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Author: John A. White

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INTRODUCTION

The supraspecific categories of the chipmunks, as in most other groups of squirrels, have been a source of controversy for many years. Before presenting new evidence and a review of older evidence bearing on the problem, it seems desirable to review briefly in chronological order, the taxonomic history of the genera and subgenera of the chipmunks.

HISTORICAL

Linnaeus (1758:64) described the eastern North American chipmunks under the name *Sciurus striatus* and based his description on that of Catesby (1743:75). The Asiatic chipmunk was first described, under the name *Sciurus sibiricus*, by Laxmann (1769:69). Schreber (1785, 4:790) separated the Asiatic and North American chipmunks into the Asiatic and American varieties. Gmelin (1788:50) followed Schreber and, employing trinomials, used the names *Sciurus striatus asiaticus* and *S. s. americanus*. Illiger (1811:83) proposed *Tamias* as the generic name of the chipmunk of eastern North America. Say (1823:45) described *Sciurus quadrivittatus*, the first species of chipmunk known from western North America.

Trouessart (1880:86-87) proposed *Eutamias* as the subgeneric name to include the western North American and Asiatic chipmunks.

Merriam (1897:189-190) raised *Eutamias* to full generic rank. In so doing he neither listed nor described any characters but wrote that “it will be observed that the name *Eutamias*, proposed by Trouessart in 1880 as a subgenus of *Tamias* is here adopted as a full genus. This is because of the conviction that the superficial resemblance between the two groups is accidental parallelism, in no way indicative of affinity. In fact the two groups, if my notion of their relationship is correct,

had different ancestors, *Tamias* being an offshoot of the ground-squirrels of the subgenus *Ictidomys* of Allen, and *Eutamias* of the subgenus *Ammospermophilus*, Merriam."

Howell (1929:23) proposed *Neotamias* as the subgeneric name for the chipmunks of western North America, of the genus *Eutamias*.

Ellerman (1940, 1:426) gave *Eutamias* and *Neotamias* equal subgeneric rank with *Tamias* under the genus *Tamias*; on pages 427-428 he quoted Merriam, as I have done above, and later, after quoting the key to the genera and subgenera of chipmunks of Howell (1929:11), Ellerman wrote (*op. cit.*: 428-429), "This key convinces me that all these forms must be referred to one genus only. The characters given to separate '*Eutamias*' from *Tamias* are based only on the absence or presence of the functionless premolar, and on the colour pattern. If colour pattern is to be used as a generic character, it seems *Citellus suslicus* will require a new name when compared with *C. citellus*, etc." And again, "The Asiatic chipmunk is intermediate between typical *Tamias* and the small American forms in many characters." To substantiate this, Ellerman (*loc. cit.*) quotes Howell (*loc. cit.*), in comparing the subgenera *Eutamias* and *Neotamias*, as follows: "'the ears [of subgenus *Eutamias*] are broad, rounded, of medium height, much as in *Tamias*; postorbital broad at base, tapering to a point, much as in *Tamias*; interorbital constriction slight, as in *Tamias*; upper molariform tooth rows slightly convergent posteriorly, as in *Tamias*.'" Ellerman (*loc. cit.*) again quotes Howell (*loc. cit.*), "'*Eutamias* of Asia resembles *Tamias* of North America and differs from American *Eutamias* in a number of characters, notably the shape of the anteorbital foramen, the postorbital process, the breadth of the interorbital region, the development of the lambdoidal crest, and the shape of the external ears. On the other hand, American *Eutamias* agrees with the Asiatic members of the genus in the shape of the rostrum, the well-defined striations of the upper incisors, the presence of the extra peg-like premolar, and in the pattern of the dorsal stripes.'"

Bryant (1945:372) wrote, "I am convinced that Ellerman's interpretation of the relationships of the chipmunks is correct." After commenting that the presence or absence of P3, "is of significance only in distinguishing between species of squirrels," Bryant adds that "The other differences between the eastern and the western chipmunks do not appear to be of sufficient phylogenetic importance to warrant the retention of the two groups as genera."

Methods, Materials, and Acknowledgments

Characters previously mentioned in the literature as having taxonomic worth for supraspecific categories of chipmunks were checked by me on specimens old enough to have worn permanent premolars. Some structural features not previously used were found to have taxonomic significance. The baculum in each of the supraspecific categories of sciurids of North America was examined; the bacula were processed by the method described by White (1951:125) to obviate "variation" caused by shriveling of the smaller bacula or breaking of the more delicate parts of the larger bacula. Mallei and hyoid bones of the genera and subgenera of the chipmunks were mostly studied in the dry state. Part of the hyoid musculature in these same groups of chipmunks was dissected.

