

Neotoma magister.

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Neotoma magister Baird, 1857

Allegheny Woodrat

Neotoma magister Baird, 1857:xlili, 498. Type locality “Carlisle Bone Cave, Pennsylvania.”

Neotoma pennsylvanica Stone, 1893:16. Type locality “near the top of Stone Mountain (2,000 ft.), Cumberland County, Penna. [Pennsylvania], some six miles from Pine Grove, at a point known as Lewis’s Cave.”

Neotoma floridana magister: Schwartz and Odum, 1957:204. Name combination.

CONTEXT AND CONTENT. Order Rodentia, suborder Myomorpha, superfamily Muroidae, family Cricetidae, subfamily Neotominae, tribe Neotomini, genus *Neotoma*, subgenus *Neotoma* (Musser and Carleton 2005); part of the *N. floridana* species-group (Birney 1973a; Burt and Barkalow 1942; Edwards and Bradley 2001; Planz et al. 1996). *N. magister* is monotypic.

DIAGNOSIS. External morphology of *N. magister* (Fig. 1) is similar to that of *N. floridana*, the only parapatric *Neotoma*. Although *N. magister* generally is larger in mass and with longer vibrissae, identification based on single measurements is unreliable because of morphometric overlap (Ray 2000). Multivariate comparisons of cranial characters (Fig. 2) separate *N. magister* and *N. floridana* primarily on size (Hayes and Richmond 1993; Ray 2000). North–south clinal variation does not account for the differences (Hayes and Richmond 1993). The most reliable character for identifying *N. magister* is the presence of a maxillovomerine notch (present in all 418 *N. magister* skulls but in only 0.2% of 457 *N. floridana* skulls—Hayes and Richmond 1993). Additionally, only 1.7% of *N. magister* skulls exhibited bifurcation of the anterior palatal spine, whereas 70.9% of *N. floridana* skulls exhibited some degree of bifurcation.

GENERAL CHARACTERS. Dorsal pelage is gray to brownish gray with more brown typically present in adults. Ventral surface is white from throat to tip of tail. Tail is long, moderately haired, and distinctly bicolored. A midventral gland is present in adults of both sexes. Mean external measurements (in mm; *SD* and *n* in parentheses) based on adult museum specimens from Alabama, Kentucky, Maryland, New Jersey, New York, North Carolina, Pennsylvania, Tennessee, Virginia, Washington, D.C., and West Virginia (Hayes and Richmond 1993) for males and females, respectively, are: length of head and body (defined as total length minus length of tail vertebrae), 227.8 (14.3, 132), 224.1 (12.0, 110); length of hind foot, 42.7 (2.0, 133), 42.2 (2.0, 112); length of ear, 30.6 (2.3, 72), 29.8 (2.8, 59). Mean external measurements (in mm; range and *n* in parentheses) based on adult museum specimens from Alabama, Kentucky, Maryland, North Carolina, Tennessee, Virginia, Washington, D.C., and West Virginia (Ray 2000) are: total length, 397.4 (311–451, 91); length of tail, 180 (147–210, 91); length of hind foot, 41.7 (35–46, 92); length of ear, 28.3 (23–34, 42). Mean body masses (in g; *SD* and *n* in parentheses) for males and females, respectively, are 357.0 (56.5, 48) and 337.0 (53.5, 36) from across the distribution (Hayes and Richmond 1993).

Mean cranial measurements (in mm; *SD* and *n* in parentheses) from Alabama, Kentucky, Maryland, New Jersey, New York, North Carolina, Pennsylvania, Tennessee, Virginia, Washington, D.C., and West Virginia (Hayes and Richmond 1993) for males and females, respectively, are: breadth at mastoids, 20.0 (0.8, 129), 19.8 (0.7, 110); breadth of metapterygoid fossa, 4.3 (0.3, 142), 4.3 (0.3, 117); breadth of rostrum, 8.4 (0.4, 144), 8.4 (0.4, 121); breadth of zygomatic plate, 4.7 (0.3, 145), 4.7 (0.3, 121); condylobasilar length, 52.1 (2.1, 120), 51.4 (2.0, 107); greatest length of skull, 54.0 (2.0, 116), 53.3 (1.8, 83); least interorbital constriction, 6.8 (0.2, 141),

6.8 (0.3, 117); length of incisive foramen, 11.2 (0.6, 141), 11.1 (0.7, 118); length of maxillary toothrow, 9.6 (0.3, 144), 9.5 (0.4, 121); length of nasals, 21.5 (1.1, 131), 21.1 (1.2, 97); length of palatal bridge, 9.6 (0.7, 142), 9.5 (0.7, 117); length of rostrum, 22.3 (1.1, 127), 21.9 (1.1, 95); zygomatic breadth, 52.1 (2.1, 120), 51.4 (2.0, 107).

