A BRIEF HISTORY OF THE NEW WORLD FLYING SQUIRRELS: PHYLOGENY, BIOGEOGRAPHY, AND CONSERVATION GENETICS

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I summarize our current understanding of the evolutionary origin and biogeographic history of the New World flying squirrels (*Glaucomys*). The emerging synthesis of flying squirrel systematics supports a monophyletic origin for the group in the early Miocene followed by a divergence of New World and Eurasian flying squirrels in the late Miocene. Today, the New World flying squirrels consist of 2 recognized species, *G. sabrinus* and *G. volans*. These 2 species are closely associated with the northern coniferous and deciduous hardwood forest biomes of North America, respectively, making them especially useful as biogeographic indicator species for these 2 forest types. Molecular systematic studies have revealed the presence of 2 distinct evolutionary lineages within *G. sabrinus* (a widespread Continental lineage and a more geographically restricted Pacific Coastal lineage). Bacular morphology and data from nuclear loci suggest recent or ongoing gene flow between these 2 lineages where they meet in the Pacific Northwest of North America. Populations of *G. volans* from eastern North America represent a 3rd distinct lineage within the genus. Mesoamerican flying squirrels (traditionally considered to be southern forms of *G. volans*) have not been examined with molecular data and may represent 1 or more additional lineages. From a biogeographic perspective, Quaternary climatic fluctuations and associated changes in the location and extent of forest habitats appear to have been important factors in promoting early evolutionary diversification within the genus; structuring of intraspecific patterns of genetic variation; and producing geographically isolated peripheral populations in high-elevation habitats at the southern extremes of each species' range, several of which are now of conservation concern. These results have broad implications for understanding the Quaternary biogeography of the coniferous and deciduous forest biomes of North America.

Key words: biogeography, boreal forest, comparative phylogeography, flying squirrel, *Glaucomys sabrinus*, *Glaucomys volans*, phylogeography, Pleistocene, Pteromyini

Flying squirrels are a diverse group of nocturnal, arboreal rodents that are highly adapted for gliding locomotion. They range in size from the 24-g pygmy flying squirrels (*Petaurillus*) to the 1.5-kg giant flying squirrels (*Petaurista*—Thorington and Heaney 1981). All flying squirrels are characterized by the presence of a membrane of skin between their wrists and ankles (a patagium) that they extend when gliding. There are 2 basic types of tail morphology (Thorington et al. 2002). In the smaller species (those less than approximately 1 kg), the lateral hairs of the tail are much longer than the dorsal and ventral hairs, resulting in a flattened, featherlike tail; in the larger species (those greater than approximately 1 kg), the tail is round in cross section. The larger species also have a uropatagium extending between their ankles and the base of the tail. This feature is lacking or greatly reduced in the smaller species.

Currently, 15 genera and 44 species of flying squirrels are recognized, with the majority (14 of the 15 genera and 42 of the 44 species) occurring in Eurasia, especially Southeast Asia (Thorington and Hoffmann 2005). The only genus to occur outside of Eurasia is *Glaucomys*; this genus is restricted to North America and Mesoamerica (Mexico plus Central America) and comprises 2 species, the northern flying squirrel (*G. sabrinus*) and the southern flying squirrel (*G. volans*).

In this paper, I summarize our current understanding of the evolution, biogeography, and conservation genetics of the New World flying squirrels. I begin with an overview of the phylogeny and taxonomy of flying squirrels in general, briefly synthesizing existing morphological and molecular studies of the group. I then focus on *Glaucomys* in particular, highlighting recent phylogeographic and conservation genetics research on the genus. In keeping with the spirit of this symposium, I have

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focused primarily on the northern flying squirrel. The close association of this species with the northern coniferous forests of North America makes it especially useful as a biogeographic indicator species. Indeed, insights gained from studies of *G. sabrinus* have been instrumental in shaping our current understanding of the Pleistocene biogeography of the boreal forest biome of North America in general. To a lesser degree, I also focus on the southern flying squirrel. Because this species is closely associated with the deciduous hardwood forests of eastern North America and the highlands of Mesoamerica, it serves as a biogeographic indicator species for this forest type, much in the same way as *G. sabrinus* does for the northern coniferous forest. Examining both species together therefore provides a broad perspective on the Quaternary biogeography of 2 of North America's most extensive forest types. In the end, I highlight what I view as important, and as yet unanswered, questions regarding the evolutionary history and biogeography of the New World flying squirrels.

## PHYLOGENY AND TAXONOMY OF LIVING FLYING SQUIRRELS

Flying squirrels traditionally have been considered a subfamily (Pteromyinae) within the family Sciuridae, which also contains tree and ground squirrels (subfamily Sciurinae; see Thorington et al. [2002] for a detailed review of the taxonomic history of flying squirrels). However, the phylogenetic position and taxonomy of flying squirrels has been the subject of considerable debate. One major issue has been whether flying squirrels arose from an ancestral lineage of tree squirrels or from an independent lineage of Eocene pyramyid rodents (de Bruijn and Ünay 1989; Mein 1970). A 2nd issue has been whether flying squirrels are monophyletic or if gliding may have arisen multiple times in the group (see Black 1963, 1972; Ellerman 1940; Hight et al. 1974; Major 1893; Thomas 1908; Thorington 1984). There also has been disagreement among researchers on the phylogenetic relationships among the 15 extant genera of flying squirrels and how these genera are related to fossil forms (McKenna 1962; Mein 1970; Thorington and Darrow 2000; Thorington et al. 1996). The relationship among living and fossil forms, as well as the 1st appearance of flying squirrels in the fossil record, is complicated by the fact that dental features once considered diagnostic of fossil flying squirrels (e.g., those described by James [1963]) have been documented in tree and ground squirrels as well (Thorington et al. 2005).

