopterygoid ridge of the alisphenoid are
 present 16
 16. The masseteric fossa stops well short of the
 maxillopremaxillary suture, and rises no
 higher than the lower edge of the lacrimal
 bone subtribe *Funisciurina*
 The masseteric fossa reaches the premaxilla
 and rises above the level of the lower edge
 of the lacrimal bone.
 subtribe *Funambulina*
 17. In lateral aspect the lip of the infraorbital
 foramen is concave, and its horizontal lower
 limb is as long as the vertical upper; the
 masseteric tubercle protrudes laterodorsally
 as a minute process on the anterior ex-
 tremity of the lip of the infraorbital fora-
 men. . subtribe *Microsciurina* of *Sciurini*
 Lateral lip of infraorbital foramen, and mas-
 seteric tubercle, are otherwise.
 . . . subtribe *Callosciurina* of *Callosciurin*

SUMMARY

DISCOVERY OF A CHARACTER of the skull that appeared to sort some of the squirrels of the subfamily Sciurinae into the tribes into which they had previously been assignable only on the basis of genital characters resulted in a search for other skull characters for a testing of the existing sciurine classification. Three of the six subfamilies proposed by Pocock (1923) and scaled down to tribes by Simpson (1945), namely, the Xerini, the Tamiasciurini, and the Marmotini, are here shown to be distinguishable by skull characters. The tribes Sciurini and Callosciurini, which possess the most consistently distinctive characters of the baculum (os penis), are accepted as valid tribes on those characters alone. These last two are found to be constituted by three and two phyla, respectively, which are distinguished by characters of the skull and which are recognized as subtribes. The sixth tribe, the Funambulini, is shown by skull characters to consist of three distinct phyla. The tribe Funambulini as restricted is accepted, and two phyla are here raised to tribal rank, the Protoxerini and the Ratufini.

Eleven phyla, six of them tribes and five the subtribes of the Sciurini and the Callosciurini, are defined and diagnosed by means of skull characters in considerable detail. Their possible relationships are discussed on the basis of such definitions and diagnoses and other available information. A key to the tribes and subtribes based on characters of the skull is offered, and many genera are for the first time given an adequate diagnosis on characters of the skull. A classification of the Sciurinae is offered which integrates as close-

ly as possible the findings of the present study with what seems validated of earlier work. This consists of eight tribes, 11 subtribes, and 37 genera.

Because the problem of whether or not the pygmy squirrels constitute a monophyletic unit had never been adequately treated, the skull character evidence for and against such a concept is here marshalled, considered, and concluded to be strongly against. The pygmy squirrel likenesses apparently represent convergence. An enumeration and comparison of the taxonomic skull characters of the genera of Sciurinae reveal indications of great conservatism in genera occupying the typical tree squirrel niche, and perhaps a basic ground squirrel niche and a long-nosed squirrel niche, whereas genera occupying other sciurine niches appear to have had greater freedom to acquire skull character specializations. The South American genus *Sciurillus* is thought to be too highly differentiated to have originated in South America, because an isthmus made that continent available to squirrels in the late Pliocene. It is suggested that it evolved in a tropical southern extremity of North America before an isthmus arose.

CONCLUSION

The squirrel subfamily, Sciurinae, has proved to be amenable to classification by skull characters when concentrated study was devoted to bringing these to light, and the validity of the previously existing, much-questioned classification on characters of the baculum is strongly affirmed and considerably refined.

APPENDIX

THE SYNOPTIC SERIES of squirrel skulls against which the characters of each taxon were checked as described in the Introduction is identified here. As the present study is primarily of suprageneric categories, the selection was made to obtain a sample that might reveal all the generic skull characters in the Sciurinae. This list is not intended to serve as a criterion for the validity of specific names. The specific names used are current ones in Chasen (1940), Ellerman (1940), Ellerman and Morrison-Scott (1951), and Miller and Kellogg (1955). Whenever the present writer departs from their allocations as to genus or subgenus, however, the departure is intended.

It is probably necessary to repeat that each new character found for a taxon was checked through a greater series (often far greater) of that particular taxon, and that the synoptic series serves only for a comparison of such a taxon with the rest of the Sciurinae for such a character. In cases in which the sample of any taxon available to the writer was small, approximately how small it was may be seen in table 1. The full size of some large samples examined in various instances is, however, not indicated in table 1.

