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Towards a uniform nomenclature for ground squirrels: the status of the Holarctic chipmunks

Abstract: The chipmunks are a Holarctic group of ground squirrels currently allocated to the genus *Tamias* within the tribe Marmotini (Rodentia: Sciuridae). Cranial, post-cranial, and genital morphology, cytogenetics, and genetics each separate them into three distinctive and monophyletic lineages now treated as subgenera. These groups are found in eastern North America, western North America, and Asia, respectively. However, available genetic data (mainly from mitochondrial cytochrome *b*) demonstrate that the chipmunk lineages diverged early in the evolution of the Marmotini, well before various widely accepted genera of marmotine ground squirrels. Comparisons of genetic distances also indicate that the chipmunk lineages are as or more distinctive from one another as are most ground squirrel genera. Chipmunk fossils were present in the late Oligocene of North America and shortly afterwards in Asia, prior to the main radiation of Holarctic ground squirrels. Because they are coordinate in morphological, genetic, and chronologic terms with ground squirrel genera, the three chipmunk lineages should be recognized as three distinct genera, namely, *Tamias* Illiger, 1811, *Eutamias* Trouessart, 1880, and *Neotamias* A. H. Howell, 1929. Each is unambiguously diagnosable on the basis of cranial, post-cranial, and external morphology.

Keywords: diagnosis; fossils; genetic distance; Holarctic; nomenclature; phylogenetics; Sciuridae.

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Introduction

The chipmunks represent a species-rich radiation of ground squirrels that range over much of northern Eurasia and North America. At present, 25 species are recognized in a single genus, *Tamias* (Thorington and Hoffmann 2005, IUCN 2014). As a group, chipmunks represent almost 9% of the 285 squirrel species recognized worldwide (Thorington et al. 2012). Their diurnal activity, conspicuousness, abundance, and distribution in areas accessible to scientists in Europe, Asia, and North America all suggest that chipmunks should be thoroughly studied and systematically well known. However, this is true neither concerning species limits nor their phylogenetic relationships.

Chipmunks are typically both conservative and variable in terms of cranial and external morphology (Merriam 1886, Allen 1890, Pocock 1923, Patterson 1983), delaying appreciation of their true species richness (Howell 1929, Hall and Kelson 1959). The number of recognized chipmunk species grew with the realization that contiguously allopatric taxa were often strikingly divergent in genital morphology (White 1953a, Callahan 1977, Sutton 1982, Patterson 1984). However, whereas preliminary studies at contact zones between chipmunk species indicated congruence between genital morphology, vocalizations, and pelage (Sutton and Nadler 1974, Patterson and Heaney 1987, Sutton 1987, Gannon and Lawlor 1989, Gannon and Stanley 1991), more sophisticated studies have documented complex cases of hybridization and introgression (Good and Sullivan 2001, Demboski and Sullivan 2003, Good et al. 2003, 2008, Hird and Sullivan 2009, Hird et al. 2010). Regional studies based on both nuclear and mitochondrial sequences have shown varying degrees of past introgression among an array of chipmunk species in western North America (Reid et al. 2012, Sullivan et al. 2014).

Assessing the lineages of chipmunks has been equally complicated. Currently, the 25 recognized species are allocated to three subgenera within the genus *Tamias*: *Tamias* Illiger, 1811 for the lone species in eastern North America; *Eutamias* Trouessart, 1880 for the one recognized Eurasian species (but see Obolenskaya et al. 2009); and *Neotamias* A. H. Howell, 1929 for 23 species from western

North America. However, for much of the last century, two genera of chipmunks were recognized (Howell 1929, 1938, Hall and Kelson 1959, Hall 1981): *Tamias* for chipmunks lacking P3 (among other characters) and *Eutamias* (including *Neotamias* as a subgenus) for forms retaining this tooth (but see Ellerman 1940 and Bryant 1945, who treated them as one). Allocating all chipmunks to a single genus became generally accepted following Nadler et al. (1977), Corbet (1978), and Ellis and Maxson (1979) and was codified by global checklists (Corbet and Hill 1980 and later editions, Honacki et al. 1982 and later editions). Although several analyses of mitochondrial and nuclear gene sequences have clarified the interspecific relationships of chipmunks (Piaggio and Spicer 2000, 2001, Reid et al. 2012) and made nomenclatural recommendations to separate them as distinct genera (Piaggio and Spicer 2001), little attention has focused on their higher-level relationships.

Collectively, chipmunks belong either in their own tribe Tamiini (Black 1963, McKenna and Bell 1997) or as the sister group to all other Holarctic ground squirrels and marmots within the tribe Marmotini (Thorington et al. 2012) of the squirrel subfamily Xerinae. The remarkable diversity of social systems among ground squirrels and marmots has invited phylogenetic analyses to document their historical relationships (e.g., Harrison et al. 2003), inadvertently uncovering paraphyly in some widely recognized groups (Herron et al. 2004). Recently, the ground squirrel genus *Spermophilus* was revised to eliminate its paraphyly with respect to both prairie dogs (*Cynomys*) and marmots (*Marmota*). Eight former subgenera of *Spermophilus* were thereby elevated to generic rank on the basis of diagnostic morphology, distinctive craniometrics, and reciprocal monophyly in molecular phylogenetic studies (Helgen et al. 2009). This revised taxonomy of ground squirrels and marmots has since been widely adopted (Thorington et al. 2012, Bradley et al. 2005, Ge et al. 2014, Roskov et al. 2014).