Thorington et al. (2002) examined intergeneric relationships among flying squirrels by conducting a cladistic analysis of 75 dental and postcranial morphological characters. They also used a constrained-tree approach to compare their results to 3 published hypotheses of flying squirrel relationships—those of McKenna (1962), Mein (1970) and Thorington and Darrow (2000). McKenna (1962) and Mein (1970) used dental characters to formulate their hypotheses, whereas Thorington and Darrow (2000) relied primarily on postcranial anatomy. The 3 hypotheses in question vary in several respects, including which genera are considered to be most closely related

to *Glaucomys* (see Thorington et al. 2002; Fig. 1). Although not all relationships were well resolved, Thorington et al. (2002) recovered a "*Glaucomys* group" comprising the genera *Glaucomys*, *Eoglaucomys*, *Iomys*, *Petinomys*, *Hylopetes*, and *Petaurillus*. Within this group, *Glaucomys* and *Eoglaucomys* occupied basal positions, suggesting that the North American and Asian flying squirrels diverged from one another relatively early in the radiation. The *Glaucomys* group recovered by Thorington et al. (2002) was identical to that proposed by Thorington and Darrow (2000), but differed from those of McKenna (1962) and Mein (1970). Thorington et al. (2002) also found support for 2 additional clades of flying squirrels: one comprising *Trogopterus*, *Aeromys*, *Belomys*, and *Pteromyscus* and the other comprising *Petaurista*, *Pteromys*, *Eupetaurus*, and *Aeretes*. Together, these latter 2 clades contain the 8 genera recognized as the "*Petaurista* group" by Thorington and Darrow (2000).

Two recent molecular studies (Mercer and Roth 2003; Steppan et al. 2004) have greatly clarified the phylogeny of squirrels, and that of flying squirrels in particular (Fig. 1). These researchers conducted phylogenetic analyses of several relatively slowly evolving genes (the *12S* mitochondrial gene and the *IRBP*, *RAG1*, and *Cmyc* nuclear gene regions). Their results agree in strongly supporting a monophyletic origin of flying squirrels. In addition, a sister relationship between flying squirrels and tree squirrels (specifically the New World tree squirrels) is strongly supported (Fig. 1). The origination of flying squirrels therefore appears to be relatively recent, approximately 18–20 million years ago (early Miocene—Mercer and Roth 2003). The divergence of the New World flying squirrels (*Glaucomys*) from Asian flying squirrels is estimated to have followed 4–6 million years later (Mercer and Roth 2003).

