

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 archaeological 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 nonporphyrin.

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
<i>S. niger</i>	Fluorescent, not burned	1	0	16	17
<i>S. niger</i>	Fluorescent, burned	0	0	2	2
<i>S. niger</i>	Not fluorescent, not burned	1	2	5	8
<i>S. niger</i>	Not fluorescent, burned	1	1	1	3
Total <i>S. niger</i>		3	3	24	30
<i>S. carolinensis</i>	Not fluorescent, not burned	5	24	20	49
<i>S. carolinensis</i>	Not fluorescent, burned	2	0	9	11
Total <i>S. carolinensis</i>		7	24	29	60
<i>Sciurus</i> sp.	Not fluorescent, not burned	1	1	1	3
<i>Sciurus</i> sp.	Not fluorescent, burned	1	0	0	1
Total <i>Sciurus</i> 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

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 [P³] 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.



(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 archaeological 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 re-

peated 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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References Cited

- Allen, Durward L.
1943 *Michigan Fox Squirrel Management*. Game Division, Department of Conservation, Lansing, MI.
- Bakken, Arnold A.
1952 Interrelationships of *Sciurus carolinensis* (Gmelin) and *Sciurus niger* (Linnaeus) in Mixed Populations. Unpub-

- lished Ph.D. dissertation, Department of Zoology, University of Wisconsin, Madison.
- Barber, Michael B.
1989 Preliminary Vertebrate Faunal Analysis: The Hall Site, Montgomery County, Virginia. Report on file at the Virginia Department of Historic Resources, Richmond.
- Barfield, Eugene B., and Michael B. Barber
1992 Archeological and Ethnographic Evidence of Subsistence in Virginia During the Late Woodland Period. In *Middle and Late Woodland Research in Virginia: A Synthesis*, edited by Theodore R. Reinhart and Mary Ellen N. Hodges, pp. 225–248. Special Publication No. 6. Archeological Society of Virginia, Richmond.
- Brown, Bruce W., and George O. Batzli
1984 Habitat Selection by Fox and Gray Squirrels: A Multivariate Analysis. *Journal of Wildlife Management* 48: 616–621.
- Carder, Nanny, Elizabeth J. Reitz, and J. Matthew Compton
2004 Animal Use in the Georgia Pine Barrens: An Example from the Hartford Site (9PU1). *Southeastern Archaeology* 23: 25–40.
- Conner, L. Mike, J. Larry Landers, and William K. Michener
1999 Fox Squirrel and Gray Squirrel Associations within Minimally Disturbed Longleaf Pine Forests. *Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies* 53:364–374.
- Dooley, Alton C., Jr., and Nancy D. Moncrief
2012 Fluorescence Provides Evidence of Congenital Erythropoietic Porphyria in 7,000-Year-Old Specimens of the Eastern Fox Squirrel (*Sciurus niger*) from the Devil's Den. *Journal of Vertebrate Paleontology* 32:495–497.
- Edwards, John, Mark Ford, and David Guynn
2003 Fox and Gray Squirrels. In *Wild Mammals of North America*. 2nd ed, edited by George A. Feldhamer, Bruce C. Thompson, and Joseph A. Chapman, pp. 248–267. Johns Hopkins University Press, Baltimore.
- Emry, Robert J., and Richard W. Thorington
1982 Descriptive and Comparative Osteology of the Oldest Fossil Squirrel, Protosciurus (*Rodentia: Sciuridae*). *Smithsonian Contributions to Paleobiology* 47:1–35.
- Fischer, Richard A., and Nicholas R. Holler
1991 Habitat Use and Relative Abundance of Gray Squirrels in Southern Alabama. *Journal of Wildlife Management* 55: 52–60.
- Flyger, Vagn, and Ephraim Y. Levin
