MAMMALIAN SPECIES Nos. 214 and 215.

Spermophilus elegans.

By David A. Zegers

Sorex fumeus.

By James G. Owens

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ERRATA

Errors appeared in *Mammalian Species* accounts 214 and 215. In account no. 214 (*Spermophilus elegans*), part of a sentence was omitted from the DIAGNOSIS section (p. 1). In the GENERAL CHARACTERS section (p. 1) of account no. 215 (*Sorex fumeus*), the cranial dimensions were incorrect by a factor of 10. Each of these sections is reprinted below with corrections. They simply can be glued on the originals.

Account No. 214

DIAGNOSIS. Total length of adult *Spermophilus elegans* ranges from 253 to 307 mm (Armstrong, 1972; Howell, 1938; Long, 1965) making *S. elegans* similar in size to *S. armatus* (280 to 303 mm) and *S. beldingi* (254 to 300 mm), larger than *S. townsendii* (167 to 271 mm), and smaller than *S. columbianus* (327 to 410 mm) (Hall, 1981). Where sympatric with *S. beldingi*, *S. elegans* can be distinguished by its longer tail, more intense cinnamon coloration on nose and underparts, and buff rather than reddish color on underside of tail. Where sympatric with *S. townsendii*, *S. elegans* can be recognized by cinnamon rather than whitish underparts, tail with buffy white borders, and larger size. Where sympatric with *S. armatus*, *S. elegans* is distinguishable by buff rather than gray underside of tail (Hall, 1981); in addition, *S. elegans* exhibits character displacement, being slightly smaller and paler than *S. armatus* where the two species are allopatric (Long, 1965). Where sympatric with *S. richardsonii*, *S. elegans* can be recognized by a hindfoot length less than 43 mm, total length less than 275 mm, a maxillary toothrow less than 10 mm, nasal length less than 17 mm, a greatest skull length 42 to 45 mm, and a zygomatic breadth less than 30 mm (Howell, 1938). In total body length, 11 of 16 cranial measurements, and 11 of 19 measurements of the axial skeleton, *S. elegans* is significantly smaller than *S. richardsonii* (Fagerstone, 1982). Although the dorsal side sometimes is more grayish or brownish and less buffy, the head and shoulders are paler and the tail is darker with paler edgings than in *S. richardsonii* (Howell, 1938), pelage color is not consistently different between *S. elegans* and *S. richardsonii* (Fagerstone, 1982). Five pairs of mammae are spaced uniformly from the upper pectoral region into the inguinal region (Burnett, 1920). Bacula have 8 to 11 distinct tooth-like projections on the distal expansion, whereas those of *S. richardsonii* have projections reduced or absent. The shaft of the baculum of *S. elegans* is twisted pronouncedly, whereas the shaft in *S. richardsonii* is twisted only slightly (Neuner and Schultz, 1979). The diploid number is 34 compared with 36 in *S. richardsonii*; the X chromosome is smaller with the centromere more medially placed; and the Y chromosome is acrocentric (rather than subtelocentric) and larger than in *S. richardsonii* (Nadler et al., 1971). *S. elegans* lacks the Tf_2 allele typical of *S. richardsonii* (Nadler et al., 1974).

Account No. 215

GENERAL CHARACTERS. Smoky shrews (Fig. 1) are large, weighing an average of 7.6 g (6.5 to 9.9; n = 30). Means and ranges of external measurements (mm) are: total length, 111.4 (101 to 122; n = 17); length of tail, 43.8 (41 to 48; n = 17); length of hindfoot, 13.2 (12 to 14; n = 17). Cranial measurements (mean, range) of New York specimens are: condylobasal length, 18.3 (17.4 to 18.5; n = 14); palatal length, 7.7 (7.2 to 8.0; n = 24); interorbital breadth, 3.7 (3.4 to 4.0; n = 25); cranial breadth, 9.1 (8.7 to 9.4; n = 12); length of maxillary toothrow, 6.7 (6.4 to 6.8; n = 26); maxillary breadth, 5.3 (5.1 to 5.6; n = 23). The cranium often is flattened (Fig. 2), sometimes extremely so (Junge and Hoffmann, 1981). In winter, the pelage is nearly concolor in general aspect; color of the dorsum may vary from slaty to deep gray or almost blackish; the venter may be a little paler and somewhat silvery. The summer pelage is dull brown dorsally and slightly paler ventrally. The tail is bicolored throughout the year; its upperparts are fuscus, below it is paler and washed with light yellow. Old specimens may have whitish-tipped hairs (Hamilton, 1940). Green (1943) described a "concolor buff" pelage from an autumn-caught juvenile *S. f. fumeus*. Geographic variation in *S. fumeus* is slight (Barbour and Davis, 1974; Bole and Moultrop, 1942; Brown and Lanning, 1954; Cameron and Orkin, 1950; Jackson, 1928; Peterson, 1966).

