SOUTHEASTERN ARCHAEOLOGY

USING FLUORESCENCE OF BONES AND TEETH TO DETECT REMAINS OF THE EASTERN FOX SQUIRREL (*SCIURUS NIGER*) IN ARCHAEOLOGICAL DEPOSITS

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*Skeletal remains of the eastern gray squirrel (*Sciurus carolinensis*) and the eastern fox squirrel (*S. niger*) are relatively common in archaeological deposits in the eastern United States. However, the teeth and skeletons of eastern fox squirrels are very similar to those of eastern gray squirrels, which has complicated or prevented definitive assignment of these remains to the species level. As part of a comprehensive study of Pleistocene and Holocene ecology and evolution in these two species, we sought a method to assign remains to* S. niger *easily and definitively in mixed assemblages. Here we describe a technique (using pink fluorescence under ultraviolet [UV] light) to assign teeth and skeletons to* S. niger. *We examined faunal deposits from several archaeological sites and confirmed that UV fluorescence can be detected in ancient* S. niger *remains. This method is effective even for isolated elements (e.g., a single incisor tooth), elements that have been burned, and those that have been extremely fragmented. This technique provides an inexpensive, nondestructive test that can definitively detect* S. niger *in mixed faunal assemblages.*

The skeletal remains of the eastern fox squirrel, hereafter fox squirrel (*Sciurus niger*), and the eastern gray squirrel, hereafter gray squirrel (*S. carolinensis*), are common in faunal deposits at archaeological sites in the eastern United States (Barfield and Barber 1992; Carder et al. 2004; Holm 2002; O'Brien and Kuttruff 2012; Smith 2011; VanDerwarker 2001). These archaeological remains are an underused, but potentially very valuable, resource for analyses of environmental conditions associated with archeological deposits and studies of the ecology and evolution of fox squirrels and gray squirrels during the Holocene and late Pleistocene. However, assignment of remains as either fox squirrel or gray squirrel can be extremely challenging, because the overall skeletal morphology of tree squirrels (genus *Sciurus*) is quite conservative, with very few differences between species (Emry and Thorington 1982). Living fox squirrels and gray squirrels are easily distinguished using differences in pelage color (Edwards et al. 2003); also, teeth and skeletal elements of the fox squirrel are often larger than those of the gray squirrel (Hall 1981). However, there is overlap in the size ranges in modern specimens of these species. The body mass of adult gray squirrels ranges from approximately 300 g to approximately 700 g, whereas adult fox squirrels range in body mass from approximately 500 g to approximately 1,300 g (Koprowski 1994a, 1994b). Furthermore, modern populations of both species currently occur in most temperate forests east of the Rocky Mountains (Hall 1981), and they often coexist in the same local habitats (Edwards et al. 2003).

These factors complicate, or prevent, researchers from definitively assigning many elements of *Sciurus* in archaeological deposits in eastern North America to the species level. As a result, many bones, bone fragments, and isolated teeth at archaeological sites can be identified as remains of animals that are in the genus *Sciurus*, but the species cannot be assigned unless the elements are from especially large individuals, or unless particular features are preserved (the gray squirrel has a tiny, peglike upper premolar tooth [P3] that is absent in the fox squirrel [Figure 1A; Hall 1981]). Thus, many studies of archaeological sites in the southeastern United States report individual elements as *Sciurus* sp., indicating that the authors are confident that the element is from an animal in the genus *Sciurus* but cannot assign the element to *S. niger* or *S. carolinensis*.

We recently demonstrated a method to definitively assign fossils to *S. niger* using 7,000-year-old specimens of the fox squirrel from a sinkhole deposit in Florida (Dooley and Moncrief 2012). This method takes advantage of the fact that modern populations of *S. niger* include individuals that display some characteristics of a condition called congenital erythropoietic porphyria (CEP; Levin and Flyger 1971). CEP is caused by mutations in the genes that code for enzymes in the biosynthetic pathway that produces heme, which is an

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important component of hemoglobin, the red pigment in vertebrate blood that allows effective delivery of oxygen to tissues (van Tuyll van Serooskerken et al. 2010).