DISTRIBUTION. The historic distribution of *N. magister* generally followed the Appalachian Mountains and Interior Highland regions of the eastern United States from western Connecticut to northern Alabama (Goodwin 1932; Poole 1940). The species is extirpated from Connecticut and New York and is restricted to a small area along the Hudson River Palisades in New Jersey (Fig. 3). The southern and western borders of the distribution approximate the Tennessee River corridor, with the exception of 3 specimens collected south of the river near Muscle Shoals, Colbert County, Alabama, that were identified as *N. magister* based on presence of the maxillovomerine notch (Hayes and Richmond 1993). Although cave deposits indicate a former more northerly distribution (Richards 1987), the modern distribution in Indiana and Ohio is restricted to the limestone escarpments near the Ohio River (Johnson 2002). To the east, the distribution follows the Blue Ridge Escarpment in Virginia, south to the northern portion of western North Carolina. In the Blue Ridge of North Carolina, *N. magister* occurs at elevations >640 m (Ray 2000). Historical records exist from the Piedmont of Maryland and Virginia along the Potomac River corridor near Great Falls, upstream from present-day Washington, D.C. (Wetmore 1923). The western extent of the distribution along the Ohio Hills in northwestern West Virginia and southwestern Pennsylvania is uncertain.

FOSSIL RECORD. Fossil remains of *N. magister* are numerous from several Pleistocene cave deposits in Indiana, Kentucky, Maryland, Ohio, Pennsylvania, Tennessee, and Virginia (Gidley and Gazin 1933, 1938; Guilday et al. 1964, 1977, 1978; Richards 1972, 1987). The oldest remains are from middle Pleistocene deposits at Cumberland Cave, Maryland, and Trout Cave, West Virginia (Kurtén and Anderson 1980). The unglaciated southern Appalachians served as a late Pleistocene refugium for *N. magister* (Birney 1973b; Guilday et al. 1964) when habitat conditions in the northern extent of the current distribution were unsuitable (Hayes and Harrison 1992).

FORM AND FUNCTION. *Neotoma magister* has long vibrissae, usually >51 mm (Ray 2000). Vibrissae number up to 50



FIG. 1. Adult *Neotoma magister* in Randolph County, West Virginia. Photograph by Steven B. Castleberry.



FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Neotoma magister* from Buncombe County, North Carolina (female, Georgia Museum of Natural History 25729). Greatest length of cranium is 48 mm.

on each side of the muzzle (Howell 1926). Black vibrissae are stiff, whereas white vibrissae are softer. A few vibrissae are black near the base becoming white on the distal half. Molt in *N. magister* progresses uniformly over the entire body (Poole 1940). Dental formula is $i\ 1/1$, $c\ 0/0$, $p\ 0/0$, $m\ 3/3$, total 16.

The midventral gland becomes active during the breeding season, especially in males (Poole 1940). The odor of the midventral gland is "marked" (Poole 1940:263).

The baculum of *N. magister* is short with a broad proximal end and lateral wings giving a U-shaped appearance (Burt and Barkalow 1942). Mean bacular measurements (in mm; range in parentheses) of 4 specimens of *N. magister* examined by Burt and Barkalow (1942) are: length, 6.79 (6.41–7.10); diameter at base: dorsoventral, 1.74 (1.45–1.98) and lateral, 3.32 (2.93–3.50); diameter of shaft: dorsoventral, 0.69 (0.60–0.86) and base, 0.82 (0.75–0.93). Penis has recurved spines that expand in the vagina, allowing a copulatory lock during mating (Howell 1926). Testes are partly abdominal, especially when reproductively active (Patterson 1933). Mean testes measurements for 3 males from West Virginia in February were 18.5 mm polar length by 11 mm diameter. Scrotum is shallow, enclosing one-third of testicles and epididymides (Patterson 1933). A prostate is present. Cowper's glands are caudal to ischiocavernosus muscle. Spongy tissue and coagulating glands surround the neck of the bladder in reproductively active individ-