RATUFINI

Ratufa bicolor gigantea, A.M.N.H. No. 83440, Assam

PROTOXERINI

Protoxerus stangeri, A.M.N.H. Nos. 50707, 50747, 54447, 55759, 86749, middle Africa

Epixerus wilsoni, U.S.N.M. Nos. 220039, 220040, 220469, middle Africa

Heliosciurus gambianus, A.M.N.H. Nos. 50475, 50764, 55730, 81322, 83277, 86216, 86744, 86752, 88134, middle Africa

FUNAMBULINI

Funambulus tristriatus, A.M.N.H. No. 54652, India

Funambulus palmarum, A.M.N.H. No. 164048, India

Funambulus pennanti, A.M.N.H. No. 164050, India

Funambulus sublineatus, U.M.M.Z. No. 81078, India

Funisciurus lemniscatus, A.M.N.H. No. 54307, French Congo

Funisciurus pyrrhopus, A.M.N.H. No. 82531, Congo

Funisciurus carruthersi, A.M.N.H. No. 82580, Congo

Funisciurus anerythrus, A.M.N.H. No. 119610, eastern Congo

Paraxerus cepapi, A.M.N.H. No. 42048, southern Rhodesia

Paraxerus alexandri, A.M.N.H. No. 50642, Congo

Paraxerus cepapi, A.M.N.H. No. 55729, Kenya

Paraxerus palliatus, A.M.N.H. No. 81324, Nyasaland

Paraxerus Böhmi, A.M.N.H. No. 55731, Belgian Congo

Paraxerus vulcanorum, A.M.N.H. No. 55763, Belgian Congo

Paraxerus emini, A.M.N.H. No. 82542, Congo

Paraxerus antoniae, A.M.N.H. No. 86874, Belgian Congo

Myosciurus pumilio, U.S.N.M. Nos. 125429, 125430, 125431, 125432, Kamerun

CALLOSCIURINA

Callosciurus prevosti, A.M.N.H. No. 102709, south Sumatra

Callosciurus notatus, A.M.N.H. No. 103936, Borneo

Callosciurus nigrovittatus, A.M.N.H. No. 102506, south Sumatra

Callosciurus caniceps, A.M.N.H. No. 54692, lower Burma

Callosciurus sladeni, A.M.N.H. No. 113465, north Burma

Callosciurus quinquestriatus, A.M.N.H. No. 114928, north Burma

Callosciurus melanogaster, A.M.N.H. No. 103136, Mentawi Islands

Callosciurus erythraeus, A.M.N.H. No. 43228, Yunnan, China

Callosciurus erythraeus, A.M.N.H. No. 54794, Burma

Callosciurus pygerythrus, A.M.N.H. No. 163507, Burma

Callosciurus imitator, A.M.N.H. No. 87449, Laos

Callosciurus (Tamiops) swinhoei, A.M.N.H. No. 111396, Szechwan, China

Callosciurus (Tamiops) maclellandi, A.M.N.H. No. 113492, north Burma

Callosciurus (Tamiops) maritimus, A.M.N.H. No. 44717, Fukien, China

Callosciurus (Tamiops) rodolphei, A.M.N.H. No. 87468, Laos

Sundasciurus lowi, A.M.N.H. No. 106910, Borneo

Sundasciurus tenuis, A.M.N.H. No. 102538, Sumatra

- Sundasciurus brookei*, U.S.N.M. No. 198746, Borneo
Sundasciurus fraterculus, A.M.N.H. No. 103160, Mentawi Islands
Sundasciurus (Aletesciurus) hippurus, A.M.N.H. No. 103964, Borneo
Sundasciurus (Aletesciurus) juvencus, A.M.N.H. No. 175468, Palawan, Philippine Islands
Sundasciurus (Aletesciurus) steeri, C.N.H.M. No. 63119, Palawan, Philippine Islands
Sundasciurus (Aletesciurus) mollendorffi, C.N.H.M. No. 63105, Culion, Philippine Islands
Sundasciurus (Aletesciurus) mindanensis, C.N.H.M. No. 80348, Mindanao, Philippine Islands
Sundasciurus (Aletesciurus) philippinensis, C.N.H.M. No. 60835, Mindanao, Philippine Islands
Nannosciurus melanotis, A.M.N.H. No. 106637, southwest Sumatra
Glyphotes simus, U.S.N.M. No. 292611, Borneo
Lariscus insignis, A.M.N.H. No. 106415, Sumatra
Lariscus niobe, A.M.N.H. No. 106421, Sumatra
Lariscus obscurus, A.M.N.H. No. 103307, Mentawi Islands
Lariscus hosei, U.S.N.M. No. 301012, Borneo
Menetes berdmorei, A.M.N.H. No. 54793, Burma
Dremomys lokriah, A.M.N.H. No. 114936, north Burma
Dremomys pernyi, A.M.N.H. No. 43999, Yunnan, China
Dremomys rufigenis, A.M.N.H. No. 113221, north Burma
Rhinosciurus laticaudatus, U.S.N.M. No. 114414, Banjak Island, near Sumatra