In all, I studied more than 1,000 skulls and skins of the subgenus *Neotamias*, approximately 50 skulls and skins of *Tamias striatus*, and 15 skulls and skins of the subgenus *Eutamias* (*Eutamias sibiricus asiaticus* from Manchuria). Numerous other specimens were examined but not in such detail.

I am grateful to Professor E. Raymond Hall for guidance in the study. For encouragement and advice I am grateful also to Doctors Robert W. Wilson, Cecil G. Lalicker, Edwin C. Galbreath, Keith R. Kelson, E. Lendell Cockrum, Olin L. Webb, and others at the Museum of Natural History, and in the Department of Zoology of the University of Kansas. My wife, Alice M. White, made the drawings and helped me in many other ways. For lending specimens I thank Dr. David H. Johnson of the United States National Museum, and Dr. George C. Rinker of the Department of Anatomy, University of Michigan.

Assistance with field work is acknowledged from the Kansas University Endowment Association, the National Science Foundation, and the United States Navy, Office of Naval Research, through contract No. NR161 791.

Evaluation of Characters

The following paragraphs treat the characters listed by Howell, Ellerman, and Bryant, and such additional characters as I have found useful in characterizing the genera and subgenera of chipmunks. Some of the findings, I think, illustrate how study of such mammalian structures as the baculum, malleus, and hyoid apparatus—structures that seem to be little influenced by the changing external environment—clarifies relationships, if these previously were estimated only from other parts of the anatomy of Recent specimens.

The structural features and characters to be discussed, or listed, below may be arranged in three categories as follows: 1) Characters in which the subgenera *Eutamias* and *Neotamias* agree but are different from the genus *Tamias*; 2) Characters in which the subgenus *Eutamias* and the

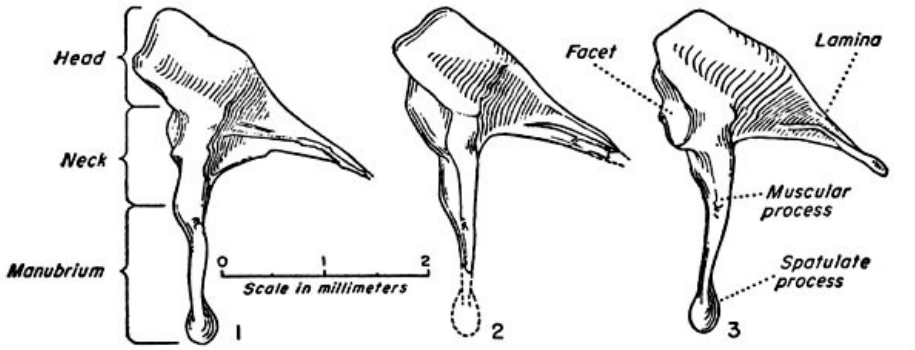
genus *Tamias* agree but are different from the subgenus *Neotamias*; 3) Structural features that are too weakly expressed to be of taxonomic use.

Characters in which the Subgenera Eutamias and Neotamias Agree, but Differ from the Genus Tamias

Structure of the Malleus.—The malleus in chipmunks is composed of a head and neck, a manubrium which has a spatulate process at the end opposite the head, and a muscular process situated about halfway between the spatulate process and the head of the malleus. An articular facet begins on the manubrium near the neck and spirals halfway around the head of the malleus. A lamina extends from the anterior edge of the head and neck, tapers to a point and joins the tympanic bulla anteriorly where there is a suture between the lamina and bulla. The lamina is one half as long as the rest of the malleus (see figs. 1-3).

The head of the malleus in *Tamias* is clearly more elongated than in *Eutamias*. The plane formed by the lamina in *Eutamias* makes an angle of approximately 90 degrees with the plane formed by the manubrium; in *Tamias* the two planes make an angle of approximately 60 degrees.

Examination of series of mallei of *Eutamias* and *Tamias* indicate that there is slight individual variation, slight variation with age, and no secondary sexual variation. Intraspecific variation in the subgenus *Neotamias* is slight, consisting of differences in size. Specimens of the subgenus *Eutamias* from Manchuria have mallei which are morphologically close to the mallei of the subgenus *Neotamias*.



Figs. 1-3. Dorsomedial views of left malleus.

Fig. 1. *Tamias striatus lysteri*, No. 11920 sex?; from Carroll Co., New Hampshire.

Fig. 2. *Eutamias sibiricus asiaticus*, No. 199637 male NM; from I-mien-po, N. Kirin, Manchuria.

Fig. 3. *Eutamias townsendii senex*, No. 165 male; from Lake Tahoe, California.