MAMMALIAN SPECIES No. 215, pp. 1–8, 3 figs.

Sorex fumeus.

By James G. Owen

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Sorex fumeus Miller, 1895

Smoky Shrew

Sorex fumeus Miller, 1895:50. Type locality Peterboro, Madison County, New York, U.S.A.

CONTEXT AND CONTENT. Order Insectivora, Superfamily Soricoidea, Family Soricidae, Subfamily Soricinae, Tribe Soricini, Genus *Sorex*. The genus *Sorex* contains approximately 59 species and is distributed within the Holarctic region. Two subspecies of *S. fumeus* are recognized (Jackson, 1928):

S. f. fumeus Miller, 1895:50, see above.
S. f. umbrosus Jackson, 1917:149. Type locality James River, Antigonish County, Nova Scotia, Canada.

DIAGNOSIS. Skull large; third unicuspid larger than fourth; width of unicuspids exceeds length; medial pigmented ridge, extending from apices of unicuspids to nearly one-half distance to cingulum, often lacking; small post-mandibular foramen may be present on at least one mandible; palate broad (Hall, 1981; Junge and Hoffmann, 1981). Hamilton (1940), Jackson (1928), Wharton (1968), and especially Junge and Hoffmann (1981) and Kirkland (1981) discussed differences between *S. fumeus* and other sympatric soricids with which it may be confused. Junge and Hoffmann (1981) developed a key to the genus *Sorex* in the United States and Canada. Caldwell and Bryan (1982) present a key to the Soricidae, including *S. fumeus*, of Kentucky.

GENERAL CHARACTERS. Smoky shrews (Fig. 1) are large, weighing an average of 7.6 g (6.5 to 9.9; n = 30). Means and ranges of external measurements (mm) are: total length, 111.4 (101 to 122; n = 17); length of tail, 43.8 (41 to 48; n = 17); length of hindfoot, 13.2 (12 to 14; n = 17). Cranial measurements (mean, range) of New York specimens are: condylobasal length, 182.4 (174 to 185; n = 14); palatal length, 76.8 (72 to 80; n = 24); interorbital breadth, 37.3 (34 to 40; n = 25); cranial breadth, 90.9 (87 to 94; n = 12); length of maxillary toothrow, 66.5 (64 to 68; n = 26); maxillary breadth, 52.9 (51 to 56; n = 23). The cranium often is flattened (Fig. 2), sometimes extremely so (Junge and Hoffmann, 1981). In winter, the pelage is nearly concolor in general aspect; color of the dorsum may vary from slaty to deep gray or almost blackish; the venter may be a little paler and somewhat silvery. The summer pelage is dull brown dorsally and slightly paler ventrally. The tail is bicolored throughout the year; its upperparts are fuscus, below it is paler and washed with light yellow. Old specimens may have whitish-tipped hairs (Hamilton, 1940). Green (1943) described a "concolor buff" pelage from an autumn-caught juvenile *S. f. fumeus*. Geographic variation in *S. fumeus* is slight (Barbour and Davis, 1974; Bole and Moultrop, 1942; Brown and Lanning, 1954; Cameron and Orkin, 1950; Jackson, 1928; Peterson, 1966).

DISTRIBUTION. The geographic distribution of *S. fumeus* (Fig. 3) is centered in the Appalachian Mountains (Handley, 1971). In Canada, it extends from the Maritime Provinces to south central Ontario. According to de Vos (1964), *S. fumeus* is expanding westward in the Great Lakes region. Soper (1961) hypothesized that *S. fumeus* may occur in extreme southeastern Manitoba. A shrew, tentatively identified as *S. fumeus*, escaped from Buckner (1957) in southeastern Manitoba. South of the Great Lakes the smoky shrew occurs west across two-thirds of Kentucky (Caldwell et al., 1982). A single specimen was reported from a disjunct area in Wisconsin (Miller, 1895). The western limit of the range is unknown (Caldwell and Bryan, 1982). At higher elevations in the Appalachian Mountains, *S. fumeus* extends as far south as northern Georgia. Near the southern terminus of its range the smoky shrew is more common at higher elevations in montane communities (Linzey and Linzey, 1968) but may descend as low as 300 m in suitable microhabitats (Howell, 1909; Schwartz, 1955). The ecological range of *S. fumeus* is primarily the upper transition and lower Canadian life zones. Literature containing distribution records but not cited elsewhere in this account include: CANADA—Ontario: Elson (1937), Saunders (1932), Soper (1920), Ussher (1939); Quebec: Manville (1961); Manitoba: Peterson and Symansky (1963). UNITED STATES—Maine: Pope (1922); Massachusetts: Parker (1939); New York: Mearns (1899), Owen (1954), Townsend (1935); Pennsylvania: Doutt et al. (1966), Kirkland (1977), Kirkland and Knipe (1979), Kirkland et al. (1979); Maryland: Gardner (1950); Virginia: Hooper and Cady (1941); West Virginia: Barbour (1950, 1951*a*); Wilson (1945); Kentucky: Barbour and Hardjasasmita (1966), Welter and Sollberger (1939); Tennessee: Smith et al. (1974), Conaway and Howell (1953); Ohio: Enders (1930), Gottschang (1981); North Carolina: Adams (1965); New England: Godin (1977). Intergradation between *S. f. umbrosus* and *S. f. fumeus* occurs in New England and western New Brunswick (Jackson, 1928).