The results of the molecular phylogenetic studies of Mercer and Roth (2003) and Steppan et al. (2004) have shaped our current understanding of flying squirrel evolution, biogeography, and taxonomy in several important ways. First, a Miocene origin of flying squirrels suggests that dental characters linking earlier Oligocene fossil teeth to modern flying squirrels may be misleading, echoing the concerns of Thorington et al. (2005). Second, the molecular data (Mercer and Roth 2003; Fig. 1B) support the same basic relationships among living genera of flying squirrels as that proposed by Thorington and Darrow (2000) and Thorington et al. (2002) based on morphological data. In particular, both sources of data support the existence of a monophyletic *Glaucomys* group containing the same 6 genera, and both indicate that the divergence of the New World flying squirrels from their Asian relatives occurred early within the radiation of this *Glaucomys* group. Using a fossil-calibrated sciurid-specific molecular clock and 3 genes, Mercer and Roth (2003) estimated that this divergence occurred approximately 14 million years ago. This is consistent with palynological data indicating that Beringia was both emergent and forested at this time and therefore could have provided a link between Asia and North America suitable for dispersal of flying squirrels (Mercer and Roth 2003; Wing 1998). Third, the finding that flying squirrels are sister to the New World tree squirrels has
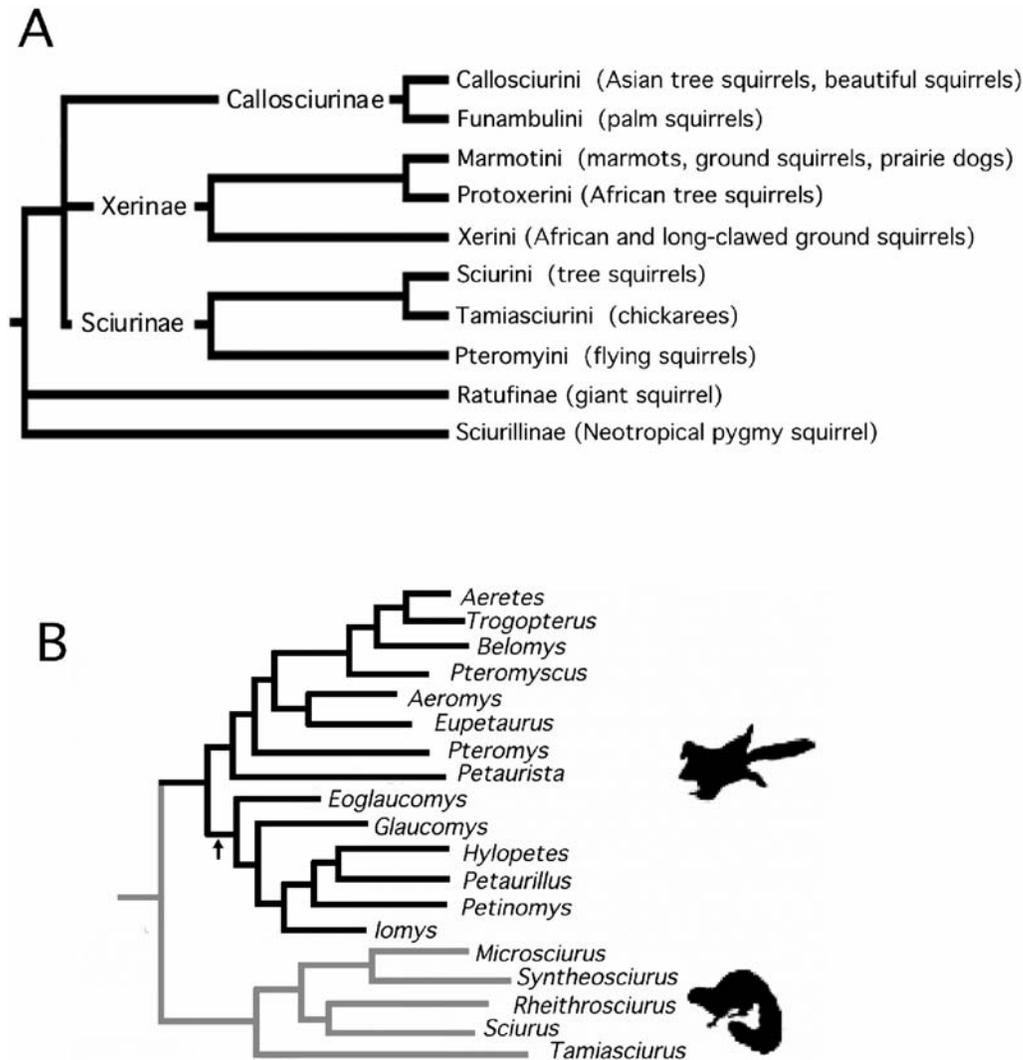
F IG . 1.—Phylogenies of flying squirrels. A) Summary of phylogenetic relationships among major lineages of squirrels showing position of flying squirrels (tribe Pteromyini) as sister to North American tree squirrels. Adapted from Steppan and Hamm (The Tree of Life Web Project, http://tolweb.org/Sciuridae/16456/2006.05.13). B) Detailed phylogenetic relationships among 14 extant genera of flying squirrels (black lines) and New World tree squirrels (gray lines) based on the molecular analysis of Mercer and Roth (2003). Arrow indicates the node defining the "*Glaucomys* group" (sensu Thorington and Darrow [2000] and Thorington et al. [2002]).