Structure of the Baculum.—In discussing the baculum in *Eutamias* and *Tamias*, it seems desirable to do so in the light of the structure of the baculum in other sciurids.

The bacula of North American sciurids are divisible into six distinct types represented by those of the genera *Spermophilus*, *Marmota*, *Sciurus*, *Tamiasciurus*, *Eutamias*, and *Glaucomys*.

The type of baculum in *Spermophilus* is spoonshaped with a ventral process that is spinelike or keellike. Also, spines usually are present along the margin of the "spoon." The base (proximal end) of the baculum is broad, and some species have a winglike process extending dorsally and partly covering a longitudinal groove. The shaft is more or less curved downward in the middle (see figs. 7, 10).

In *Marmota* the baculum is greatly enlarged at the posterior end and forms a shieldlike surface. The ventral surface of the base is flattened and the ventral surface of the shaft curves slightly ventrally then dorsally to the tip. The dorsal region of the base culminates in a point, from which there is a ridge that extends anteriorly and that tapers rapidly into the shaft near the tip. The tip, dorsally, has a slight depression surrounded by knobs, which are more or less well defined, and which resemble, topographically, the spines described for *Spermophilus* (see fig. 8).

In *Sciurus* the baculum is semispoonshaped and asymmetrical. There is a winglike process on one side and a spine, which projects lateroventrally, on the other side of the tip. The base of the baculum is broad but not so broad as in most species of *Spermophilus*. Extending posteriorly from the region of the tip, at which point a spine projects lateroventrally, there is a ridge, which is often partly ossified and that extends to a point near the base (see fig. 4).

In *Tamiasciurus* the baculum is absent or vestigial (Layne, 1952:457-459).

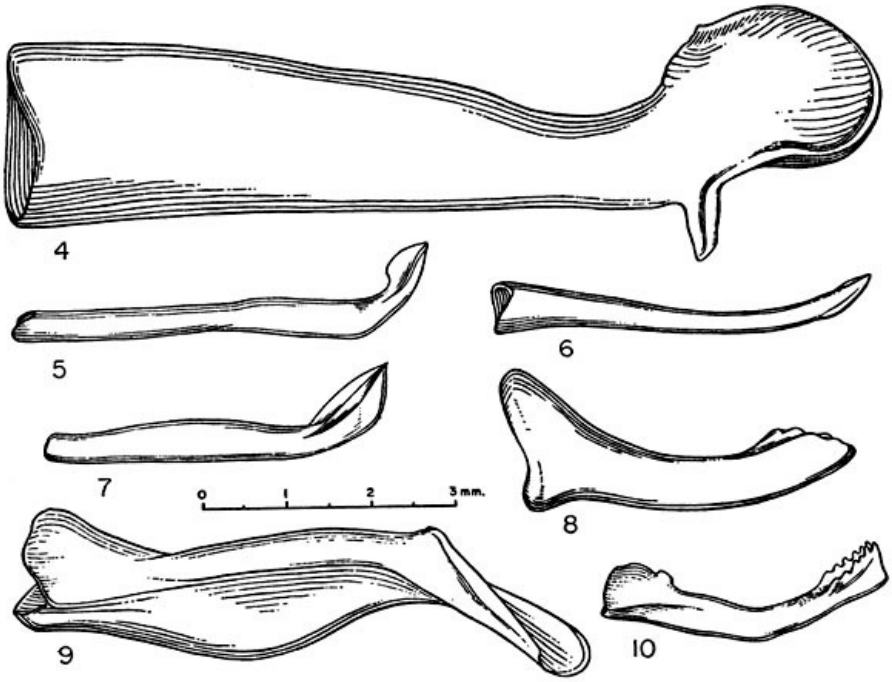
In *Eutamias* the baculum is broad at the base and the shaft tapers distally to the junction of the shaft and tip, or the base is only slightly wider than any part of the shaft. The tip often forms an

abrupt angle with the shaft and there is a keel on the dorsal surface of the tip (see figs. 5, 6).

The baculum in *Glaucomys* is the most distinctive of that of any American sciurid. According to Pocock (1923:243-244), "The baculum [of *G. volans*] is exceedingly long and slender, slightly sinuous in its proximal third, and inclined slightly upwards distally. The extreme apex is bifid, the lower process being rounded, the upper more pointed. On the left side there is a long crest running from the summit of the upper terminal process and ending abruptly behind the left side about one-third of the distance from the proximal end of the bone. It lies over a well-marked groove, and there is a second shallower groove on the right side of the bone." The baculum of *G. sabrinus* is markedly wider, more flattened and shorter than in *G. volans*. The crest, which is also present in *G. volans*, starts from the upper terminal process and extends to the base of the baculum on the left side. There is a knoblike process on the crest at a point three fourths the length of the baculum from its base. The distal one third of the baculum curves sharply but smoothly upwards (see fig. 9).