Recently, Ge et al. (2014) produced a timetree of Sciuridae suggesting that the earliest divergences among chipmunks are as old as or older than splits among the Holarctic ground squirrels. However, their analysis was calibrated at multiple nodes within the Xerinae, and the constraints on these nodes could have contributed to their result. Specifically, Ge and colleagues constrained the earliest divergence among Holarctic ground squirrels to be 16 Mya but imposed no constraints on the age of chipmunks. Systemic bias in molecular age estimates has been demonstrated in numerous studies (Ho and Jermiin 2004, Jansa et al. 2006, Norris et al. 2015). Deep branches may be underestimated relative to more recent branches (Ho and

Larson 2006), especially in situations where fast-evolving genes have become saturated (Hugall et al. 2007, Dornburg et al. 2014). If such systemic bias is present, it may affect both chipmunks and Holarctic ground squirrels equally, but the bias would be corrected only for the Holarctic ground squirrels, thanks to the presence of a calibrating fossil. A similar analysis without age constraints is needed to confirm whether the apparent age of chipmunk lineages results from their underlying genetics.

Assigning ranks to supraspecific groups is ultimately a subjective exercise, although some have argued that higher taxa are real natural entities (Humphreys and Barraclough 2014). Group names are referents for sets of taxa, and extended arguments have been made for adopting a rankless system (e.g., de Queiroz 2006). However, most biologists regard the taxonomic ranks as a nested system for information storage and retrieval (Mayr 1969, Hawksworth 2010). The value of any hierarchical system depends on coordinate rankings for coordinate entities, and this value is particularly great for sister taxa, where biological comparisons are most meaningful (Benton 2007). Relative to other squirrel genera, how different are the three chipmunk lineages currently regarded as subgenera? In particular, how do evolutionary differences among chipmunks compare to those among the ground squirrels that comprise their sister group? The taxonomic rank accorded to the chipmunk lineages should be comparable to the ranks separating other equivalent groups of Marmotini.

To address these questions, we compiled available evidence from morphology, paleontology, and genetics. We analyzed genetic sequence data generated in previously published studies across the Marmotini using both distance metrics and a Bayesian approach to estimate relative divergence times. We also compared these relative estimates to calibrated estimates of divergence times and to the fossil record itself.

Materials and methods

Genetic data were obtained from already-generated sequences deposited in GenBank (<http://www.ncbi.nlm.nih.gov/genbank/>). Cytochrome *b* (*Cytb*) is the only gene where sequence data are currently available for representatives of the three subgenera of chipmunks. Although sequences have been generated for exon 1 of the interphotoreceptor binding protein (*IRBP*) in sciurids (DeBry and Sagel 2001, Mercer and Roth 2003, Roth and Mercer 2008), they are available for only two of the chipmunk lineages (*Tamias* and *Eutamias*), are otherwise very limited in relevant taxon sampling, and present the additional problem

that different studies sequenced different regions of the gene. Due to these limitations, we restricted our analysis of *IRBP* to observing a handful of representative pairwise comparisons of related genera using exon 1 but analyzed the *Cytb* data in greater depth. The complete *Cytb* gene (1140 bp) was analyzed for 65 species of Marmotini and seven outgroup sciurids, whereas *IRBP* data (1093 bp) were analyzed for eight taxa. GenBank accession numbers are listed in Appendix 1.

Sequences were aligned using Clustal W (<http://www.clustal.org/clustal2/>) (Larkin et al. 2007) and modified by eye. Pairwise genetic distances (both uncorrected p and maximum likelihood) were calculated with PAUP* [version 4.0b8 (<http://paup.software.informer.com/download/>)], Swofford 2003], and statistics were calculated in R (R Development Core Team 2011). The appropriate model of evolution for *Cytb* (HKY+ Γ) and *IRBP* (TrN+ Γ) were determined using the AIC option in jModeltest (<http://www.jModeltest.org>) (Darriba et al. 2012).

Nodal support and relative divergences times were estimated using BEAST [version 1.8.1 (<http://beast.bio.ed.ac.uk>), Drummond et al. 2012]. Relative ages were estimated instead of absolute ages in order to ensure that the genetic data could be evaluated independently of fossil information. Because the best available fossils to calibrate this analysis are at or near the nodes of interest (see Ge et al. 2014), any molecular dating analysis that employs these fossils *a priori* may unduly reflect age estimates based on paleontology instead of genetics. Because our goal in this study was not to determine the best estimates of divergence times but instead to evaluate how levels of divergence compare across the Marmotini, we estimated *relative* ages based exclusively on genetic data. Trees derived solely from genetic data can then be calibrated *a posteriori* in order to obtain absolute age estimates without distorting their branching order (Conroy and van Tuinen 2003, Norris et al. 2015).