CEP has been reported in at least eight mammalian species besides *S. niger* (Richard et al. 2008; Rivera and Leung 2008; Samman 1991; van Tuyll van Serooskerken et al. 2010). Symptoms of CEP (also known as Günther's disease when it affects humans) (Richard et al. 2008) usually include anemia, cutaneous photosensitivity, and/or acute neurological attacks (van Tuyll van Serooskerken et al. 2010). Surprisingly, fox squirrels do not display any of these debilitating symptoms of CEP (Levin and Flyger 1973).

CEP is an atypical condition in most species, because it is usually the result of rare, spontaneous mutations (van Tuyll van Serooskerken et al. 2010). However, in *S. niger*, the condition exists in most or all individuals (Flyger and Levin 1977; Spradling et al. 2000) and has been reported in modern populations of fox squirrels from widely separated localities, including Pennsylvania, Michigan, Maryland, Texas, and Oklahoma (Turner 1937; Allen 1943; Levin and Flyger 1971, 1973; Spradling et al. 2000). The prevalence of CEP in fox squirrels indicates that the mutation causing this condition is either harmless or advantageous to this species (Turner 1937; Levin and Flyger 1971, 1973).

Animals with CEP accumulate excess uroporphyrin I in their bones, causing them to fluoresce pink under ultraviolet (UV) light (Flyger and Levin 1977; Turner 1937). Levin and Flyger (1973) conducted laboratory studies to investigate physiological details of CEP in live fox squirrels. They included live gray squirrels in their study as controls. Levin and Flyger (1973) reported high concentrations of uroporphyrin I in the bones, teeth, blood, soft tissues, and urine of fox squirrels, but not gray squirrels, which they characterized as being nonporphyric.

After learning that bones of modern fox squirrels fluoresce, and after demonstrating that subfossil remains of *S. niger* fluoresce under UV light (Dooley and Moncrief 2012), we hypothesized that archaeological remains of this species in Holocene deposits might also exhibit this property. To test for fluorescence in archaeofaunal remains, we examined a series of specimens from three sites in Virginia that have radiocarbon dates earlier than A.D. 1500 (Klein and Theriot 1999; Rotenizer 1992; Thompson 1989).

We selected these three pre-contact sites because each included numerous specimens that previous researchers (Barber 1989; Whyte 1989, 2002) had assigned to *Sciurus* sp., *S. carolinensis*, and *S. niger*. Our objectives did not include comprehensive reanalysis and reinterpretation of faunal evidence from the three sites. Specimens from those sites were simply used to determine whether or not fluorescent properties we have already demonstrated in *S. niger* (Dooley and Moncrief 2012) were also observable in archaeological remains. Unlike fossils, remains in archaeological deposits are often burned and may be extremely fragmented as a result of taphonomic processes such as butchering and using bones as tools or decorative objects. The purpose of this study was to test fluorescence in ancient remains of *Sciurus* in archaeological deposits in order to develop a diagnostic method to assign archaeological specimens (including those that are burned and fragmented) definitively to *S. niger*.

Methods

We examined archaeological collections from three sites in Botetourt and Montgomery counties, Virginia (Bessemer [44BO26], Hall [44MY33], and Mount Joy [44BO2]), that are housed by the Virginia Department of Historic Resources (VDHR). All specimens examined were from intact features that were not contaminated with modern materials. Features from these sites have been radiocarbon dated as follows: Bessemer, A.D. 1235–1345 (Thompson 1989); Hall, A.D. 1277–1282 (Rotenizer 1992); and Mount Joy, A.D. 1162–1435 (Klein and Theriot 1999).