necessitated a change in the traditional taxonomy for the family Sciuridae, which treated flying squirrels as a distinct subfamily (Pteromyinae) sister to all other living squirrels. Thorington and Hoffmann (2005) recently revised the classification of squirrels accordingly; the 5 major lineages identified by Mercer and Roth (2003) and Steppan et al. (2004) are now treated as subfamilies (Ratufinae, Sciurillinae, Sciurinae, Xerinae, and Callosciurinae) and the flying squirrels are now considered a tribe (Pteromyini) within the subfamily Sciurinae (Fig. 1A).

The emerging synthesis of flying squirrel phylogeny therefore indicates that flying squirrels are monophyletic and most closely related to the New World tree squirrels. Flying squirrels appear to have originated in the early to middle Miocene. The New World flying squirrels (*Glaucomys*) appear to have diverged from Asian flying squirrels relatively early in the history of the group, most likely in the late Miocene.

Together, the sister relationship of the Pteromyini with the New World tree squirrels (Sciurinae), the current geographic distribution of the Pteromyini (which includes both Asia and North America), and the phylogenetic position of *Glaucomys* (Fig. 1) relative to Asian forms, suggest that trans-Beringian dispersal has played an important role in shaping the evolutionary history of flying squirrels.

SYSTEMATICS, BIOGEOGRAPHY, AND CONSERVATION GENETICS OF *GLAUCOMYS*

The 2 species of New World flying squirrels are morphologically similar to one another in many respects (see Dolan and Carter 1977; Wells-Gosling and Heaney 1984). However, *G. sabrinus* is considerably larger than *G. volans* (approximately 75–140 g for the former versus 46–85 g for the latter)
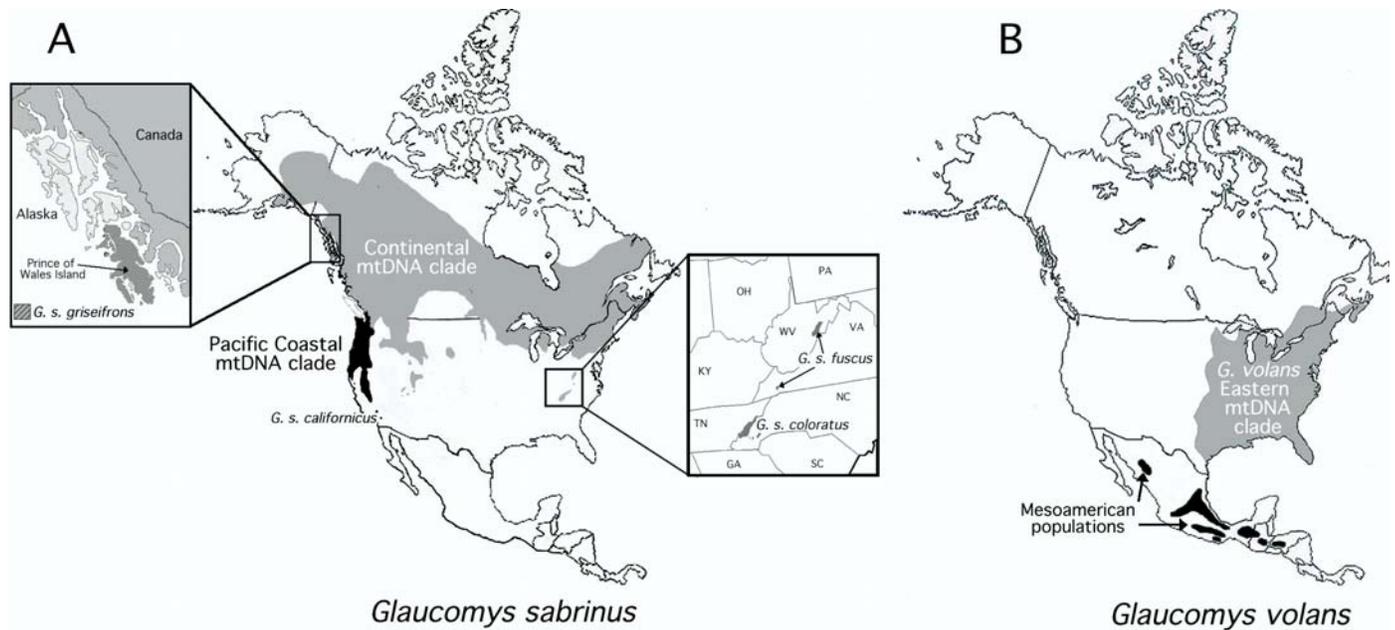
FIG. 2.—Geographic distributions of the New World flying squirrels (*Glaucomys*). A) Geographic distribution of the northern flying squirrel (*G. sabrinus*) with the Pacific Coastal mitochondrial DNA (mtDNA clade) shown in black and the Continental mtDNA clade shown in gray. The 2 clades overlap geographically in a narrow region in northwestern North America (see text). Subspecies of *G. sabrinus* that are listed as endangered at the state, federal, or international level are labeled. More detailed maps (insets) are provided for *G. s. fuscus* and *G. s. coloratus* from the Appalachian Mountains and *G. s. griseifrons* from the Alexander Archipelago of southeastern Alaska (note that in the latter, flying squirrels have not been documented to occur on the lightly shaded islands). B) Geographic distribution of the southern flying squirrel (*G. volans*). All populations of *G. volans* surveyed from eastern North America belong to a single mtDNA clade (gray). The disjunct populations of *G. volans* in Mesoamerica (black) have not been examined with molecular data. Geographic distributions of taxa and mtDNA clades are modified from Wilson and Ruff (1999), Arbogast (1999), Bidlack and Cook (2001), and Arbogast et al. (2005).

and males of the 2 species have highly differentiated bacula that are considered diagnostic. In most cases, the 2 species also occupy different forest types; *G. sabrinus* tends to be closely associated with northern coniferous forests and adjacent ecotones, whereas *G. volans* is found primarily in deciduous hardwood forests. As a result, the 2 species have largely non-overlapping geographic distributions (Fig. 2). However, areas of sympatry do exist where northern coniferous and deciduous hardwood forest types come into contact, such as in northeastern North America and in the Appalachian Mountains. The geographic distributions of both species are characterized by the presence of multiple disjunct populations at the southern edge of their respective ranges. In the case of *G. sabrinus*, this includes several subspecies that are listed as endangered at the federal or state level (e.g., *G. s. californicus*, *G. s. fuscus*, and *G. s. coloratus*; Fig. 2). In the case of *G. volans*, this includes 6 subspecies that occur only in disjunct areas of high-elevation oak and oak–pine habitat in Mesoamerica (Dolan and Carter 1977).

Systematics.—Over the last decade, several studies (e.g., Arbogast 1999; Arbogast et al. 2005; Bidlack and Cook 2001, 2002; Demboski et al. 1998a; Petersen and Stewart 2006) have used molecular genetic approaches to examine the evolutionary history, biogeography, and conservation genetics of *Glaucomys*. Together these analyses have revealed that *Glaucomys* is monophyletic relative to Asian flying squirrels and that the genus comprises at least 3 distinct lineages: 2 within

G. sabrinus (a widespread Continental lineage and a Pacific Coastal lineage) and at least 1 within *G. volans* (Figs. 2 and 3). These 3 lineages within *Glaucomys* appear to have diverged from one another in the early to middle Pleistocene (Arbogast 1999). This estimate is relatively recent given the late-Miocene date estimated for the divergence of *Glaucomys* and Asian flying squirrels (Mercer and Roth 2003). However, little is known about the evolution of North American flying squirrels in the intervening period because of a lack of pre-Pleistocene fossils that can be conclusively diagnosed as ancestral to *Glaucomys* (Wells-Gosling and Heaney 1984).