The BEAST analysis was performed with a single calibration at the chipmunk vs. ground squirrel+marmot split using a normal distribution where mean=1.0 and standard deviation=0.0001 in order to yield results that round to 1.0 within three decimal places. The uncorrelated lognormal relaxed molecular clock model was used, the mean substitution rate was not fixed, and the Yule speciation model applied. The program was run for 30,000,000 generations, sampled every 3000 generations with a burn-in of 1000. Runs were visualized using Tracer 1.6 (<http://www.mybioinformatics.com/tracer-1-5-analyse-results-bayesian-mcmc-programs-beast-mrbayes.html>) (Rambaut et al. 2014), and all effective sample sizes (ESS) were verified to be greater than 300.

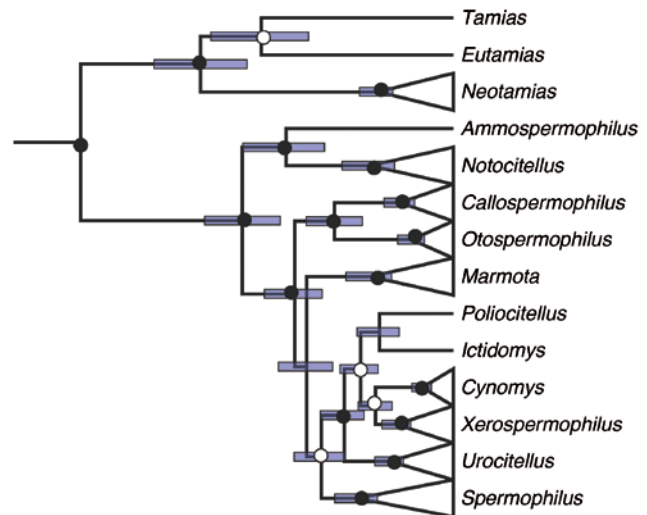


Figure 1: Maximum clade credibility tree from BEAST showing relative ages. Tree is scaled with respect to the origin of the tribe Marmotini (*sensu stricto*), which was fixed with an age of 1.0. Error bars represent 95% highest posterior density (HPD) ranges. Filled circles indicate posterior probability (PP)=1.0, whereas open circles indicate PP>0.95. Unlabeled nodes have PP<0.95. Outgroup taxa have been removed from image, and nodes have been collapsed below the level of genus for ease of visualization.

Results

The BEAST analysis recovered the chipmunks and Holarctic ground squirrels and marmots as a strongly supported monophyletic group (Figure 1). The Asian rock squirrels, *Sciurotamias*, were not recovered as part of this clade (Supporting Information 1). The focal clade contains two strongly supported subgroups, corresponding to the chipmunks on one hand and the Holarctic ground squirrels and marmots on the other (Figure 1). Results suggest that a *Neotamias* vs. *Tamias*+*Eutamias* split represents the next evolutionary divergence within Marmotini (median height=0.678; 95% highest posterior density [HPD]=0.554–0.803). In fact, the 95% HPD for chipmunks is earlier and non-overlapping with the nodes of the ground squirrels and marmots, excepting only the origin of that clade (median=0.566; 95% HPD=0.464–0.667) and its earliest divergence event, the *Ammospermophilus* vs. *Callospermophilus* split (median=0.449; 95% HPD=0.346–0.565).

The results also suggest that the younger *Tamias* vs. *Eutamias* node (median=0.515; 95% HPD=0.388–0.650) is also older than all but the oldest node within the ground squirrels and marmots. The 95% HPD for this chipmunk divergence overlaps several intergeneric divergences within the ground squirrel lineage, but it does not overlap with that of the *Poliocitellus*+*Ictidomys*+

Cynomys+Xerospermophilus clade (median=0.249; 95% HPD=0.201–0.304) or its subclades. There are no examples in the Marmotini where 95% HPD values for within-genus evolution overlap with the splits among the three chipmunk lineages. The earliest within-genus divergence recovered was within *Spermophilus* (median=0.256; 95% HPD=0.203–0.317).

The divergence of chipmunks vs. ground squirrels+marmots is documented in the fossil record by *Nototamias* and *Miospermophilus*, both present in the Gerin-gian (26.3–30.8 Mya; Late Oligocene) of Nebraska (Pratt and Morgan 1989, Korth 1992, Bailey 2004). If 26.3 Mya is applied as an *a posteriori* calibration, the earliest divergence between chipmunk lineages would be dated to 17.8 Mya (95% HPD=14.6–21.1 Mya), and the *Tamias* vs. *Eutamias* split would be dated to 13.5 Mya (95% HPD=10.2–17.1 Mya). In contrast, the earliest divergence in the ground squirrel+marmot clade would be dated to 14.9 Mya (95% HPD=12.2–17.5 Mya), the *Poliocitellus* vs. *Ictidomys* split (the most recent intergeneric node recovered) would be dated to 5.2 Mya (95% HPD=3.8–6.8 Mya), and the divergence of crown *Spermophilus* would be dated to 6.7 Mya (95% HPD=5.3–8.3 Mya).