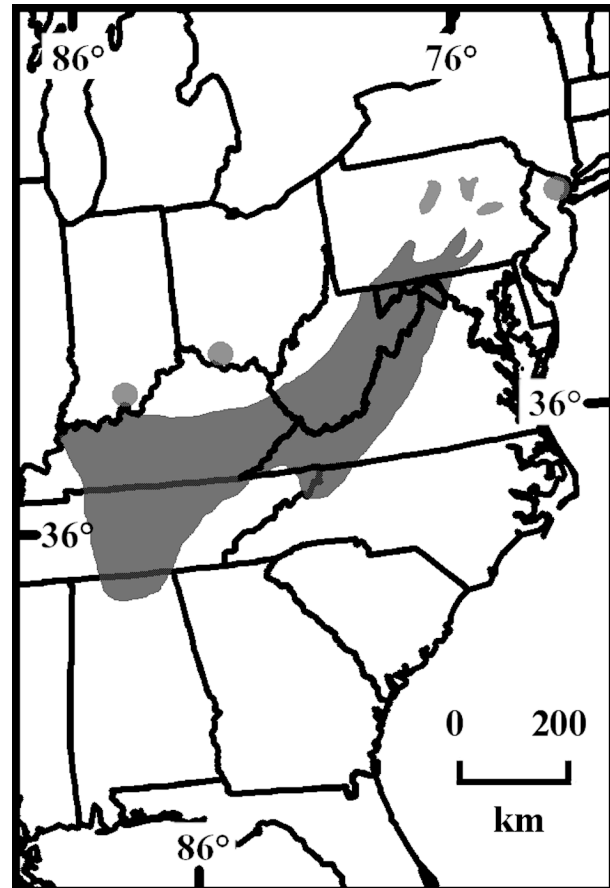


FIG. 3. Distribution of *Neotoma magister* in the eastern United States.

uals. Ovaries are covered by fat and folds of the oviducts. Uterus is bicornus and converges into a broad U-shape.

Water consumption by captive *N. magister* ranged from 0 to 250 ml of free water per 48 h (Newcombe 1930; Poole 1940). Free-ranging *N. magister* generally have year-round access to water in streams and seepage water in or near caves and rock outcrops.

ONTOGENY AND REPRODUCTION. The breeding season is variable depending on location. Specimens from southeastern Pennsylvania produced 2 or 3 litters per year between mid-March and October (Poole 1940). In western Virginia, breeding occurs year-round, but most young are born between May and October (Mengak 2002a). The gestation period is 30–36 days (Poole 1940). Typical litter sizes range from 1 to 4, with means of 2.0 (Poole 1940) and 2.3 (Mengak 2002a). Sexual maturity is attained at 3–4 months (Poole 1940). Individuals may give birth at 10 months (Poole 1940).

Young are pink and naked at birth and weigh 15–17 g (Mengak 2002a; Poole 1936, 1940). By day 5, young are covered by fine hair and are fully furred at 2 weeks. Eyelids are conspicuously black until eyes open. Eyes become sensitive to light at 2 weeks and are fully open at 3 weeks (Poole 1936). Tail remains hairless until ca. 3 weeks. Mean growth rates of juveniles (body mass ≤ 175 g) and subadults (176–225 g) in western Virginia were 1.26 and 0.95 g/day, respectively (Mengak 2002a). Mother and young remain together until individual young weigh ≥ 115 g (Mengak 2002a). *N. magister* can live to 48 months in captivity (Poole 1940) and to 58 months in the wild (Mengak et al. 2002).

Young are reared in nests constructed of bark, grasses, roots, and shredded wood fibers (Poole 1940). The outside of the nest is constructed of coarse materials, and the inside is lined with finer materials (Newcombe 1930; Poole 1940). Nests have an outside diameter of 460 mm and a nest cavity diameter of 120 mm (Poole 1940). Nests typically are located in inaccessible rock crevices or on ledges in caves.