For each site, we recorded data for elements from squirrels of the genus *Sciurus* using comparative material from the Mammal Collection of the Virginia Museum of Natural History to identify elements and to assign each specimen to the species level, if possible (see Notes for collection information related to the modern comparative specimens used in this study). After identifying each element, we assigned a unique identifier (DM number), and then we noted the degree of fragmentation and whether or not it appeared to be charred or burned. We also used an Ultra Light ULG1 UV flashlight to examine fluorescence patterns. This light emitted at 400 nanometers, which is near the peak fluorescence of uroporphyrin I (Rimington 1960). These lights are relatively inexpensive (less than U.S. $15), and they are readily available because they are used to detect fluorescent inks and dyes applied to currency to deter counterfeiting, and they are used to detect urine and blood stains in forensic investigations.

Fluorescent elements were assigned to *S. niger*. We then noted the size of the archaeological specimen in relation to the comparative fox squirrel and gray squirrel material, taking into account skeletal features detailed by Hall (1981) and Emry and Thorington (1982). We assigned to *S. carolinensis* all fully fused elements of *Sciurus* that did not fluoresce and were similar in size to or smaller than the comparative gray squirrel material. We assigned to *S. niger* all elements of *Sciurus* that did not fluoresce and were similar in size to or larger than the comparative fox squirrel material. We assigned to *Sciurus* sp. all fully fused elements of *Sciurus* that did not fluoresce and were intermediate in

Table 1. Number of *Sciurus* specimens identified as eastern fox squirrel (*Sciurus niger*), eastern gray squirrel (*S. carolinensis*), and *Sciurus* sp. at three sites in Virginia, with the number of burned and fluorescent specimens reported for each site.

Species	Condition	Bessemer 44BO26 Botetourt Co.	Hall 44MY33 Montgomery Co.	Mount Joy 44BO2 Botetourt Co.	Total Number of Specimens Examined
S. niger	Fluorescent, not burned	1	0	16	17
S. niger	Fluorescent, burned	0	0	2	2
S. niger	Not fluorescent, not burned	1	2	5	8
S. niger	Not fluorescent, burned	1	1	1	3
Total *S. niger*		**3**	**3**	**24**	30
S. carolinensis	Not fluorescent, not burned	5	24	20	49
S. carolinensis	Not fluorescent, burned	2	0	9	11
Total *S. carolinensis*		**7**	**24**	**29**	**60**
Sciurus sp.	Not fluorescent, not burned	1	1	1	3
Sciurus *sp.*	Not fluorescent, burned	1	0	0	1
Total *Sciurus* sp.		**2**	**1**	**1**	**4**
Total number of specimens examined		**12**	**28**	**54**	**94**

size relative to the comparative material of fox squirrels and gray squirrels. We did not observe any fluorescent elements of *Sciurus* that were similar in size to or smaller than the comparative *S. carolinensis* material.

We photographed all archaeological specimens in visible light, and, if the specimen fluoresced, we also photographed it in UV light. This photographic method did not require any special lenses or equipment (other than the UV flashlight), but the best results were obtained in total darkness. We used a large panel of black fabric (draped over the camera, flashlight, and specimen) to block out ambient light when we were unable to darken the room completely.

Results

We observed pink fluorescence in 19 elements (Table 1). Five of the 19 specimens were intermediate in size relative to the comparative material of fox squirrels and gray squirrels. We assigned 60 specimens to *S. carolinensis* and 30 to *S. niger*, but we were unable to assign four specimens to the species level (Table 1). In addition to the maxilla, tibia, innominate, dentary, and scapula shown in Figure 1, we observed fluorescence in the following elements: rib, radius, ulna, humerus, isolated incisor, basisphenoid, pterygoid, alisphenoid, and squamosal. Fluorescence in some archaeological specimens of *S. niger* (e.g., the scapula shown in Figure 1) equaled the intensity we observed in modern specimens. Others exhibited less intense, more diffuse evidence of fluorescence that was difficult to photograph. We observed fluorescence in two specimens that appeared to have been burned (the dentary and the innominate in Figure 1) and in those that were extremely fragmented (e.g., isolated incisors, isolated squamosal, isolated maxilla, isolated basisphenoid and pterygoid, and isolated alisphenoid).