1977 Animal Model: Normal Porphyria of Fox Squirrels (*Sciurus niger*). *American Journal of Pathology* 87:269–272.
- Hall, E. Raymond
1981 *The Mammals of North America*. 2nd ed. John Wiley and Sons, New York.
- Hogue, S. Homes
2003 The Application of a Small-Mammal Model in Paleo-environmental Analysis. In *Blackland Prairies of the Gulf Coastal Plain: Nature, Culture, and Sustainability*, edited by Evan Peacock and Timothy Schauwecker, pp. 48–63. University of Alabama Press, Tuscaloosa.
- Holm, Mary Ann
2002 Vertebrate Subsistence Practices along the Dan River at the Time of Contact. In *The Archaeology of Native North Carolina, Papers in Honor of H. Trawick Ward*, edited by Jane M. Eastman, Christopher B. Rodning, and Edmond A. Boudreaux, III., pp. 65–75. SEAC Special Publication 7, Biloxi, MS.
- Jackson, H. Edwin, and Susan L. Scott
2003 Patterns of Elite Faunal Utilization at Moundville Alabama. *American Antiquity* 68:552–572.
- Klein, Michael J., and Tyler S. Theriot
1999 *The Mount Joy Site (44BO2): Ceramic Analysis*. Center for Historic Preservation, Mary Washington College, Fredericksburg, VA. Submitted to the Virginia Department of Historic Resources, Richmond.
- Koprowski, John L.
1994a *Sciurus niger*. *Mammalian Species* 479:1–9.
1994b *Sciurus carolinensis*. *Mammalian Species* 480:1–9.
- 2005 The Response of Tree Squirrels to Fragmentation: A Review and Synthesis. *Animal Conservation* 8:369–376.
- Levin, Ephraim Y., and Vagn Flyger
1971 Uroporphyrinogen III Cosynthetase Activity in the Fox Squirrel (*Sciurus niger*). *Science* 174:59–60.
- 1973 Erythropoietic Porphyria of the Fox Squirrel *Sciurus niger*. *Journal of Clinical Investigations* 52:96–105.
- McMillan, R. Bruce, and Walter E. Klippel
1981 Post-Glacial Environmental Change and Hunting-Gathering Societies of the Southern Prairie Peninsula. *Journal of Archaeological Science* 8:215–245.
- Means, D. Bruce
2006 Vertebrate Faunal Diversity of Longleaf Pine Ecosystems. In *The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration*, edited by Shibu Jose, Eric J. Jokela, and Deborah L. Miller, pp. 157–213. Springer, New York.
- Nixon, Charles M., and Lonnie P. Hansen
1987 *Managing Forests to Maintain Populations of Gray and Fox Squirrels*. Technical Bulletin 5. Illinois Department of Conservation, Springfield.
- O'Brien, Michael J., and Carl Kuttruff
2012 The 1974–75 Excavations at Mound Bottom, a Palisaded Mississippian Center in Cheatham County, Tennessee. *Southeastern Archaeology* 31:70–86.
- Pavao-Zuckerman, Barnett
2000 Vertebrate Subsistence in the Mississippian-Historic Transition. *Southeastern Archaeology* 19:135–144.
- Richard, Emmanuel, Elodie Robert-Richard, Cecile Ged, Francois Moreau-Gaudry, and Hubert de Verneuill
2008 Erythropoietic Porphyrias: Animal Models and Update in Gene-Based Therapies. *Current Gene Therapy* 8:176–186.
- Rimington, Claude
1960 Spectral-Absorption Coefficients of Some Porphyrins in the Soret-Band Region. *Biochemical Journal* 75:620–623.
- Rivera, Dario F., and Luke K.-P. Leung
2008 A Rare Autosomal Recessive Condition, Congenital Erythropoietic Porphyria, Found in the Canefield Rat *Rattus sordidus* Gould 1858. *Integrative Zoology* 3:216–218.
- Rotenizer, David E.
1992 *The Hall Site (44My33): Rescue Excavations at a Late Woodland Occupation along the South Fork of Roanoke River in Southeastern Montgomery County, Virginia*. New River Valley and Roanoke Area Chapters, Archaeological Society of Virginia. Submitted to the Virginia Department of Historic Resources, Richmond.