ECOLOGY. The presence of rock habitats, such as boulder fields, caves, cliff faces, or talus slopes, is the limiting factor for occurrence regardless of vegetation type (Heisler 1941; Newcombe 1930; Poole 1940). *N. magister* occurs in a wide variety of forest types, including northern hardwood (composed of sugar maple [*Acer saccharum*], yellow birch [*Betula alleghaniensis*], and American beech [*Fagus grandifolia*]) and red spruce (*Picea rubens*)–eastern hemlock (*Tsuga canadensis*) at higher elevations (>800 m) in the Allegheny Mountains in Maryland, Pennsylvania, and West Virginia. The species occurs in mixed-mesophytic and mixed-oak (*Quercus*)–pine (*Pinus*) forest types throughout its distribution (Castleberry et al. 2002a, 2002c; Fassler 1974; M. T. Mengak, in litt.). Sandstone rock outcrops occupied by *N. magister* in north-central West Virginia occur on steeper slopes, are wider, have less leaf litter accumulation, and have fewer understory trees than do unoccupied rock outcrops (Myers 1997). In eastern Kentucky, *N. magister* occupies rock outcrops on steep slopes with high overstory tree densities (Bommarito 1999). *N. magister* tolerates a variety of forest stand age and structure conditions but selects foraging areas with diverse understory vegetation (Castleberry et al. 2002c).

Mean home-range sizes of 37 individuals radiotracked from May to August in east-central West Virginia were 6.5 ha for males ($n = 19$) and 2.2 ha for females ($n = 18$ —Castleberry et al. 2001). Mean home-range sizes of 7 individuals on the same study area from October to December were 0.49 and 0.78 ha, respectively, for males ($n = 3$) and females ($n = 4$ —Hornsby et al. 2005). Mean home-range size was 0.18 ha for 4 females radiotracked from January to April in western Virginia (Mengak 2002b). *N. magister* restricts its movement away from rock habitats in late fall and winter when little green vegetation is available and cached foods are consumed (Hornsby et al. 2005).

In eastern Pennsylvania, *N. magister* consumes various vegetative and fruiting parts of woody plant species, including black birch (*Betula lenta*), American chestnut (*Castanea dentata*), flowering dogwood (*Cornus florida*), apple (*Malus pumila*), bear oak (*Quercus ilicifolia*), black cherry (*Prunus serotina*), rhododendron (*Rhododendron maximum*), mountain ash (*Sorbus americana*), and eastern hemlock (Poole 1940). Fronds of the common polypody fern (*Polypodium vulgare*) were common in stomach contents of *N. magister* in central Pennsylvania (Heisler 1941). The most common food items consumed (from highest to lowest by percentage in the diet) in xeric oak–pine forests in the Ridge and Valley of Virginia and eastern West Virginia were blackberry (*Rubus*) leaves, fungi, greenbrier (*Smilax*) leaves, acorns, and oak leaves (Castleberry et al. 2002a). In mesic, mixed oak–northern hardwood and red spruce–hemlock forests in the Allegheny Plateau of West Virginia, the most common foods were (from highest to lowest by percentage in the diet) fungi, acorns, holly (*Ilex*) and blueberry (*Vaccinium*) fruit, fern (*Dryopteris*), and lichen. Acorns are an important component of the diet, and consumption typically reflects annual and seasonal availability (Castleberry et al. 2002a).

Neotoma magister accumulates large piles of sticks and other debris, referred to as middens, underneath overhanging rock ledges, which often are at crevice openings (Heisler 1941; Newcombe 1930; Poole 1940). Although their specific functions are unknown, middens are common deposition sites for food items such as green vegetation and fungi, as well as nonfood items. *N. magister* deposits feces and urine at latrine sites located on clean, flat rock surfaces (Poole 1940). Both sexes deposit scent from the midventral gland near latrine areas (S. B. Castleberry, in litt.).