Keeping in mind that the baculum in the North American sciurids can be classified into six structural groups, as given above, the baculum in each of the subgenera *Eutamias* and *Neotamias* and in the genus *Tamias* is briefly described.

In the subgenus *Neotamias* the baculum resembles a leg and foot of man, with a narrow ridge (keel) in the center of the "instep" of the foot (Howell 1929:27). The tip (=foot) curves dorsally at the distal end (see figs. 5, 6).



Figs. 4-10. Lateral views of right side (except left-lateral view in fig. 9) of baculum.

Fig. 4. *Sciurus aureogaster aureogaster*, No. 37000; from 70 km. S C. Victoria (by highway), and 6 km. W of highway, Tamaulipas.

Fig. 5. *Eutamias quadrimaculatus*, No. 95780 BS; from Mountains near Quincy, Plumas Co., California.

Fig. 6. *Eutamias sibiricus asiaticus*, No. 199632 NM; from 120 mi. up the Yalu River, Korea.

Fig. 7. *Tamias striatus lysteri*, No. 193493 NM; from Locust Grove, New York.

Fig. 8. *Marmota flaviventer dacota*, No. 41641; from 1½ mi. E Buckhorn, 6,150 ft., Weston Co., Wyoming.

Fig. 9. *Glaucomys sabrinus bangsi*, No. 15079; from 10 mi. NE Pinedale, 8,000 ft., Sublette Co., Wyoming.

Fig. 10. *Spermophilus armatus*, No. 14888; from W end Half Moon Lake, 7,900 ft., Sublette Co., Wyoming.

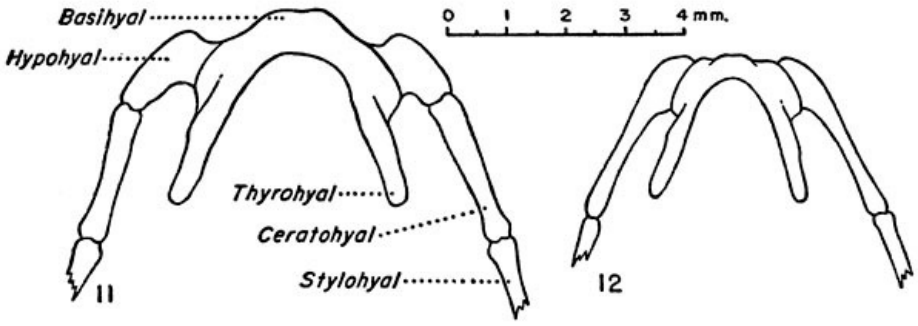
In the subgenus *Eutamias*, the baculum "tapers gradually from base to tip, the distal portion upturned in an even curve and slightly flattened ..." (*op. cit.*:26). Microscopic examination reveals that there is a faint keel on the dorsal surface of the tip.

Eutamias, like *Callosciurus*, *Menetes*, *Dremomys*, *Lariscus*, *Rhinosciurus*, and *Nannosciurus*, has a keel on the dorsal surface of the tip of the baculum (compare figures 5 and 6 with the

descriptions and figures in Pocock, 1923:217-225).

In *Tamias* the baculum is "a slender bone 4.5-5 millimeters in length, nearly straight, upturned at the tip and slightly expanded into the shape of a narrow spoon or scoop, with a slight median ridge on the under surface." (Howell *op. cit.*:13.) The "median ridge" is a keel on the ventral surface. In having a keel on the ventral surface of the tip, the baculum of *Tamias* is comparable to that of *Spermophilus*.

Examination of series of bacula of the subgenus *Neotamias* and the genus *Tamias* indicates, as in the case of the mallei, that there is slight individual variation and slight variation with age. In the subgenus *Neotamias* interspecific variation in the baculum is considerable, but the general plan of structure remains constant. From this study of variation of the baculum in American chipmunks, it can be extrapolated that the baculum in the Asiatic *Eutamias* would show little individual variation in structure. I have seen only two bacula of the Asiatic *Eutamias*.



Figs. 11-12. Ventral views of the hyoid apparatus in *Tamias* and *Eutamias*.

Fig. 11. *Tamias striatus venustus*, No. 11072 female; from Winslow, Washington Co., Arkansas.

Fig. 12. *Eutamias minimus operarius*, No. 5376 male; from 14 mi. N El Rito, Rio Arriba Co., New Mexico.