Discussion

We have demonstrated that some remains of *Sciurus* from archaeological deposits display the same fluorescent properties as modern specimens of *S. niger*. We observed pink fluorescent properties in burned elements and in those that were fragmented (Table 1, Figure 1). Because of their fluorescent properties, we were able to assign to *S. niger* some elements (such as ribs, scapulae, and isolated incisors) that we would not have been able to assign beyond *Sciurus* sp. otherwise. Previous reports of faunal analyses for these three sites

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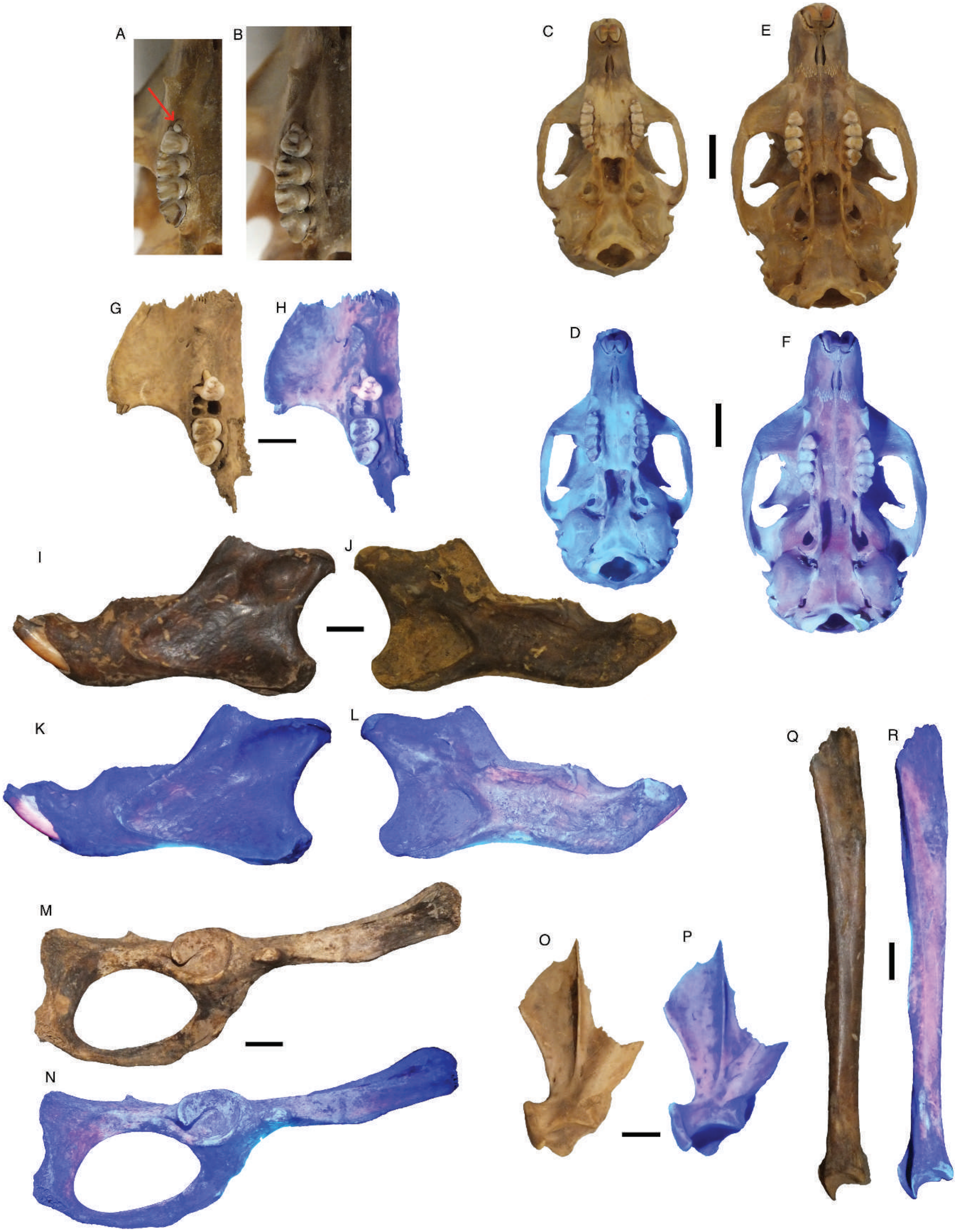
Figure 1. Skeletal elements of modern and subfossil *Sciurus*, as seen in visible light and ultraviolet light: (A) right palate, ventral view, of modern *S. carolinensis* (VMNH 33842 [VMNH 422 under old catalog]); (B) right palate, ventral view, of modern *S. niger* (VMNH 33776, [VMNH 356 under old catalog]) (note the peglike upper pre-molar tooth [P^3] present in *S. carolinensis* [arrow] but not in *S. niger*; (C, D) cranium, ventral view of modern *S. carolinensis* (VMNH 35689 [VMNH 2269 under old catalog]); (E, F) cranium, ventral view of modern *S. niger* (VMNH 35711 [VMNH 2291 under old catalog]); (G, H) right maxilla, ventral view, of subfossil *S. niger* (DM060); (I–L) left dentary of subfossil *S. niger* (DM045) (I, K, labial view, and J, L, lingual view); (M, N) right innominate, lateral view, of subfossil *S. niger* (DM043); (O, P) right scapula, lateral view, of subfossil *S. niger* (DM061); (Q, R) right tibia, lateral view of subfossil *S. niger* (DM042). A, B, C, E, G, I, J, M, O, and Q were photographed using visible light; D, F, H, K, L, N, P, and R were photographed using ultraviolet light. Scale bars for C–F are 10 mm; all other scale bars are 5 mm. Elements shown in G–R are from Mt. Joy (44BO2), Botetourt County, Virginia. See Notes for collection information about modern specimens shown in A–F.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(Barber 1989; Whyte 1989, 2002) did not reference collection catalog numbers of individual specimens. Therefore, we cannot compare our analysis of particular elements to the assignments other researchers made for the same specimens.