Neotoma magister commonly occurs in habitats occupied by the northern short-tailed shrew (*Blarina brevicauda*), southern red-backed vole (*Myodes gapperi*), rock vole (*Microtus chrotorrhinus*), white-footed deermouse (*Peromyscus leucopus*), North American deermouse (*P. maniculatus*), cinereus shrew (*Sorex cinereus*), rock shrew (*S. dispar*), smoky shrew (*S. fumeus*), and red squirrel (*Tamiasciurus hudsonicus*—Castleberry et al. 2003; Heisler 1941; Sands 1951). Rafinesque's big-eared bat (*Corynorhinus rafinesquii*), Townsend's big-eared bat (*C. townsendii*), common raven (*Corvus corax*), long-tailed weasel (*Mustela frenata*), eastern small-footed myotis (*Myotis leibii*), eastern spotted skunk (*Spilogale putorius*), and American black bear (*Ursus americanus*) often use the same rock habitats as *N. magister* for denning, roosting, or nesting. Potential predators of *N. magister* include great horned owls (*Bubo virginianus*), timber rattlesnakes (*Crotalus adamanteus*), other snakes, bobcats (*Lynx rufus*), striped skunks (*Mephitis mephitis*),

gray foxes (*Urocyon cinereoargenteus*), eastern spotted skunks, and long-tailed weasels (Balcom and Yahner 1996; Poole 1940). Raccoons (*Procyon lotor*) host the ascarid nematode *Baylisascaris procyonis*, which causes fatal neurological disease in intermediate and aberrant hosts. *B. procyonis* has been implicated in population declines of *N. magister* in the northern parts of the range (LoGiudice 2001, 2003; Owen et al. 2004). *N. magister* is at greater risk of infection than other small mammals because of its propensity to collect and cache food and nonfood items, including feces that may contain *B. procyonis* eggs. *N. magister* regularly collected simulated raccoon feces at raccoon latrine sites (LoGiudice 2001).

A diverse assemblage of ectoparasites, including chiggers, fleas, mites, and ticks, occurs with *N. magister* in Indiana (Cudmore 1986). Two flea (*Eptedia cavernicola* and *Orchopeas pennsylvanicus*) and 1 tick (*Ixodes angustus*) species are known from *N. magister* in West Virginia (Castleberry et al. 2003). The *Neotoma*-specific flea, *O. pennsylvanicus*, is common throughout the distribution (Benton 1971; Castleberry et al. 2003; Cudmore 1986). The protozoan parasite *Eimeria neotoma* was documented in a single female in central Pennsylvania (Sands 1951).

Although populations in the northern and western peripheries of the distribution have experienced dramatic declines in recent years (Balcom and Yahner 1996), *N. magister* is still believed to be common in appropriate habitats in the central and southern parts of the range. *N. magister* is relatively abundant in portions of western North Carolina (Ray 2000) and is commonly associated with cave entrances in the limestone regions of central Tennessee (Kennedy and Harvey 1980). In Kentucky, the species is more abundant in sandstone cliffs throughout the Cumberland Plateau than in the Highland Rim and largely absent in the Bluegrass regions (Barbour and Davis 1974; Bommarito 1999; Fassler 1974). Population estimates for 2 sites in the Blue Ridge of western Virginia studied intensively over an 11-year period ranged from 0 to 24.1 individuals, with long-term averages of 6.3 and 10.6 (M. T. Mengak, in litt.).

BEHAVIOR. *Neotoma magister* is agonistic toward conspecifics (Poole 1940). Adult home ranges overlap extensively, but each individual defends a unique den site (Castleberry et al. 2001; Kinsey 1977). In captivity, adult females secure the best den sites for breeding and rearing young, adult males and juveniles reside in communal aggregations, and subordinate individuals avoid confrontation by avoiding dominant females (Kinsey 1977). When confined at high densities, *N. magister* forms dominance hierarchies, displays high levels of aggression, and lacks communal aggregations (Kinsey 1977). Males become more aggressive in fall when they compete intensively for nest sites.

In high-density captive populations, body mass and occupancy of nest boxes are positively correlated with social rank (Kinsey 1976). Time spent sitting outside nest boxes and frequency of distress vocalizations are correlated negatively with social rank. Intermediate-rank individuals have more sexual encounters than do alpha individuals. In similar-sized captive groups of *N. fuscipes macrotus* and *N. magister*, the latter species exhibits higher levels of aggression and does not form communal aggregations (Kinsey 1976).

Adult *N. magister* generally are not vocal but may vocalize when fighting or injured (Poole 1940). In captivity, various vocalizations, include “squeaking” and “whimpering” (Mengak and Zadnik 2005). Young commonly squeal while in the nest (Poole 1940). Males make a “low-pitched raspy sound” when following a female before mating (Kinsey 1976; Mengak and Zadnik 2005). *N. magister* produces nonvocal sounds used to orient in the dark when ambient sounds are minimal (Dunning and Payne 1979).