Structure of the Hyoid Apparatus.—The hyoid apparatus in the chipmunks is made up of an arched basihyal with a thyrohyal attached to each limb of this "arch." To each junction between the "arch" and the thyrohyals, a hypohyal is attached by ligaments to a flat articular surface. A ceratohyal then is attached posteriorly to the hypohyal and a stylohyal ligament is attached to each ceratohyal posteriorly. The stylohyal is loosely attached along its sides to the tympanic bulla and finally attached, at the posterior end, to the bulla at a point slightly ventral and posterior to the auditory meatus.

In the genus *Eutamias* the hypohyal and ceratohyal are completely fused in adults, the suture between these two bones being visible in juvenal specimens (see fig. 12).

In the genus *Tamias* the hypohyal and ceratohyal remain distinct throughout life. The hypohyal may frequently be divided into two parts, a variation which is also present in *Marmota*.

The musculature associated with the hyoid apparatus in *Eutamias* and *Tamias* is as described by Bryant (1945:310, 316) for the Nearctic squirrels. However, the conjoining tendon of the anterior and posterior pairs of digastric muscles is ribbonlike in *Eutamias* and rodlike (rounded in cross section) in *Tamias*.

The presence or absence of P3 and the projection of the anterior root of P4 in relation to the masseteric knob.—Only rarely is P3 absent in *Eutamias* or present in *Tamias*. P3 in specimens of old adult *Eutamias*, shows wear, thus suggesting that P3 is functional in older chipmunks. In *Eutamias*, which normally has a P3, the anterior root of P4 projects to the outside of the masseteric knob, whereas in *Tamias*, which normally lacks a P3, the anterior root of P4 projects directly to the masseteric knob or to the lingual side of this structure. The projection of the anterior root of P4 seems to be correlated with the presence or absence of P3. However, in a specimen of *Tamias striatus rufescens* (No. 11117 KU), the left P3 is present, yet the anterior root of P4 still projects to the lingual side of the masseteric knob.

Ellerman (1940:48) and Bryant (1945:368-369, 372) think that the presence or absence of P3 is not of generic significance in chipmunks, since P3 is vestigial and probably is in the process of being lost, and since this character is rarely used as a generic character in other sciurids. I think that the presence or absence of P3, together with the projection of the anterior root of P4 in relation to the masseteric knob, is of generic significance, for, squirrels in general have retained the dentition and dental formula of a primitive rodent, and any change in the pattern of the teeth or in dental formula is, in my opinion, of a fundamental nature.

Length of tail in relation to total length.—The tail in *Eutamias* is more than 40 per cent of the total length, whereas in *Tamias* the tail is less than 38 per cent of the total length. In this respect

Tamias resembles most ground squirrels of the genus *Spermophilus*.

Color pattern.—The chipmunks vary but little in color pattern, for, even in *Eutamias dorsalis*, which is one of the most aberrant of the chipmunks in color pattern, the pattern is characteristic of *Eutamias*.

The width of the longitudinal stripes is uniform in *Eutamias* whereas in *Tamias* the dorsal, longitudinal light stripes are more than twice as wide as the other stripes.

In *Eutamias*, only the two lateralmost dark stripes are short, whereas in *Tamias* all four of the lateral dark stripes are short; none extends to the rump or to the shoulder.

The dark median stripe is present in both *Eutamias* and *Tamias* as well as in other genera such as *Callosciurus* and *Menetes* (Ellerman 1940:390).

Characters in which the Subgenus Eutamias and the Genus Tamias Agree, but Differ from the Subgenus Neotamias

Shape of the infraorbital foramen.—In the subgenus *Eutamias* and in the genus *Tamias* the infraorbital foramen is rounded, whereas in most species of the subgenus *Neotamias* the foramen is slitlike. In *Eutamias townsendii*, however, the infraorbital foramen is rounded as much as in the subgenus *Eutamias* and in the genus *Tamias*.

Width of the postorbital process at base.—The postorbital process is broader at the base in the subgenus *Eutamias* and in the genus *Tamias* than in most species of the subgenus *Neotamias*. In *E. townsendii*, however, this process is relatively as broad as in the subgenus *Eutamias* and in the genus *Tamias*.

Position of the supraorbital notch in relation to the posterior notch of the zygomatic plate.—In the subgenus *Eutamias* and in the genus *Tamias* the supraorbital notch is distinctly anterior to the posterior notch of the zygomatic plate, whereas in the subgenus *Neotamias*, the supraorbital notch is only slightly anterior to the posterior notch of the zygomatic plate. This difference may be correlated with differences in size, since specimens of the subgenus *Eutamias* and the genus *Tamias* are larger than specimens of the subgenus *Neotamias*.