Not all elements we assigned to *S. niger* fluoresced, and we did not observe fluorescent elements at all three sites.

There are several possible explanations for these results. It is possible that we mistakenly assigned to *S. niger* nonfluorescent elements that are actually *S. carolinensis* or another species. It is also possible that Virginia populations of *S. niger* from the late prehistoric period exhibit polymorphisms for CEP, similar to those suggested by Spradling et al. (2000) for some modern western populations of *S. niger*. They (Spradling et al. 2000) reported fluorescence in only about 70 percent of individuals in populations from Oklahoma and Texas. Spradling et al. (2000) conceded the possibility that curatorial treatments for cleaning modern skeletal material might have negatively affected the fluorescent properties of some of the specimens they examined. That is, they allow that all fox squirrels may have CEP and that their bones should fluoresce, but that curatorial treatments may alter uroporphyrin I, causing it to lose fluorescence. So CEP may be undetectable in some modern squirrels because of chemicals used to process the skeletons. Spradling et al. (2000) performed a test in which they boiled the skull of a single modern specimen in sodium carbonate for five minutes then dried it at 80 degrees C for eight hours. They reported that the dried skull fluoresced as before. In the end, Spradling et al. (2000) discounted such curatorial treatments as an explanation for the fact that they observed less than 100 percent fluorescence in the 157 modern specimens they examined, and they concluded that bone fluorescence (and, by inference, CEP) is a polymorphic character in *S. niger*.