Comparisons based on *Cytb* genetic distances exhibit a similar pattern. Pairwise genetic distances (both HKY+ Γ and uncorrected *p*) between chipmunk lineages were completely non-overlapping with pairwise distances

found among congeneric species (Figure 2). Within-genus HKY+ Γ distances ranged up to 0.1565 (0.1264 for uncorrected *p*), whereas pairwise distances between chipmunk lineages ranged from 0.2149 to 0.2749 (uncorrected *p*=0.1518 to 0.1785 – Table 1). These values fall at the upper end of pairwise distances between genera of ground squirrels and marmots (HKY+ Γ distance=0.0992–0.2845; uncorrected *p*=0.0900–0.1842). The results for the *IRBP* data (Table 1) yielded a distance for *Tamias* vs. *Eutamias* (TrN+ Γ =0.0226; uncorrected *p*=0.0211) somewhat smaller than the mean distance found between genera of ground squirrels and marmots (TrN+ Γ =0.0271; uncorrected *p*=0.0250) but well within the range observed for between-genera comparisons (TrN+ Γ =0.0114–0.0398; uncorrected *p*=0.0110–0.0357).

Discussion and conclusions

The BEAST analysis strongly supported the monophyly of the chipmunks and the Holarctic ground squirrels and marmots to the exclusion of all other squirrels tested (Supporting Information 1). Interestingly, our analysis excluded the Asian rock squirrels *Sciurotamias*, which are typically treated as members of the Marmotini (Thoring-ton et al. 2012). *Sciurotamias* was recovered well outside

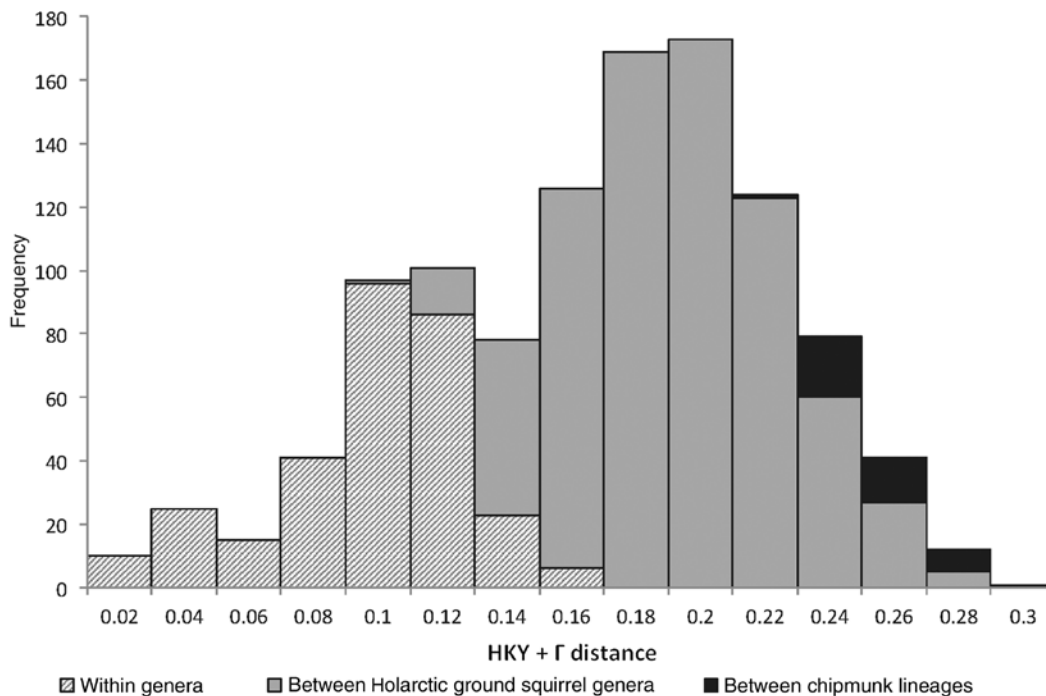


Figure 2: Histogram showing the distribution of pairwise genetic distances (HKY+ Γ) of *Cytb* among members of the tribe Marmotini. Distances among the three clades of chipmunks do not overlap intrageneric examples of any other taxon.

Table 1: Select pairwise comparisons between taxa.