The mitochondiral DNA (mtDNA) phylogeny of *Glaucomys* (Fig. 3) reveals that the Continental and Pacific Coastal clades of *G. sabrinus* are not sister to one another. Rather, the former appears to be sister to a clade comprising *G. volans* from the eastern United States. Minimum levels of corrected pairwise sequence divergence in the mtDNA cytochrome-*b* gene (*Cytb*) between all 3 clades are similar (approximately 4%), suggesting that they diverged from one another within a relatively short period of time in the early to middle Pleistocene (Arbogast 1999). Although examination of these data hints that *G. sabrinus* may comprise 2 cryptic species, subsequent comparisons of bacular morphology (R. W. Thorington, Jr., and B. S. Arbogast, in litt.) and analysis of nuclear markers (Arbogast et al. 2005) have failed to detect species-level differences between the Continental and Pacific Coastal
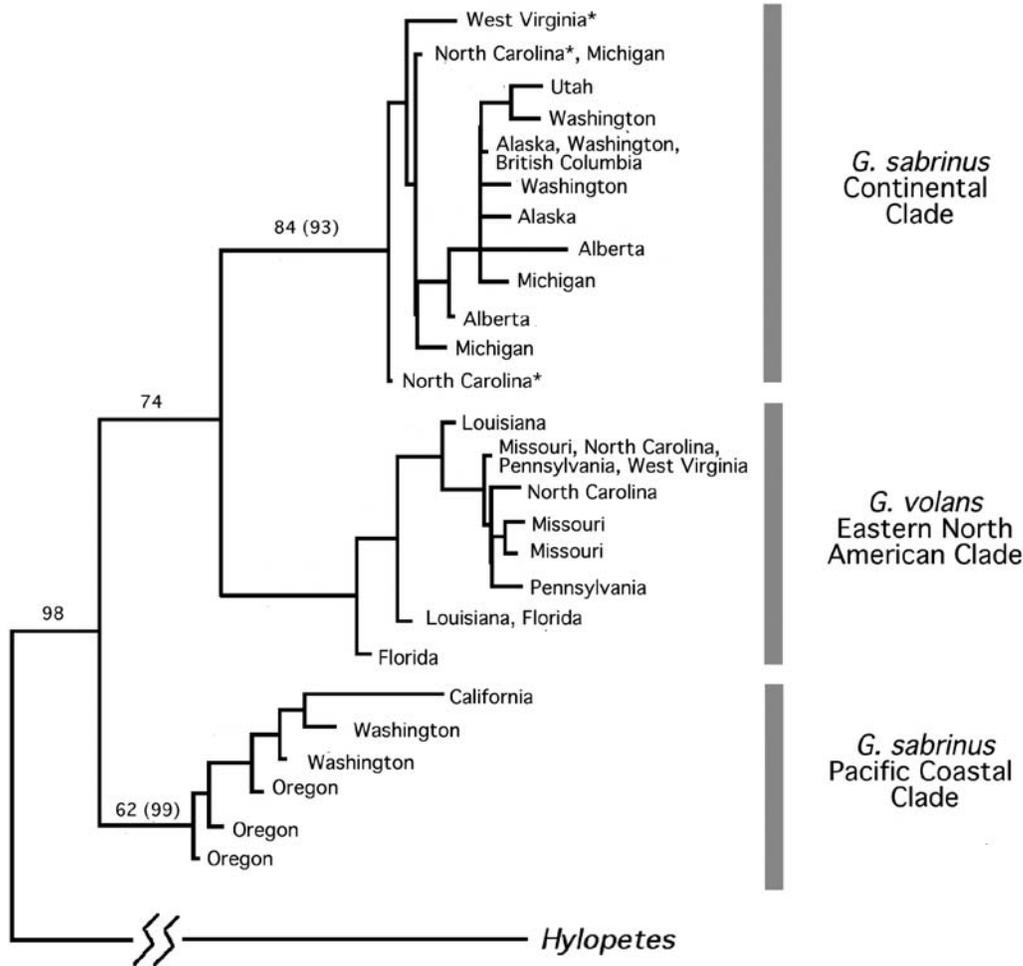
FIG. 3.—Neighbor-joining tree showing evolutionary relationships among populations of the 2 species of *Glaucomys* based on analysis of the mitochondrial DNA cytochrome-*b* gene (adapted from Arbogast et al. 2005). This tree is presented as a phylogram (branch lengths are proportional except for that between *Hylopetes* and the ingroup taxa). Bootstrap values > 50% for the outgroup analysis are shown above the line at each node, followed parenthetically by those estimated with the outgroup taxon removed (see Arbogast et al. [2005] for details). Localities (state or province abbreviations and number of individuals showing a given haplotype) are indicated at each terminal branch. Haplotypes found in the endangered southern Appalachian subspecies of *G. sabrinus* are indicated by asterisks.

mtDNA clades of this species. Therefore, recent or ongoing gene flow between these 2 clades seems likely, and they appear to represent a single biological species despite their well-differentiated mitochondrial genomes. In contrast, both nuclear and mtDNA markers clearly distinguish *G. volans* from both clades of *G. sabrinus* (Arbogast et al. 2005). Given that the 3 mtDNA clades of *Glaucomys* appear to have diverged from one another relatively recently, and that nuclear markers support current taxonomy, the paraphyly of *G. sabrinus* observed in the mtDNA gene tree (Fig. 3) may simply represent incomplete lineage sorting (Arbogast 1999).

Biogeography.—The contemporary large-scale population genetic structures of both *G. sabrinus* and *G. volans* appear to have been strongly influenced by historical changes in the distribution of North American forests throughout the Quaternary (Arbogast 1999). Over the past 2 million years, North America has experienced 20 or more glacial–interglacial cycles (Cox and Moore 2005). During interglacial periods, the northern distributional limits of North American forests may have approached those of today; however, the distributions of both coniferous and deciduous forest types would have been pushed far to the south of their present ranges during glacial periods (J. M. Adams and H. Faure [eds.], QEN members, Oak Ridge National Laboratory, Tennessee, *Review and atlas of palaeovegetation: preliminary land ecosystem maps of the world since the last glacial maximum,* http://www.esd.ornl.-gov/ern/qen/adams1.html). Examination of the mtDNA data suggests that contemporary populations of *Glaucomys* are derived from ancestral populations isolated in 3 separate forested refugia (1 corresponding to each of the 3 mtDNA clades in Fig. 3). Based on a molecular clock estimated for *Cytb* of rodents, Arbogast (1999) proposed that these clades initially diverged in the early- to middle-Pleistocene; if correct, this would implicate a pre-Wisconsinan vicariant event(s), such as one of the earlier glacial cycles of the Pleistocene, as the source of the initial diversification within *Glaucomys*.