Degree of convergence of the upper tooth-rows.—The rows of upper cheek-teeth converge posteriorly in the subgenus *Eutamias* and in the genus *Tamias*, except that in some specimens of *E. sibiricus asiaticus* the rows of upper cheek-teeth are nearly parallel to each other. In most species of the subgenus *Neotamias* the rows of upper cheek-teeth are nearly parallel to each other, although in the specimens that I have seen of *E. townsendii*, the upper rows of cheek-teeth converge posteriorly.

Degree of constriction of the interorbital region.—The interorbital region is more constricted in most species of the subgenus *Neotamias* than in the subgenus *Eutamias* and the genus *Tamias*. In specimens of *E. t. townsendii* of the subgenus *Neotamias*, however, the degree of constriction of the interorbital region is approximately the same as in the subgenus *Eutamias* and the genus *Tamias*.

Shape of the pinna.—The pinna is narrower and more pointed in the subgenus *Neotamias* than in the subgenus *Eutamias* and the genus *Tamias*.

Structural Features that are too Weakly Expressed to be of Taxonomic Use

The following alleged characters have been mentioned in the literature. Since the degree of expression of these features is so slight, or since there is marked variation within one or more natural groups of chipmunks, no reliance is here placed on these features. They are as follows: (1) Degree of the posterior projection of the palate; (2) relative size of the auditory bullae; (3) position, in relation to P4, of the notch in the posterior edge of the zygomatic plate; (4) size of m3 in relation to m2; (5) degree of development of the mesoconid and ectolophid of the lower molars; (6) shape and length of the rostrum; (7) degree of distinctness of minute longitudinal grooves on the upper incisors.

A variation that does not readily fall in any one of the three categories mentioned above is the degree of development of the lambdoidal crest. The crest is least developed in the subgenus *Neotamias* and most developed in the genus *Tamias*. The larger the skull, the more the lambdoidal crest is developed; seemingly, therefore, the degree of development is an expression of size of the skull and may be determined by heterogonic growth.

Discussion

As shown in table 1, there are ten characters by means of which *Eutamias* and *Tamias* can be separated consistently. The subgenus *Eutamias* occurs on the Asiatic side and the subgenus *Neotamias* occurs on the North American side of Bering Strait, yet the two subgenera agree in the ten features referred to. Although the subgenus *Neotamias* and the genus *Tamias* occur together in parts of the United States and Canada, they differ in the ten features, indicating that the subgenera *Eutamias* and *Neotamias* are more closely related to each other than either is to *Tamias*.

Table 1.—Characters by Means of Which the Genera Eutamias and Tamias Can Be Distinguished

Character	*Eutamias*	*Tamias*
Shape of head of malleus.	not elongated.	elongated.
Angle formed by planes of lamina and manubrium of malleus.	approximately 90 degrees.	approximately 60 degrees.
Position of keel on tip of baculum.	dorsal.	ventral.
Relation of hypohyal and ceratohyal bones of hyoid apparatus.	fused in adults.	never fused.
Appearance in cross section of conjoining tendon of anterior and posterior digastric muscles.	flattened.	rounded.
Presence or absence of P3.	present.	absent.
Projection of anterior root of P4 in relation to masseteric knob.	buccal.	lingual.
Length of tail in relation to total length.	more than 40 per cent.	less than 38 per cent.
Width of longitudinal stripes.	subequal.	median pair of light stripes twice as wide as others.
Length of lateral longitudinal light stripes.	outermost pair short.	both pairs short.

It must be pointed out here that the subgenus *Neotamias* always differs from both the subgenus *Eutamias* and the genus *Tamias* in pointed *versus* rounded pinna of ear (see table 2) and in the supraorbital notch being slightly posterior to or even with, instead of distinctly anterior to, the posterior notch of the zygomatic plate. The relative position of these two notches, however, seems to be a matter of relative (heterogonic) growth. Further, the base of the postorbital process of the frontal usually is narrower (relative to the length of the process) in the subgenus *Neotamias* but there is a gradation in this feature in *Neotamias* culminating in the species *E. townsendii* in which the bases of the processes are relatively as broad as in the subgenus *Eutamias* and the genus *Tamias*. The same condition obtains in the shape of the infraorbital foramen which is subovate to rounded in the subgenus *Neotamias* and always rounded in the other chipmunks.

Table 2.—Characters by Means of Which the Subgenus Eutamias and the Genus Tamias May Be Distinguished from the Subgenus Neotamias

Character	subgenus *Neotamias*	subgenus *Eutamias*	genus *Tamias*
Shape of infraorbital foramen.	subovate to rounded.	always rounded.	always rounded.
Relative width of the postorbital process at base.	narrow to broad.	broad.	broad.
Position of supraorbital notch in relation to posterior notch of zygomatic plate.	even with or slightly posterior.	anterior.	anterior.
Convergence, posteriorly, of upper tooth-rows.	not always.	not always.	always.
Degree of constriction of interorbital region.	slight to marked.	marked.	marked.
Shape of pinna.	long and pointed.	broad and rounded.	broad and rounded.