Comparison	IRBP uncorrected p	IRBP TrN+Γ	Cytb uncorrected p	Cytb HKY+Γ
<i>Tamias</i> – <i>Eutamias</i>	0.0211	0.0226	0.1686	0.2459
<i>Ammospermophilus</i> – <i>Callospermophilus</i>	0.0238	0.0254	0.1649	0.2342
<i>Ictidomys</i> – <i>Marmota</i>	0.0238	0.0258	0.1387	0.1750
<i>Cynomys</i> – <i>Xerospermophilus</i>	0.0257	0.0283	0.1018	0.1165
<i>Tamias</i> – <i>Dremomys</i>	0.0732	0.09436	0.2002	0.3682
<i>Marmota</i> – <i>Dremomys</i>	0.0677	0.08523	0.2105	0.4009
Mean distance between Holarctic ground squirrel genera	0.0250 (0.0110–0.0357)	0.0271 (0.0114–0.0398)	0.1410 (0.0900–0.1842)	0.1826 (0.0992–0.2845)
Mean distance between chipmunk lineages	–	–	0.1638 (0.1518–0.1785)	0.2424 (0.2149–0.2749)
Mean distance within genera	–	–	0.0788 (0.0026–0.1264)	0.0874 (0.0025–0.1565)

Values are either uncorrected p distances or maximum likelihood distances. Ranges are shown in parentheses.

this clade, in a poorly supported grouping with tree squirrels and flying squirrels (Supplemental Figure 1), but we cannot reject the possibilities that *Sciurotamias* is sister to the Marmotini *sensu stricto* or belongs in a different part of the tree. Ge et al. (2014), for example, suggested an affinity between Asian *Sciurotamias* and African Proxerini. Additional taxonomic and genetic sampling will be needed to securely place *Sciurotamias*. In the following discussion, we use Marmotini *sensu stricto* to refer to the well-supported clade of chipmunks plus Holarctic ground squirrels and marmots and consider the placement of *Sciurotamias incertae sedis* (Table 2).

The *Cytb* analyses offer unambiguous evidence that the three chipmunk lineages are at least as distinct as any recognized genus of Holarctic ground squirrels and marmots. They appear to have diverged earlier than many of the intergeneric splits within their sister lineage (Figure 1). Our relative timetree is consistent with the analysis of Ge et al. (2014), based on *a priori* calibrations, so that neither appears to be an artifact of the methodology employed. Neither the estimated divergence dates nor *Cytb* genetic distances of chipmunk lineages overlap the within-genus diversification of the ground squirrels and marmots. Amounts of sequence divergence between the three chipmunk lineages are typical of the divergences between other genera of Marmotini (Figure 2). They actually exceed in magnitude those that distinguish many familiar squirrel groups, including *Cynomys*, *Marmota*, and the various lineages that were long united under *Spermophilus*.

The *IRBP* data were less conclusive (Table 1), in part for the methodological reasons cited earlier. The genetic distance between *Tamias* and *Eutamias* fell within the range of between-genus comparisons among ground squirrels and marmots but, unlike *Cytb*, were not higher

than most of these comparisons. *IRBP* sequences were unavailable for the *Neotamias* lineage, which was more divergent in terms of *Cytb*.

The absence of a good nuclear dataset is clearly a limitation to assessing genetic divergence among chipmunk lineages; this highlights the need for additional data collection. Saturation of fast-evolving mitochondrial genes is known to limit their effectiveness in recovering older divergence events (Simon et al. 1994). Nevertheless, the

Table 2: Revised classification of Marmotini (Sciuridae: Xerinae), based on Thorington et al. (2012), Ge et al. (2014), and this study, with known species richness estimates of included genera.

Tribe Marmotini Pocock, 1923 (16 genera, 97 species)
Chipmunks (3 genera, 25 species)
<i>Eutamias</i> Trouessart, 1880 (1) ^a
<i>Neotamias</i> A. H. Howell, 1929 (23)
<i>Tamias</i> Illiger, 1811 (1)
Holarctic ground squirrels and marmots (12 genera, 70 species)
<i>Ammospermophilus</i> Merriam, 1892 (5)
<i>Callospermophilus</i> Merriam, 1897 (3)
<i>Cynomys</i> Rafinesque, 1817 (5)
<i>Ictidomys</i> J. A. Allen, 1877 (3)
<i>Marmota</i> Blumenbach, 1779 (15)
<i>Notocitellus</i> A. H. Howell, 1938 (2)
<i>Otospermophilus</i> Brandt, 1844(3)
<i>Poliocitellus</i> A. H. Howell, 19938 (1)
<i>Spermophilus</i> F. Cuvier, 1825 (15)
<i>Uroditellus</i> Obolenskij, 1927 (12)
<i>Xerospermophilus</i> Merriam, 1892 (4)
? Asian rock squirrels (1 genus, 2 species) ^b
<i>Sciurotamias</i> Miller, 1901 (2)

^aSee Obolenskaya et al. (2009) for evidence that *Eutamias sibiricus* contains three distinctive populations that may take rank as species. ^bMay not belong to the Marmotini (see Discussion and Supplemental Information 1).

limitations of fast-evolving genes are expressed as lack of support for clades, not as the spurious appearance of well-supported nodes. *Cytb* has frequently been used in mammals to assess phylogenetic relationships above the family level (e.g., Agnarsson et al. 2011) and has been shown to be surprisingly effective at these deeper nodes (Tobe et al. 2010). As noted earlier, although saturation may introduce systemic bias in age estimates (Hugall et al. 2007, Dornburg et al. 2014), such bias should influence both the chipmunk and Holarctic ground squirrel clades equally as long as no calibrating fossils are incorporated *a priori*. At present, the best available dataset (*Cytb*) provides a compelling and unambiguous argument that the three chipmunk lineages exhibit genus-level genetic differentiation. Determining the implications of these genetic differences for chipmunk nomenclature requires an assessment of evolutionary and historical relationships.