HYOSCIURINA

- Hyosciurus heinrichi*, A.M.N.H. No. 101309, Celebes
Exilisciurus exilis, A.M.N.H. No. 103962, Borneo
Exilisciurus whiteheadi, U.S.N.M. No. 292640, Borneo
Exilisciurus concinnus, M.C.Z. No. 35233, Basilan, Philippine Islands
Exilisciurus surrutilis, C.N.H.M. No. 56155, Mindanao, Philippine Islands
Rubrisciurus rubriventer, A.M.N.H. No. 101322, Celebes
Prosciurillus leucomus, A.M.N.H. No. 101331, Celebes
Prosciurillus obscurus, A.M.N.H. No. 101354, Celebes
Prosciurillus murinus, A.M.N.H. No. 2776, Celebes

SCIURINA

- Sciurus vulgaris*, A.M.N.H. Nos. 36597, 92145, 97801, 87087, 56795, 45803, 18436, England, Sweden, Siberia, Mongolia, and China

- Sciurus carolinensis*, A.M.N.H. Nos. 2647, 2209, Minnesota and Florida
Sciurus aberti, A.M.N.H. No. 8615, Arizona
Sciurus griseus, A.M.N.H. No. 144816, Oregon
Sciurus arizonensis, A.M.N.H. No. 4492, Arizona
Sciurus apache, A.M.N.H. No. 21230, Mexico
Sciurus niger, A.M.N.H. Nos. 2508, 93215, 137339, Louisiana, Virginia, and Kansas
Sciurus alleni, A.M.N.H. No. 147988, Mexico
Sciurus aureogaster, A.M.N.H. No. 63805, Mexico
Sciurus nayaritensis, A.M.N.H. No. 1281, Mexico
Sciurus polioptus, A.M.N.H. No. 26082, Mexico
Sciurus oculatus, A.M.N.H. No. 10886, Mexico
Sciurus yucatanensis, A.M.N.H. No. 91184, Mexico
Sciurus sinaloensis, A.M.N.H. No. 23937, Mexico
Sciurus socialis, A.M.N.H. No. 2410, Mexico
Sciurus deppei, A.M.N.H. No. 70507, Guatemala
Sciurus griseoflavus, A.M.N.H. No. 70509, Guatemala
Sciurus variegatoides, A.M.N.H. No. 128971, Honduras
Sciurus (Tenes) anomalus, A.M.N.H. Nos. 178783, 178784, Transcaucasia, Soviet Union
Reithrosciurus macrotis, A.M.N.H. Nos. 103710, 103733, Borneo
Guerlinguetus cuscinus, A.M.N.H. No. 16560, Peru
Guerlinguetus gilvularis, A.M.N.H. No. 76949, Venezuela
Guerlinguetus ingrami, A.M.N.H. No. 36488, Brazil
Guerlinguetus ignitis, A.M.N.H. No. 36490, Bolivia
Guerlinguetus iquiriensis, A.M.N.H. No. 149145, Brazil
Guerlinguetus (Hadrosiurus) igniventris, A.M.N.H. No. 34375, Colombia
Guerlinguetus (Hadrosiurus) urucumus, A.M.N.H. No. 37074, Brazil
Guerlinguetus (Hadrosiurus) flammifer, A.M.N.H. No. 16943, Venezuela

MICROSCIURINA

- Microsciurus alfari*, A.M.N.H. No. 142391, Costa Rica
Microsciurus similis, A.M.N.H. No. 32499, Colombia
Microsciurus isthmus, A.M.N.H. No. 33182, Colombia
Microsciurus napi, A.M.N.H. No. 68150, Ecuador
Microsciurus mimulus, A.M.N.H. No. 34162, Colombia
Microsciurus (Leptosciurus) pucherani, A.M.N.H. No. 33700, Colombia
Microsciurus (Leptosciurus) salentensis, A.M.N.H. No. 34368, Colombia