These differences of *Neotamias* are so slight in comparison with the similarities (ten features mentioned above) that *Neotamias* here is accorded only subgeneric rank under the genus *Eutamias*, instead of generic rank.

Howell's (1929) arrangement of the genera and subgenera of chipmunks is judged to be correct as indicated by the following arrangement that I propose.

Genera and Subgenera

Genus **Eutamias** Trouessart

Eutamias Trouessart, E. L. Catal. Mamm. viv. et foss., Rodentia, in Bull. Soc. d'Etudes Sci. d'Angers, 10:86-87, 1880. Type *Sciurus striatus asiaticus* Gmelin.

Eutamias, Merriam, C. H., Proc. Biol. Soc. Washington, 11:189-190, July 1, 1897.

Eutamias, Howell, A. H., N. Amer. Fauna, 52:26, November 30, 1929.

Tamias, Ellerman, J. R., The families and genera of living rodents. British Mus. (Nat. Hist.), 1:426, June 8, 1940.

Tamias, Bryant, M. D., Amer. Midland Nat., 33:732, March 1945.

Diagnosis.—Skull lightly built, narrow; postorbital process light and weak; lacrimal not elongated; infraorbital foramen lacks canal, relatively larger than in most sciurids; P3 present; head of malleus not elongated; plane of manubrium of malleus 90 degrees to plane of lamina; hypohyal and ceratohyal bones of hyoid apparatus fused in adults; conjoining tendon between anterior and posterior sets of digastric muscles ribbonlike; keel on dorsal side of tip of baculum; tail more than 40 per cent of total length; five longitudinal dark stripes evenly spaced and subequal in width; two lateral dark stripes short.

Subgenus **Eutamias** Trouessart

Eutamias Trouessart, E. L. Catal. Mamm. viv. et foss., Rodentia, in Bull. Soc. d'Etudes Sci. d'Angers 10:86-87, 1880. Type *Sciurus striatus asiaticus* Gmelin.

Eutamias, Howell, A. H., N. Amer. Fauna, 52:26, November 30, 1929.

Eutamias, Ellerman, J. R., The families and genera of living rodents. British Mus. (Nat. Hist.), 1:426, June 8, 1940.

Eutamias, Bryant, M. D., Amer. Midland Nat. 33:732, March 1945.

Diagnosis.—Size large; lambdoidal crest moderately developed; supraorbital notches distinctly anterior to posterior notch of zygomatic plate; baculum with faint keel on dorsal surface of tip which curves upward; pelage coarse; ears broad, rounded, of medium height.

Geographic range.—Palearctic. West to Dvina and Kama rivers, Vologda, and Kazan, in European Russia. South to southern Ural Mountains, Altai Mountains; Kansu, Szechwan, Shensi, Shansi, and Chihli provinces of China; Manchuria and Korea. East to Hokkaido Island, Japan; Kunashiri Island, southern Kurile Islands; Sakhalin Island, and Yakutsk, Siberia. North nearly to Arctic Coast in Siberia and European Russia (Ellerman and Morrison-Scott 1951:503).

Subgenus **Neotamias** Howell

Neotamias Howell, A. H., N. Amer. Fauna, 52:26, November 30, 1929. Type, *Eutamias merriami* J. A. Allen [=*Tamias asiaticus merriami* J. A. Allen].

Neotamias, Ellerman, J. R., The families and genera of living rodents. British Mus. (Nat. Hist.), 1:426, June 8, 1940.

Neotamias, Bryant, M. D., Amer. Midland Nat., 33:372, March, 1945.

Diagnosis.—Size small to medium; lambdoidal crest barely discernible; supraorbital notches even with, or posterior to, posterior notch of zygomatic plate; baculum with distinct keel on dorsal surface of tip which curves upward; pelage silky; ears long and pointed.

Geographic range.—Western Nearctic. West to Pacific Coast. South to Lat. 20°30' in Baja California and to northwestern Durango and southeastern Coahuila, Mexico. East to eastern New Mexico, westernmost Oklahoma, eastern Colorado, Wyoming, northwestern Nebraska, western and northwestern South Dakota, western and northwestern North Dakota, northeastern Minnesota, northern Wisconsin and Upper Peninsula of Michigan, and eastern Ontario. North to southwestern shore of Hudson Bay, southern shore of Great Slave Lake and Yukon River, Yukon.