In morphological terms, the chipmunk lineages are at least as distinctive from one another as are the various lineages of ground squirrels. In the last truly comprehensive revision of living forms, Howell (1938) treated *Tamias* and *Eutamias* as distinct genera, while retaining *Callospermophilus*, *Ictidomys*, *Notocitellus*, *Otospermophilus*, *Poliocitellus*, and *Xerospermophilus* all as subgenera of *Spermophilus*. White (1953b) even placed *Tamias* and *Eutamias*+*Neotamias* in separate tribes (Marmotini and Callosciurini, respectively). Although studies based on immunology, karyology, and electrophoresis offered inconclusive and sometimes conflicting evidence of chipmunk sister groups (Hight et al. 1974, Nadler et al. 1977, Levenson et al. 1985), DNA sequence analyses have reliably recovered the three groups of chipmunks as distinct and monophyletic (Piaggio and Spicer 2000, 2001, Herron et al. 2004, Reid et al. 2012). Different phylogenetic methods and datasets applied to chipmunk lineages tend to recover different sister pairs (Ellis and Maxson 1979, Levenson et al. 1985, Herron et al. 2004), indicating a quasi-trichotomy. The ectoparasite complements of fleas and sucking lice infesting the North American lineages *Tamias* and *Neotamias* are exclusive and non-overlapping, suggesting that neither has been derived from the other and both have been long separated (Jameson 1999).

Until recently, the only timetrees available for squirrels were either coarse and for the entire family (e.g., Mercer and Roth 2003) or else focused on other clades (Harrison et al. 2003, Roth and Mercer 2008). Using three internal calibration points on the subfamily Xerinae, Ge et al. (2014) reconstructed the earliest evolution of Marmotini as being in Asia but most of its diversification, including the divergence of chipmunks and ground squirrels (which they dated to 22.7–29 Mya), as taking place in North America. Fossil relatives

of both chipmunks (*Nototamias*) and ground squirrels (*Miospermophilus*) both appear in Nebraska deposits that date back to the Geringian (Late Oligocene, 26.3–30.8 Mya; Pratt and Morgan 1989, Korth 1992, Bailey 2004), but these taxa are well established from numerous localities by the Oligocene-Miocene boundary (~24 Mya). Chipmunk fossils are also known from this same time period in Asia (23.8–26 Mya; *Eutamias* indet., Qiu 1988; Meng et al. 2008) and from the Middle Miocene in Europe (11–18 Mya; *Tamias eviensis*, Doukas 2003, Koufos 2006).

In contrast, Ge et al. (2014) dated the initial radiation of crown-group ground squirrels to 14.76–17.93 Mya. Harrison et al. (2003) had earlier dated this same event to 10–14 Mya. In the timetree of Ge et al. (2014), no currently recognized crown for ground squirrel or marmot genera has a 95% CI that even overlaps with the most recent of the chipmunk divergences; all divergences among living ground squirrel lineages took place subsequently, mainly during the late Miocene. These dates are broadly consistent with the dates of more than 4600 fossil sciurids gleaned from NOW (Fortelius 2015) and the Paleobiology Database (paleobiodb.org) (compiled as Appendix 2 of Ge et al. 2014). Most extant genera of caviomorph and phiomorph rodents can also be traced to divergences that took place during the Miocene (Patterson and Upham 2014, Upham and Patterson In press). The Middle Miocene origin for chipmunk lineages that is suggested by both fossils and molecular dating falls comfortably within the range typically associated with genus-level divergence (Holt and Jönsson 2014).

Since Howell's revisions of chipmunks (1929) and ground squirrels (1938), no author has challenged the reciprocal monophyly of the three chipmunk lineages. Nor is it difficult to diagnose *Tamias*, *Neotamias*, and *Eutamias* in terms of cranial, post-cranial, and external morphology, genital bones, cytogenetics, or DNA sequences. Failure to recognize these groups as distinct genera has stemmed from their unquestioned membership in a single lineage and the mosaic of pleisiomorphic and apomorphic characters that have been used to define them. Unquantified impressions that the chipmunks are more similar to one another than are the ground squirrels can now be quantitatively refuted by genetic comparisons. Within-group genetic variation (particularly within species-rich *Neotamias*) certainly does not dwarf between-group distances (Figures 1 and 2). The three chipmunk groups stand readily as valid genera, and continued use of antiquated nomenclature clouds the systematic relationships of nearly 9% of the world's squirrel species. A revised classification of the Marmotini is presented in Table 2.

Because the literature containing diagnostic characters of chipmunks (Howell 1929, 1938, White 1953b) is

now dated and widely scattered, revised diagnoses of the genera are here collected and appended. The section “Included species” contains the proper scientific name and authorship of each of the 25 currently recognized species. The distinction and integrity of these lineages is such that these three genera have no additional synonyms other than *Sciurus*, used in the 18th century; in the course of history, all chipmunk species have been recognized under *Tamias* and all but *Tamias striatus* have been recognized under *Eutamias*. Only the western North American forms have been called *Neotamias* (e.g., Piaggio and Spicer 2001).