The phylogeographic structures of *G. sabrinus* and *G. volans* suggest that the most recent (Wisconsinan) glaciation also had important impacts on the biogeographic histories of these species. For example, today most of northern North America is occupied by the Continental mtDNA clade of *G. sabrinus* (Figs. 2 and 3). Within this clade, haplotypes from the Appalachian Mountains are basal and there is a general southeast-to-northwest geographic structuring of haplotypes. This pattern is consistent with a northward and westward post-Wisconsinan range expansion from a southeastern refugium. Allozyme data also support this scenario (Arbogast et al. 2005); populations from Alaska at the far northwestern extreme of the range of *G. sabrinus* exhibit much lower levels of poly-morphism and average individual heterozygosity than those from further to the south and east, and private alleles occur only within the southern Appalachian populations of *G. sabrinus*, at the far southeastern extreme of the species' range. This type of geographic structuring of allozyme variation is predicted to occur in species that have undergone an ice-age cycle of range contraction and expansion (Hewitt 1996). Analyses of mtDNA and microsatellite variation in populations of *G. sabrinus* from Alaska are consistent with a late-Pleistocene–Holocene recolonization of the region (Bidlack and Cook 2001, 2002). Both pollen and fossil evidence also are consistent with the hypothesis that the Continental clade of *G. sabrinus* underwent a rapid postglacial expansion out of a southeastern refugium. For example, the pollen record indicates that although boreal tree species such as spruce (*Picea*) were restricted to the south-central United States during the Wisconsinan glacial maxi-mum, they expanded quickly to recolonize Alaska by approximately 8,000 years ago (Ritchie 1987). Similarly, late Pleistocene remains of *G. sabrinus* have been found in several localities in the eastern and southeastern United States, including Peccary Cave, Arkansas, far to the south of the current range of the species (Kurtén and Anderson 1980; Wells-Gosling and Heaney 1984). The disjunct populations of *G. sabrinus* currently found in the Appalachian Mountains (Fig. 2A) thus appear to be late Pleistocene relicts, isolated from more northern, continuous populations of the species as the distribution of boreal forest shifted northward following the most recent glacial retreat (Arbogast 1999; Arbogast et al. 2005; Weigl 1969).

The Pacific Coastal mtDNA clade of *G. sabrinus*, compris-ing populations currently found west of the Cascades and Sierra Nevada in Washington, Oregon, and California, appears to be derived from an ancestral population that persisted in a coniferous forest refugium that existed along the Pacific Coast of the United States (Arbogast 1999). Within this clade, haplotypes from Oregon are basal, suggesting that this may have been an important refugial area (Fig. 3). In contrast to the evidence supporting a rapid post-Wisconsinan range expansion of the Continental mtDNA clade of *G. sabrinus*, the Pacific Coastal mtDNA clade appears to have expanded its range only slightly northward following glacial retreats—a pattern char-acteristic of those taxa comprising the contemporary Pacific Coast mammalian fauna (Dalquest 1948). This apparent asymmetry of postglacial recolonization may be a direct consequence of the Laurentide ice sheet of eastern North America retreating earlier or more quickly than the Cordilleran ice sheet of western North America (Cox and Moore 2005).

Today, the Continental and Pacific Coastal clades of *G. sabrinus*, although largely nonoverlapping geographically, do come into contact in a narrow region of the Pacific Northwest of North America (Fig. 2A). Specifically, the 2 clades appear to meet (and even overlap) in the Puget Sound region of northwestern Washington and in the southern Okanogan Highlands of southwestern British Columbia, Canada (B. S. Arbogast, in litt.). This area of the Pacific Northwest of North America has been identified as having a relatively high incidence of hybridization (between nominal species and subspecies) across a diverse array of animals, and it has been considered an important "suture zone," or zone of secondary contact between previously isolated biotas (Remington 1968). Comparative phylogeographic studies have revealed that many mammals associated with the northern coniferous forests of North America (e.g., the American black bear [*Ursus americanus*], the American marten [*Martes americana*], voles of the genus *Clethrionomys* [now referred to *Myodes*], and tree squirrels of the genus *Tamiasciurus*) exhibit a similar phylo-geographic discontinuity in the Northwest (Arbogast and Kenagy 2001; Demboski et al. 1999; Stone and Cook 2000; Wooding and Ward 1997). The geographically congruent phylogeographic discontinuities in these mammals suggest that they may have responded in a concerted fashion to vicariance in the environmental history of the region; this realization has had important implications for understanding the historical assembly of the contemporary community of boreal forest mammals in North America (see Arbogast and Kenagy 2001).

Relationships among haplotypes within the mtDNA clade corresponding to *G. volans* (Fig. 3) suggest a south-to-north pattern of postglacial recolonization in this species as well (Arbogast 1999; Arbogast et al. 2005). Haplotypes from Florida and Louisiana are basal in this clade, and more northern haplotypes are all closely related to one another. A recent analysis of mtDNA variation in *G. volans* that included populations of this species from southeastern Canada (Petersen and Stewart 2006) confirms this geographic pattern. These results are consistent with the paleovegetation record (Davis 1983) in supporting a northward postglacial recolonization of eastern North America by *G. volans* out of a southeastern deciduous forest refugium that existed in the Gulf Coast region of North America during the most recent glacial maximum. Adams and Faure (http://www.esd.ornl.gov/ern/qen/adams1. html) suggested that such a refugium may have been smaller and more fragmented than previously thought (Davis 1983). However, because the genetics of populations of *G. volans* from Mesoamerica have not been examined, it remains to be seen how they will contribute to the overall historical biogeo-graphic picture for *Glaucomys*.