The midventral gland is used to scent-mark objects, leaving a yellowish brown stain on the adjacent fur (Kinsey 1976). Males scent-mark by pressing the body against objects, using the front feet to drag the body along to deposit scent. When sexually active, the midventral gland becomes discolored by secretion and soil picked up by rubbing the gland over rocks and substrate (Poole 1940). Use of scent for orientation in caves and crevices is limited because cave floors are not a continuous substrate (Dunning and Payne 1979).

Neotoma magister is strongly nocturnal (Zervanos 1969). Red light is perceived as white light, reducing activity (Zervanos and Davis 1968). Daily activity begins ca. one-half hour after sunset

and continues for several hours before tapering off, but peaks again near dawn (Poole 1940; Zervanos 1969).

CONSERVATION STATUS. Throughout its range, *N. magister* has declined coincident with the decline of the American chestnut and, more recently, with a decline in oak abundance (Castleberry et al. 2002a; Miller and Kochenderfer 1998; Schuler 2004; Wright and Kirkland 2000). In Pennsylvania, sites formerly occupied by *N. magister* have forests with fewer oak and more coniferous species than currently occupied locations (Balcom and Yahner 1996). Although *N. magister* is present in areas with human activity, forest conversion and fragmentation is greater at extirpated sites than at currently occupied sites. Clear-cutting and 2-aged regeneration harvesting (removing all trees except 6–10 residual trees/ha) in the central Appalachian hardwood region of West Virginia have minimal direct impact on *N. magister* if the forest overstory is retained immediately surrounding outcrops and intact forest is maintained on 1 adjacent side (Castleberry et al. 2001). Limited clear-cutting and 2-aged harvesting near outcrops can benefit *N. magister* by providing abundant soft mast and succulent vegetation that is consumed in spring and summer (Castleberry et al. 2002a). Extirpation of *N. magister* in the Northeast where raccoon densities are high may be mediated by the parasite *B. procyonis* (LoGiudice 2001, 2003), but no evidence supports this relationship in other areas (Owen et al. 2004).

GENETICS. *Neotoma magister* has $2n = 52$ chromosomes (Ray and Webster 2004). Two autosome pairs are large subtelocentric, 2 pairs are small subtelocentric, and 21 pairs are large to small acrocentrics. The X chromosome is large subtelocentric and the Y chromosome is medium subtelocentric.

Patterns of variation at *N. magister* microsatellite loci indicate significant genetic differentiation among geographically distinct populations throughout the distribution with isolation-by-distance as the likely isolating mechanism (Castleberry et al. 2000, 2002b). Although genetically distinct, relatively frequent gene flow occurs among *N. magister* subpopulations at geographically proximate rock habitats. The remnant population in New Jersey exhibits greatly reduced genetic diversity compared to other populations throughout the distribution (Castleberry et al. 2002b).

A possible zone of hybridization between *N. magister* and *N. floridana haematoresia* exists in Burke County, North Carolina (Ray 2000). Although analysis of mitochondrial DNA (mtDNA) D-loop sequences identified 3 of 5 specimens from the area as *N. magister* and 2 as *N. f. haematoresia*, all were identified as *N. magister* based on cranial measurements and presence of a maxillovomerine notch.

Variation in mtDNA cytochrome-*b* sequences suggests that *N. magister* is included in a distinct clade with *N. albigula*, *N. floridana*, and *N. goldmani* (Edwards and Bradley 2002). *N. magister* is considered a sister species to *N. floridana* (Edwards and Bradley 2001).

REMARKS. *Neotoma* is the combined form of the Greek words *neos*, new or young, and *tomos*, cutting (Stangl et al. 1993). The specific name refers to the Latin word for master or teacher. Schwartz and Odum (1957) suggested that *N. magister* be included as a subspecies of *N. floridana* based on cranial and external morphology. Analyses of external and cranial morphology (Hayes and Richmond 1993), mtDNA restriction sites (Hayes and Harrison 1992; Planz et al. 1996), and mtDNA cytochrome-*b* sequences (Edwards and Bradley 2001, 2002) support the recognition of *N. magister* as a distinct species. Baker et al. (2003) and Jones et al. (1997) use the common name Appalachian woodrat.

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