***Tamias* Illiger, 1811**

Diagnosis Median dark dorsal stripe narrow and flanked by two paler stripes more than twice its width; all four of the dark stripes short, none extending onto the rump or shoulder; ears broad, rounded at the tips; tail <40% total length; antorbital foramen rounded (suborbicular); posterior border of the zygomatic notch reaches level of P4–M1; postorbital process long and broad basally; well-developed lambdoidal crest; palate long, extending well beyond the plane of the last molars; auditory bullae relatively small; upper incisors with weak or no longitudinal striations; a single upper premolar (P4), whose anterior root projects buccal to the masseteric knob; upper molar series slightly convergent posteriorly; head of the malleus elongate, the planes formed by the lamina and manubrium ca. 60°; hypohyal and ceratohyal elements of hyoid apparatus separate in adults; conjoining tendon between anterior and posterior sets of digastric muscles rounded in cross-section; baculum nearly straight, upturned at tip, with slight median ridge on ventral surface. Karyotype 2N=38; Giemsa-stained chromosomes show at least nine structural rearrangements from the pattern shown by *Neotamias* (Nadler et al. 1977).

Type species *Sciurus striatus* Linnaeus, 1758.

Included species *Tamias striatus* (Linnaeus, 1758) – Eastern chipmunk.

***Eutamias* Trouessart, 1880**

Diagnosis Dorsal stripes all subequally spaced; lateral pair of dark stripes shorter than median trio, which reach onto shoulder and rump; antorbital foramen suborbicular; ears broad, rounded at the tips; tail 40–50% total length; posterior border of the zygomatic notch extends only

to level of P4; postorbital process broad basally; well-developed lambdoidal crest; palate short, extending to or just behind the plane of the last molars; auditory bullae relatively large; upper incisors with numerous distinct longitudinal striations; normally two upper premolars, the anterior root of P4 projects lingual to the masseteric knob; upper molar series slightly convergent posteriorly; head of the malleus not elongated, the planes formed by the lamina and manubrium ca. 90°; hypohyal and ceratohyal elements of hyoid apparatus completely fused in adults; conjoining tendon between anterior and posterior sets of digastric muscles ribbonlike; baculum gradually tapering from base to tip, evenly curved at tip, with a microscopic ridge on the dorsal surface. Karyotype 2N=38, with two to three autosomal and one Y chromosome rearrangement separating it from either of the North American lineages (Nadler et al. 1977).

Type species *Sciurus striatus asiaticus* Gmelin, 1788.

Included species *Eutamias sibiricus* (Laxmann, 1769) – Siberian chipmunk.

Comment

Recent studies of call notes (Pisanu et al. 2013) indicate regional heterogeneity of Eurasian chipmunks, and morphology and *Cytb* sequences indicate three distinctive geographic populations in Eastern Asia (Obolenskaya et al. 2009). Sequence divergence between these forms (>10% in *Cytb* sequences) is sufficiently great that they may represent distinct species (Lee et al. 2008), but studies focused on contact zones are needed to establish the rank of these taxa.

***Neotamias* A. H. Howell, 1929**

Diagnosis Dorsal stripes all subequal in width; lateral pair of dark stripes shorter than medial trio; ears narrower, more pointed at the tips; tail 40–50% total length; antorbital foramen slitlike (narrowly oval); posterior border of the zygomatic notch extends only to level of P4; postorbital process gracile at base; lambdoidal crest barely discernable; palate short, extending to or just behind the plane of the last molars; auditory bullae relatively large; upper incisors with numerous distinct longitudinal striations; two upper premolars; the anterior root of P4 projects lingual to the masseteric knob; upper molar series approximately parallel; head of the malleus

not elongated, the planes formed by the lamina and manubrium ca. 90°; hypohyal and ceratohyal elements of hyoid apparatus completely fused in adults; conjoining tendon between anterior and posterior sets of digastric muscles ribbonlike; baculum highly variable but abruptly angled at tip with a prominent dorsal ridge (“keel”). Karyotype 2N=38, “A” and “B” karyotypes, differing from each other by a single pericentric inversion of the smallest autosome (Nadler et al. 1977).

Type species *Tamias asiaticus merriami* J. A. Allen, 1889.