Conservation genetics.—Several studies have examined the genetics of populations of *Glaucomys* that are of conservation concern. In the southern Appalachians, 2 subspecies of *G. sabrinus* (*G. s. coloratus* and *G. s. fuscus*) that are restricted to isolated stands of high-elevation boreal forests (Fig. 2A) are

listed as endangered at the federal level (Demboski et al. 1998b; Weigl 2007). Analysis of allozyme variation has revealed that these 2 subspecies possess several private alleles, making them genetically distinct and important contributors to the overall genetic variability of the species (Arbogast et al. 2005). Analysis of mtDNA variation indicates that these populations contain some haplotypes that are unique and some that also occur outside the Appalachian region (e.g., Michigan; Fig 3). Based on this combined information, Arbogast et al. (2005) argued that the endangered southern Appalachian populations of *G. sabrinus* should be considered distinct management units for conservation purposes (sensu Moritz 1994). Together, examination of available mtDNA and allozyme data indicates that levels of genetic variability within the endangered Appalachian subspecies of *G. sabrinus* are reduced relative to conspecific populations, but are not low compared to populations of the widespread southern flying squirrel (Arbogast et al. 2005) Although future decreases in genetic variability are a potential problem for populations of *G. sabrinus* from the spruce–fir islands of the southern Appalachians, the most immediate threat to the persistence of these populations is likely to be habitat loss (Weigl 2007; Weigl et al. 1999). The spruce–fir and spruce–fir–hardwood ecotonal habitats of *G. s. fuscus* and *G. s. coloratus* are being negatively impacted by introduced pests, acid precipitation, and disturbance of upland hardwoods by human activities.

In southeastern Alaska, the Prince of Wales flying squirrel (*G. s. griseifrons*) has been the subject of similar conservation concern (Demboski et al. 1998b). This endemic subspecies is restricted to Prince of Wales and several nearby islands in the southwestern portion of the Alexander Archipelago (Bidlack and Cook 2001, 2002; Fig. 2). Large portions of suitable habitat (nearly 50% on some islands) have been logged over the past half-century and many remaining areas are not protected (Demboski et al. 1998b; Smith and Nichols 2003). Analyses of microsatellite and mtDNA markers (Bidlack and Cook 2001, 2002; Demboski et al. 1998a) have confirmed the original description of *G. s. griseifrons* (based on morphological characters—Howell 1934). There appears to be no contemporary gene flow between flying squirrels inhabiting the Prince of Wales Island complex and other populations in southeastern Alaska (Bidlack and Cook 2002). These genetic analyses (Bidlack and Cook 2001, 2002; Demboski et al. 1998a) also have revealed that populations of *G. s. griseifrons* have severely reduced genetic variation, likely as the result of an early Holocene founder event from a mainland source population.

Glaucomys s. griseifrons was listed as a federal C2 candidate in 1974, but was delisted by the United States Fish and Wildlife Service in 1986; however, the most recent assessment of this subspecies considers it to be "endangered" on the basis of the subspecies' highly restricted distribution and immediate threats to its habitat (Demboski et al. 1998b; IUCN red list of threatened species, *Glaucomys sabrinus*, http://www.iucnredlist.org). Given that both genetic and morphological data indicate that *G. s. griseifrons* is a distinct and endemic taxon (Bidlack and Cook 2001, 2002; Demboski et al. 1998a), it is essential that forest management plans for

the region include provisions to maintain healthy and viable populations of this unique subspecies of flying squirrel.

Several additional subspecies of *G. sabrinus* are of conservation concern. One subspecies, *G. s. californicus*, is considered a federal C2 candidate taxon and a species of special concern in the state of California; this subspecies is found only in the San Bernardino and San Jacinto mountains (and possibly the San Gabriel Mountains) of southern California (Demboski et al. 1998b). The current population status and levels of genetic variability of these high-elevation populations is unknown, but their small and fragmented distribution makes them susceptible to many of the same problems as those described above for the endangered Appalachian and Prince of Wales subspecies. Other populations of *G. sabrinus* that are of potential conservation concern include those found in the Black Hills of South Dakota (*G. s. bangsi*) and the Rocky Mountains of southern Utah (*G. s. murinauralis* and *G. s. lucifugus*). These subspecies also have highly fragmented, islandlike distributions at the southern periphery of the species' range (Wells-Gosling and Heaney 1984). Their current population, genetic, and conservation status is unknown.

In the case of *G. volans*, multiple studies (e.g., Arbogast 1999; Arbogast et al. 2005; Petersen and Stewart 2006) have documented levels of genetic variability across the range of the species in eastern North America that are surprisingly low, especially given the large, relatively contiguous distribution of many of the populations in question. However, low levels of genetic variability, a lack of phylogeographic structuring, or both also have been observed in a broad array of other animal and plant taxa from this geographic region (Soltis et al. 2006). Examination of the genetic data for *G. volans* suggests that this species may have experienced repeated or severe historical bottlenecks associated with a reduction in suitable deciduous forest habitat in eastern North America during glacial cycles of the Pleistocene (Arbogast et al. 2005). This scenario also may explain why other sciurids closely associated with the hardwood forest biome of eastern North America, such as *Sciurus niger* and *S. carolinensis*, also exhibit relatively low levels of genetic variability (Moncreif 1998). However, it also is possible that contemporary populations of *G. volans* in eastern North America are the result of a late Pleistocene range expansion following a founder event from Mesoamerica; this too would lead to limited genetic variation across the eastern North American portion of the species' range. A lack of genetic data for the Mesoamerican populations of *G. volans* prevents definitively distinguishing between these 2 scenarios at this time. Regardless of the underlying cause, the relatively low levels of genetic variability present in *G. volans* from eastern North America could have important implications for future management and conservation of the species. This is especially true for small and geographically isolated populations at the northern periphery of the species' range, such as that found in Nova Scotia, Canada (Petersen and Stewart 2006).