It is also possible that all fox squirrels have CEP and that all remains from archaeological sites should fluoresce but that uroporphyrin I in some archaelogical remains loses fluorescence because of conditions related to deposition at some archaeological sites. We are currently conducting a series of experiments to address the possibility that physical and chemical alteration of uroporphyrin I (as a result of chemical treatments not considered by Spradling et al. [2000]) may diminish or extinguish the fluorescent properties of skeletal elements of *S. niger*. We are also examining modern specimens from throughout the geographic range of this species to investigate systematically the frequency at which fluorescence occurs in modern populations. Regardless of the frequency at which fluorescence occurs in modern or ancient populations of *S. niger*, and regardless of the physical and chemical factors that may diminish or extinguish fluorescent properties of uroporphyrin I, we maintain that fluorescent bones or teeth can be assigned unequivocally to *S. niger*. That is, although it is possible (for various reasons) that not all *S. niger* elements are fluorescent, we contend that all fluorescent sciuruid elements in archaeological deposits in eastern North America are *S. niger*.

Patterns of faunal utilization can provide evidence of spatial and chronological changes in cultural, social, and ecological factors that affected subsistence of Native Americans (Barfield and Barber 1992; Pavao-Zuckerman 2000). Faunal analysts use ecological characteristics of modern populations of animals to infer evidence of ecological conditions at or near an archaeological site or of ecological conditions otherwise exploited by site occupants. Modern populations of fox squirrels and gray squirrels share many ecological characteristics (Steele and Koprowski 2001). Both species require mature temperate forests for food, nest sites, and protection from predators (Koprowski 2005). Additionally, because these squirrels do not hibernate, the presence and persistence of populations of both species are especially dependent on the presence of mature trees that produce winter-storable foods (acorns and nuts), including oaks (*Quercus*), hickories (*Carya*), and walnuts (*Juglans*) (Edwards et al. 2003; Koprowski 1994a, 1994b; Steele 2008). The American chestnut (*Castanea dentata*) was also an important cacheable food source until the early 1900s, when it was almost eliminated by a fungus (Whitney 1994). Pines, especially *Pinus palustris*, are an important element of squirrel habitat in the southeastern United States (Weigl et al. 1989). Therefore, remains of both squirrels are evidence of the presence of a mature, temperate forest environment (with a substantial component of *Quercus*, *Carya*, *Juglans*, or *Castanea* and sometimes *Pinus*) at or near an archaeological site or of ecological conditions otherwise exploited by site occupants.

Although these species have similar requirements for food and shelter, there are differences in the habitats they typically occupy, providing evidence that may allow a more detailed characterization of forest type. Fox squirrels usually occupy mature, upland forest with relatively sparse understory, whereas gray squirrels typically occupy mature hardwood forest, often with dense understory (Edwards et al. 2003). Both species, however, inhabit a variety of forest types throughout their range, reflecting variability in tree species composition, canopy closure, and understory conditions (Edwards et al. 2003). The species often occur together in the same local habitats.

In the midwestern United States, fox squirrels and gray squirrels occur primarily in habitats dominated by oaks, but squirrel presence and abundance varies with stand density, stand size, and past land-use practices (Bakken 1952). A higher percentage of oak and reduced understory development may favor fox squirrels over gray squirrels (Edwards et al. 2003). Factors such as extensive timber harvesting, heavy grazing, and repeated burnings that reduce overstory and understory density while increasing the number of early successional species of plants favor fox squirrels over gray squirrels. Size of the forest patch may also influence species occurrence, with larger patches favoring gray squirrels (Brown and Batzli 1984) and smaller patches with extensive ''edge'' between forest and field favoring fox squirrels (Nixon and Hansen 1987).