- Microsciurus (Leptosciurus) medellinensis*, A.M.N.H. No. 42356, Colombia
Simosciurus stramineus, A.M.N.H. Nos. 34684, 34687, Ecuador
Syntheosciurus poasensis, A.M.N.H. No. 131723, Costa Rica
Syntheosciurus (Mesosciurus) griseogena, A.M.N.H. No. 31526, Venezuela
Syntheosciurus (Mesosciurus) saltuensis, A.M.N.H. No. 15233, Columbia
Syntheosciurus (Mesosciurus) chapmani, A.M.N.H. 36163, Venezuela
Syntheosciurus (Mesosciurus) valdiviae, A.M.N.H. 37673, Colombia
Syntheosciurus (Mesosciurus) meridensis, A.M.N.H. No. 21337, Venezuela
Syntheosciurus (Mesosciurus) quindianus, A.M.N.H. No. 62792, Colombia

SCIURILLINA

- Sciurillus pusilus*, A.M.N.H. Nos. 76185, 94749, 94751, 94756, 95724, Brazil and Peru

MARMOTINI

- Eutamias sibericus*, A.M.N.H. Nos. 45834, 45310, 33989, Mongolia, Korea, and China
Eutamias minimus, A.M.N.H. No. 20672, British Columbia, Canada
Eutamias townsendi, A.M.N.H. No. 1424, Washington
Eutamias amoenus, A.M.N.H. No. 33378, Oregon
Eutamias alpinus, A.M.N.H. No. 12582, California
Eutamias quadrivittatus, A.M.N.H. No. 120611, Idaho
Eutamias merriami, A.M.N.H. No. 4241, California
Tamias striatus, A.M.N.H. No. 77697, New Jersey
Spermophilus citellus, A.M.N.H. No. 33141, north China
Spermophilus undulatus, A.M.N.H. No. 45735, Mongolia
Spermophilus pygmaeus, A.M.N.H. No. 87089, Russia
Spermophilus major, A.M.N.H. No. 97802, Russia
Spermophilus columbianus, A.M.N.H. No. 124953, British Columbia
Spermophilus tridecemlineatus, A.M.N.H. No. 137350, Colorado
Spermophilus franklini, A.M.N.H. No. 3462, Minnesota

- Spermophilus beecheyi*, A.M.N.H. No. 122035, Nevada
Spermophilus annulatus, A.M.N.H. No. 2107, Mexico
Spermophilus lateralis, A.M.N.H. No. 131938, New Mexico
Spermophilus tereticaudus, A.M.N.H. No. 7296, Arizona
Ammospermophilus leucurus, A.M.N.H. No. 8281, California
Cynomys leucurus, A.M.N.H. No. 70454, Colorado
Cynomys ludovicianus, A.M.N.H. No. 41407, Montana
Cynomys gunnisoni, A.M.N.H. No. 131862, New Mexico
Cynomys parvidens, A.M.N.H. No. 140086, Utah
Marmota marmota, A.M.N.H. No. 146619, Germany
Marmota caudata, A.M.N.H. No. 54623, Kashmir, India
Marmota bobak, A.M.N.H. No. 45688, Mongolia
Marmota caligata, A.M.N.H. No. 127750, Northwest Territories, Canada
Marmota flaviventris, A.M.N.H. No. 7444, South Dakota
Marmota monax, A.M.N.H. No. 3514, Minnesota

TAMIASCIURINI

- Tamiasciurus hudsonicus*, A.M.N.H. Nos. 21882, 19856, 834, 166333, 11869, 140069, 1717, North Carolina, Ohio, Arizona, Utah, California, British Columbia, and Alaska
Sciurotamias davidianus, A.M.N.H. No. 45370, Shansi, China
Sciurotamias (Rupes) forresti, U.S.N.M. No. 255138, Szechwan, China

XERINI

- Xerus (Geosciurus) inaurus*, A.M.N.H. No. 81766, 42713, 83650, south Africa
Xerus (Geosciurus) princeps, A.M.N.H. No. 86479, Angola
Xerus (Euxerus) erythropus, A.M.N.H. Nos. 81060, 50816, 82751, 66195, Abyssinia, Congo, British East Africa, and Sierra Leone
Xerus rutilus, A.M.N.H. Nos. 54011, 13556, 81242, British Somaliland (2), Abyssinia
Atlantoxerus getulus, B.M. Nos. 98.7.4.39, 98.7.4.10, 2.1.7.5, 2.1.7.6, 22.5.30.16, 32.4.4.3, all Morocco
Spermophilopsis leptodactylus, A.M.N.H. Nos. 174336, 178788, 178789, near Caspian Sea

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