Genus **Tamias** Illiger

Tamias Illiger, J. K. W., Prodromus Syst. Mam. Avium, pp. 83, 1811. Type, *Sciurus striatus* Linnaeus.

Tamias, Howell, A. H., N. Amer. Fauna, 52:26, November 30, 1929.

Tamias, Ellerman, J. R., The families and genera of living rodents. British Mus. (Nat. Hist.), 1:426, June 8, 1940.

Tamias, Bryant, M. D., Amer. Midland Nat. 33:372, March, 1945.

Diagnosis.—Skull lightly built, narrow; postorbital process small and weak; lacrimal not elongated; infraorbital foramen lacks canal, relatively larger than in most sciurids; P3 absent; head of malleus elongated; plane of manubrium of malleus forms 60 degree angle with plane of lamina; hypohyal and ceratohyal bones of hyoid apparatus fused in adults; conjoining tendon of anterior and posterior digastric muscles rounded in cross section; keel on ventral surface of tip which curves upward in baculum; tail less than 38 per cent of total length; five longitudinal dark and four longitudinal light stripes present but two dorsal light stripes at least twice as broad as other stripes; four lateral dark stripes short.

Geographic range.—Eastern Nearctic. West to Turtle Mountains, North Dakota; eastern North Dakota, eastern South Dakota, Nebraska, Kansas, and Oklahoma. South to southern

Louisiana, Mississippi, Alabama, northwestern Georgia. East to Atlantic Coast from South Carolina to Nova Scotia. North to northeastern Quebec and southern tip of Hudson Bay.

Discussion

Chipmunks are small striped squirrels that inhabit the Holarctic Realm and that are found in similar niches in each of the three regions: Palearctic, western Nearctic, and eastern Nearctic. Ellerman (1940) and Bryant (1945) placed the chipmunks in three subgenera, corresponding to the regions mentioned above, under the one genus *Tamias*. Critical examination of new and old evidence reveals, nevertheless, that the subgenera *Eutamias* and *Neotamias* of the genus *Eutamias* are more closely related to one another than either is to the genus *Tamias*. This relationship can be seen clearly in the structure of the malleus, baculum, hyoid apparatus, hyoid musculature, the presence or absence of P3, the projection of the anterior root of P4 in relation to the masseteric knob, and in the color pattern.

Because the genera *Eutamias* and *Tamias* occupy similar ecological niches, the structural similarities that permit these animals to be called chipmunks, show convergence, and thus can be assumed to be adaptive. These similarities are in the molars, in shape of the skull, in color pattern and in other features which have been used by many systematists to interpret the phylogenetic relationships of the squirrels. Pocock (1923:211), however, reviewed the taxonomic literature on sciurids and wrote: “The conclusion very forcibly suggested by the literature of the subject is the untrustworthiness of such characters.” Pocock (*op. cit.*), correctly in my opinion, then established a supraspecific classification of the sciurids based almost exclusively on the structure of the baculum and glans penis. I have studied the baculum in chipmunks and in all the major supraspecific groups of Nearctic squirrels. The bacula of the Nearctic squirrels and those of the Palearctic and Indian squirrels, other than the chipmunks, are described and figured by Pocock (*op. cit.*).

The baculum in *Eutamias*, in general plan of structure, resembles the baculum in the genera *Callosciurus*, *Menetes*, *Rhinosciurus*, *Lariscus*, *Dremomys*, and *Nannosciurus*, of the tribe Callosciurini Simpson. The baculum in *Tamias*, in general plan of structure, resembles that in *Spermophilus* (=*Citellus*) and *Cynomys* of the tribe Marmotini Simpson. These tribes, designated by Simpson (1945:79), are based on the corresponding subfamilies defined by Pocock (1923:239-240) primarily on differences in the structure of the baculum. I assign *Tamias* to the tribe Marmotini. I assign *Eutamias* to the tribe Callosciurini, but do so only tentatively because I have not, at first hand, studied the bacula of most of the Callosciurini. The fossil record is too incomplete to reveal the time when the two tribes diverged. The subgenera *Eutamias* and *Neotamias* are closely related. Indications are that the divergence of the two subgenera occurred, geologically, but a short time ago, possibly in Pleistocene time.

Conclusions

1. *Eutamias* and *Tamias* are distinct genera of chipmunks.

2. The subgenera *Eutamias* and *Neotamias* are valid, for, *Eutamias sibiricus* differs from all the species of the subgenus *Neotamias* to a greater degree than these species differ from one another.

3. The genera *Eutamias* and *Tamias* probably evolved from two distinct lines of sciurids; one line (*Eutamias*) is represented by the tribe Callosciurini, and the other (*Tamias*) by the tribe Marmotini.

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