Included species *Neotamias alpinus* (Merriam, 1893) – Alpine chipmunk; *Neotamias amoenus* (J. A. Allen, 1890) – Yellow-pine chipmunk; *Neotamias bulleri* (J. A. Allen, 1889) – Buller’s chipmunk; *Neotamias canipes* (Bailey, 1902) – Gray-footed chipmunk; *Neotamias cinereicollis* (J. A. Allen, 1890) – Gray-collared chipmunk; *Neotamias dorsalis* (Baird, 1855) – Cliff chipmunk; *Neotamias durangae* (J. A. Allen, 1903) – Durango chipmunk; *Neotamias merriami* (J. A. Allen, 1889) – Merriam’s chipmunk; *Neotamias minimus* (Bachman, 1839) – Least chipmunk; *Neotamias obscurus* (J. A. Allen, 1890) – California chipmunk; *Neotamias ochrogenys* (Merriam, 1897) – Yellow-cheeked chipmunk;

Neotamias palmeri (Merriam, 1897) – Palmer’s chipmunk; *Neotamias panamintinus* (Merriam, 1893) – Panamint chipmunk; *Neotamias quadrimaculatus* (Gray, 1867) – Long-eared chipmunk; *Neotamias quadrivittatus* (Say, 1822) – Colorado chipmunk; *Neotamias ruficaudus* (A. H. Howell, 1920) – Red-tailed chipmunk; *Neotamias rufus* (Hoffmeister and Ellis, 1979) – Hopi chipmunk; *Neotamias senex* (J. A. Allen, 1890) – Shadow chipmunk; *Neotamias siskiyou* (A. H. Howell, 1922) – Siskiyou chipmunk; *Neotamias sonomae* (Grinnell, 1915) – Sonoma chipmunk; *Neotamias speciosus* (Merriam, 1890) – Lodgepole chipmunk; *Neotamias townsendii* (Bachman, 1839) – Townsend’s chipmunk; *Neotamias umbrinus* (J. A. Allen, 1890) – Uinta chipmunk.

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Appendix

Appendix 1: GenBank accession numbers for taxa used in this study.

Cytb: *Ammospermophilus harrisi* AF157926*; *Callosciurus prevostii* AB499914; *Callospermophilus lateralis* AF157950*; *Callospermophilus madrensis* AF157946; *Callospermophilus saturatus* AF157917; *Cynomys gunnisoni* AF157930*; *Cynomys ludovicianus* JQ885590; *Cynomys mexicanus* DQ106852; *Cynomys parvidens* AF157929; *Dremomys pernyi* HQ698363*; *Eutamias sibiricus* KF990333*; *Glaucomys volans* AF157921; *Ictidomys mexicanus* AF157852*; *Marmota broweri* JN024621*; *Marmota caligata* FJ438940; *Marmota olympus* JF313271; *Neotamias alpinus* KJ452914; *Neotamias amoenus* AY121090; *Neotamias canipes* KJ139459; *Neotamias cinereicollis* KJ139547; *Neotamias dorsalis* KJ139583; *Neotamias durangae* JN042437; *Neotamias merriami* JN042549; *Neotamias minimus* KJ453081; *Neotamias obscurus* JN042551; *Neotamias panamintinus* KJ453106; *Neotamias quadrimaculatus* JN042497; *Neotamias quadrivittatus* KJ139530; *Neotamias ruficaudus* JN042448; *Neotamias rufus* KJ139468; *Neotamias senex* JN042532; *Neotamias siskiyou* JN042509; *Neotamias sonomae* JN042530; *Neotamias speciosus* JN042483; *Neotamias townsendii* JN042504; *Neotamias umbrinus* KJ139640; *Notocitellus adocetus* AF157843; *Notocitellus annulatus* AF157849; *Otospermophilus atricapillus* JF925312; *Otospermophilus beecheyi* AF157918; *Otospermophilus variegatus* AF157878; *Poliocitellus franklinii* AF157894; *Ratufa bicolor* NC023780; *Sciurotamias davidianus* KC005710; *Sciurus carolinensis* FJ200744; *Spermophilopsis leptodactylus* AF157865; *Spermophilus alashanicus* AF157868; *Spermophilus citellus* KC971254; *Spermophilus dauricus* AF157871; *Spermophilus fulvus* AF157913; *Spermophilus major* AF157903; *Spermophilus pallidicauda* AF157866; *Spermophilus pygmaeus* AF157910; *Spermophilus relictus* AF157867; *Spermophilus suslicus* AF157897; *Spermophilus xanthoprymnus* AF157909; *Tamias striatus* JN042555*; *Uroditellus armatus* AF157901; *Uroditellus beldingi* AF157881; *Uroditellus brunneus* AF157952; *Uroditellus columbianus* AF157882; *Uroditellus elegans* AF157891; *Uroditellus parryi* AF157931; *Uroditellus richardsoni* AF157914; *Uroditellus townsendi* AF157938; *Uroditellus undulatus* AF157912; *Uroditellus washingtoni* AF157936; *Xerospermophilus mohavensis* AF157928*; *Xerospermophilus perotensis* AF157840; *Xerospermophilus spilosoma* DQ106854; *Xerospermophilus tereticaudus* AF157941; *Xerus rutilus* AY452690.

IRBP: *Ammospermophilus harrisi* AY227583; *Callospermophilus lateralis* AY227586; *Cynomys leucurus* AY227584; *Dremomys pernyi* HQ698525; *Eutamias sibiricus* AB253981; *Ictidomys tridecemlineatus* AF297278; *Marmota monax* AJ427237; *Tamias striatus* JN414824; *Xerospermophilus mohavensis* JX065593.

Cytb sequences used as representative examples in Table 1 are marked with an asterisk.

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