Compared to populations in eastern North America, little is known about the conservation status or genetics of the disjunct populations of *G. volans* occupying the highlands of Mesoamerica. The montane oak–pine forests of the region

are considered to be one of the most highly threatened habitats in the world (World Wildlife Fund, 2006, *WWF Global 200: a science-based global ranking of the Earth's most biologically outstanding terrestrial, freshwater and marine habitats,* http://www.panda.org/about_wwf/where_we_work/ecoregions/about/index.cfm), and it is likely that populations of flying squirrels have gone locally extinct in some formerly occupied areas. However, given the paucity of specimens and distributional data for *G. volans* in Mesoamerica, it seems likely that this species may occur in a number of areas where it has not yet been documented (Dolan and Carter 1977). Clearly, of all the New World flying squirrels, the Mesoamerican populations represent the most serious and substantial gap in terms of our current knowledge of basic distributional data, population status, and conservation genetics.

UNANSWERED QUESTIONS AND FUTURE DIRECTIONS

The last decade has brought many new insights into the evolution and biogeography of flying squirrels in general, and the New World flying squirrels in particular. However, many intriguing questions remain. First, there is a gap of more than 12 million years between the divergence of *Glaucomys* and Asian flying squirrels in the late Miocene (Mercer and Roth 2003) and the Pleistocene diversification of the 3 major mtDNA lineages within *Glaucomys* (Arbogast 1999). What was happening during this intervening period remains a mystery. Second, the Pacific Coastal and Continental mtDNA clades of *G. sabrinus* appear to be in secondary contact in the Pacific Northwest (Arbogast et al. 2005). Examination of allozyme data suggests recent or ongoing gene flow between the 2 clades. However, the emergence of new molecular approaches for assaying variation in the nuclear genomes of mammals (Avise 2004) provides an opportunity to examine patterns of gene flow in this geographic region in much finer detail. These types of approaches should allow researchers to document the extent and directionality of gene flow and to address fundamental questions about the relative roles of geographic, genetic, and ecological factors in shaping the evolution of this species. Third, the Pacific Northwest phylogeographic discontinuity within *G. sabrinus* has been important in developing hypotheses about the historical assembly of the boreal forest biome of North America (Arbogast and Kenagy 2001). However, despite the existence of distinct Pacific Coastal and Continental mtDNA clades in *G. sabrinus* and a variety of other boreal forest taxa, it has not been possible to determine if these patterns are all the result of a single event, or if they have been produced at different times in the past. The cyclic nature of Pleistocene glacial cycles makes the latter a distinct possibility. The development of multilocus coalescent approaches (Hickerson et al. 2006; Jennings and Edwards 2005) raises the exciting possibility of being able to test these competing hypotheses within a rigorous statistical framework. This will be essential to understanding the evolution of the boreal forest ecosystem of North America and the place of flying squirrels within it. Fourth, the genetics, ecology, and conservation status of several southern peripheral

isolates of *G. sabrinus* (e.g., those in the San Bernardino and San Jacinto mountains of southern California, the Black Hills of South Dakota, and Rocky Mountains of southern Utah) are not well documented and should be investigated. Finally, in terms of their phylogenetic position and biogeographic history, the Mesoamerican populations of *Glaucomys* remain enigmatic. These populations are considered to represent subspecies of *G. volans*, and morphological analyses tend to support this view (Braun 1988). However, several recent genetic studies of small mammals from the highlands of Mesoamerica have revealed a surprising number of cryptic species. Examples include mice of the genera *Peromyscus* and *Reithrodontomys* (Sullivan et al. 1997, 2000) and pocket gophers of the genera *Cratogeomys* and *Pappogeomys* (Demastes et al. 2002). This suggests that there could be similar cryptic diversity within the flying squirrels of Mesoamerica. Therefore, in the absence of genetic information, it remains unclear whether the Mesoamerican flying squirrels are the result of a recent dispersal from eastern North America, or vice versa. It is also possible that Mesoamerican flying squirrels represent a more divergent, cryptic lineage(s) that has retained ancestral morphological similarities to *G. volans*. Answering these questions is central to fully appreciating the evolution and biogeographic history of the New World flying squirrels and the forest biomes with which they are associated.

CONCLUSIONS

The New World Flying squirrels are a unique component of the forest ecosystems of North and Central America. Their origin can be traced back to an initial divergence of all flying squirrels from tree squirrels in the Miocene, followed subsequently by divergence of New World and Asian forms in the late Miocene. An important period of diversification occurred within *Glaucomys* in the early to middle Pleistocene, resulting in at least 3 distinct evolutionary lineages and 2 biological species within *Glaucomys*. The most recent glacial cycle also appears to have had an important impact on contemporary patterns of genetic variation within *Glaucomys*. Multiple lines of evidence support a scenario wherein distinct lineages of *Glaucomys* were isolated in separate forest refugia during the Wisconsinan glacial maximum, followed by northward expansion as glaciers retreated. In the case of *G. sabrinus*, this has resulted in a zone of secondary contact and gene flow in the Pacific Northwest of North America. Although many questions remain, *G. sabrinus* and *G. volans* have emerged as important biogeographic model species for northern coniferous and deciduous hardwood forests, respectively; future work on these species promises to generate many additional insights and hypotheses regarding the evolution and biogeography of 2 of the New World's most extensive forest types.

study. B. Blake, J. Cook, L. Heaney, and fellow participants in this symposium (W. Smith, J. Scheibe, R. Thorington, and P. Weigl) provided many valuable comments that helped improve the manuscript and A. Schwandt-Arbogast provided assistance with preparation of figures.

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Special Feature Editor was Barbara H. Blake.