- Samman, Samir, Susan H. Fussell, and Clive I. Rose
1991 Porphyria in a New Zealand White Rabbit. *Canadian Veterinary Journal* 32:622-623.
- Scott, Susan L.
1983 Analysis, Synthesis, and Interpretation of Faunal Remains from the Lubbub Creek Archaeological Locality. In *Prehistoric Agricultural Communities in West Central Alabama*, edited by Christopher S. Peebles, pp. 272-290. University of Michigan. Submitted to the U.S. Army Corps of Engineers, Mobile District.
- Smith, Bruce D.
2011 The Cultural Context of Plant Domestication in Eastern North America. *Current Anthropology* 52(Su4):5471-5484.
- Spradling, Kimberly D., Bonnie L. Blossman-Myer, and Frederick B. Stangl
2000 Polymorphic Nature of Cranial Fluorescence in the Fox Squirrel (*Sciurus niger*) from Texas and Oklahoma. *Texas Journal of Science* 52:327-334.
- Stafford, C. Russell, Ronald L. Richards, and C. Michael Anslinger
2000 The Bluegrass Fauna and Changes in Middle Holocene Hunter-Gatherer Foraging in the Southern Midwest. *American Antiquity* 65:317-336.
- Steele, Michael A.
2008 Evolutionary Interactions Between Tree Squirrels and Trees: A Review and Synthesis. *Current Science* 95: 871-876.
- Steele, Michael A., and John L. Koprowski
2001 *North American Tree Squirrels*. Smithsonian Institution Press, Washington, DC.
- Styles, Bonnie W., and Walter E. Klippel
1996 Mid-Holocene Faunal Exploitation in the Southeastern United States. In *Archaeology of the Mid-Holocene Southeast*, edited by Kenneth E. Sassaman and David G. Anderson, pp. 115-133. University Press of Florida, Gainesville.
- Styles, Bonnie W., and R. Bruce McMillan
2009 Archaic Faunal Exploitation in the Prairie Peninsula and Surrounding Regions of the Midcontinent. In *Archaic Societies Diversity and Complexity Across the Midcontinent*, edited by Thomas E. Emerson, Dale L. McElrath, and Andrew C. Fortier, pp. 39-80. State University of New York Press, Albany.
- Thompson, Stephen M.
1989 Radiocarbon Dates. In *Archaeological Investigations at the Bessemer Site (44BO26): A Late Woodland Period and Page Component Village Site on the Upper James River, Virginia*, edited by Thomas R. Whyte and Steven M. Thompson, pp. 140-148. Archaeological Research Center, James Madison University, Harrisonburg, VA. Submitted to the Virginia Department of Transportation, Richmond.
- Turner, William J.
1937 Studies on Porphyria. I. Observations on the Fox-squirrel, *Sciurus niger*. *Journal of Biological Chemistry* 118: 519-530.
- VanDerwarker, Amber
2001 *An Archaeological Assessment of Pre-Columbian Fauna in the Roanoke River Basin*. Research Report No. 21. Research Laboratories of Archaeology, University of North Carolina, Chapel Hill.
- van Tuyl van Serooskerken, Anne-Moniek, Pamela Poblete-Gutierrez, and Jorge Frank
2010 The Porphyrias: Clinic, Diagnostics, Novel Investigative Tools and Evolving Molecular Strategies. *Skin Pharmacology and Physiology* 23:18-28.
- Warren, Randy C., and George A. Hurst
1980 Squirrel Densities in Pine-Hardwood Forests and Streamside Management Zones. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 34:492-498.
- Weigl, Peter D., Michael A. Steele, Lori J. Sherman, James C. Ha, and Terry S. Sharpe
1989 The Ecology of the Fox Squirrel (*Sciurus niger*) in North Carolina: Implications for Survival in the Southeast. *Bulletin of the Tall Timbers Research Station* 24:1-93.
- Whitney, Gordon G.
1994 *From Coastal Wilderness to Fruited Plain: A History of Environmental Change in Temperate North America from 1500 to the Present*. Cambridge University Press, Cambridge.
- Whyte, Thomas R.
1989 Faunal Remains. In *Archaeological Investigations at the Bessemer Site (44BO26): A Late Woodland Period and Page Component Village Site on the Upper James River, Virginia*, edited by Thomas R. Whyte and Steven M. Thompson, pp. 214-243. Archaeological Research Center, James Madison University, Harrisonburg, VA. Submitted to the Virginia Department of Transportation, Richmond.
- 2002 Archaeofaunal Remains from the Late Prehistoric Mount Joy Site in Botetourt County, Virginia. *Banisteria* 20:45-52.