Fox squirrels and gray squirrels also occupy a wide range of forest types in the southeastern United States, and coexistence in local areas is common (Edwards et al. 2003). Southeastern fox squirrels typically occupy mature, open upland-pine and pine-hardwood forest types such as longleaf pine savanna, longleaf pine–turkey oak, and the edge habitats (ecotones) between longleaf pine and other vegetation types (Conner et al. 1999; Koprowski 1994a). Means (2006) and Weigl et al. (1989) report that *S. niger* in the southeastern United States is an ecological specialist of longleaf pine flatwoods, sandhills, and clay hills because there is a coevolved interdependence between longleaf pine, the fox squirrel, and hypogeous fungi. Southeastern gray squirrels, in contrast, typically occupy stands having a substantial hardwood component among the canopy trees, such as mixed hardwood-pine (Warren and Hurst 1980) and bottomland hardwood forests (Fischer and Holler 1991).

Habitat associations of squirrels have been used as indicators of forest types by faunal analysts. McMillan and Klippel (1981), Stafford et al. (2000), and Styles and Klippel (1996) interpreted the predominance of gray squirrels as evidence of mature, closed, mesic forests at early Holocene sites in the midwestern United States. Styles and McMillan (2009) used a decrease in the ratio of squirrels to deer as evidence for inferring a change in the vegetation of the Prairie Peninsula and surrounding areas of the midwestern United States from mesic, closed forests during the early Holocene to more open forests in mid-Holocene.

In the southeastern United States, Scott (1983) analyzed two faunal assemblages (agricultural and prehistoric, non-agricultural) from a multicomponent site (Lubbub Creek) in Alabama. She interpreted an increase in the ratio of remains of fox squirrels to those of gray squirrels as evidence of environmental disturbance associated with agriculture. Noting that gray squirrels occupy closed deciduous forests, Scott (1983) hypothesized that fox squirrels replaced gray squirrels as agricultural fields and subsequent secondary forest growth replaced these forests at the Lubbub Creek site. Similarly, Jackson and Scott (2003) used an increase in the ratio of gray squirrels relative to those of fox squirrels as evidence for reforestation of abandoned fields at the Moundville site in Alabama. In another study in the Southeast, Hogue (2003) used remains of fox squirrels and gray squirrels (along with other small mammals) to infer landscape alterations associated with agriculture at two sites (Josey Farm and Yarborough) in the Black Belt physiographic region of Mississippi.

Because researchers attempt to assign all faunal remains to the species level in order to study faunal utilization by Native Americans, we suggest that our test will benefit archaeologists. We have described an inexpensive, nondestructive method for detecting the presence of *S. niger* in mixed faunal deposits. This method is effective even for isolated elements (e.g., a single incisor tooth), elements that have been burned, and those that have been extremely fragmented. Thus we suggest this method can provide previously unavailable, detailed evidence for interpreting patterns of tree squirrel utilization, which may, in turn, provide data for spatial and chronological changes in ecological factors that affected subsistence of Native Americans in the eastern United States.

Notes

Collections. Modern specimens used in this study are housed at the Virginia Museum of Natural History, Martinsville, Virginia (VMNH). Specimens we examined from archaeological deposits are housed by the Virginia Department of Historic Resources (VDHR), Roanoke, Virginia, and Richmond, Virginia. For fluorescence, we compared VDHR specimens to a modern specimen of *S. niger* (VMNH new number 35711, [VMNH 2291 under old catalog]), an adult female, collected October 2, 1995, in Bedford County, Virginia, and a modern specimen of *S. carolinensis* (VMNH new number 35689, [VMNH 2269 under old catalog]), an adult female, collected May 25, 1993, in Henry County, Virginia. The other modern specimens included in Figure 1 are *S. carolinensis* (VMNH 33842 [VMNH 422 under old catalog]), an adult male, collected October 28, 1993, in Dorchester County, Maryland, and *S. niger* (VMNH 33776, [VMNH 356 under old catalog]), an adult male, collected August 30, 1992 in Baker County, Georgia.

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