FOSSIL RECORD. Pleistocene remains of *S. fumeus* were reported as follows: Virginia—Natural Chimneys, Augusta County (Guilday, 1962); Clark's Cave, Bath County (Guilday et al., 1977). Pennsylvania—New Paris Sinkhole No.4, Bedford County (Guilday et al., 1964). Tennessee—Baker Bluff Cave, Sullivan County (Guilday et al., 1978). West Virginia—Eagle Cave, Pendelton County (Guilday and Hamilton, 1973). In reviewing the Pleistocene history of the Appalachian mammalian fauna, Guilday (1971) postulated that *S. fumeus* possibly originated in or within the vicinity of the Appalachians. In postglacial times, populations of smoky shrews expanded throughout the Appalachian uplift, crossed the St. Lawrence River, and extended into their present distribution (Handley, 1971).

FORM AND FUNCTION. The smoky shrew has two molts annually. In New York the molt into winter pelage commences from mid-September to early October, with males entering the molt earlier than females (Hamilton, 1940). Jackson (1928) found that most specimens attained a complete winter pelage by late October to early November, although a few individuals were in full winter fur by early October. The molt from winter to summer pelage extended from late April to late June in New York (Hamilton, 1940). Jackson (1928) found indications in a few specimens from the southern part of the distribution of the species that the summer molt may begin by mid-April but that most molted in May. A male from Roan Mountain, North Carolina, showed early signs of the summer molt on 19 April but another specimen from the same area had worn

FIGURE 1. Photograph of *Sorex fumeus* (courtesy of Rodger W. Barbour).

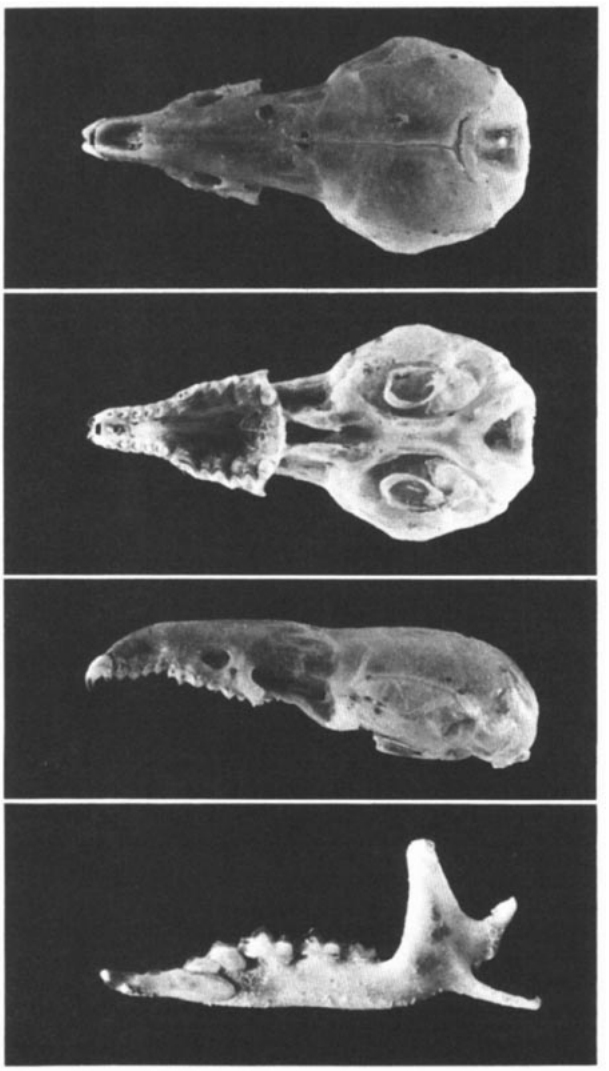

FIGURE 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Sorex fumeus* (AMNH 166895, male from Tompkins County, New York). Condylobasal length of skull is 18.1 mm. Photo by S. K. Smith.

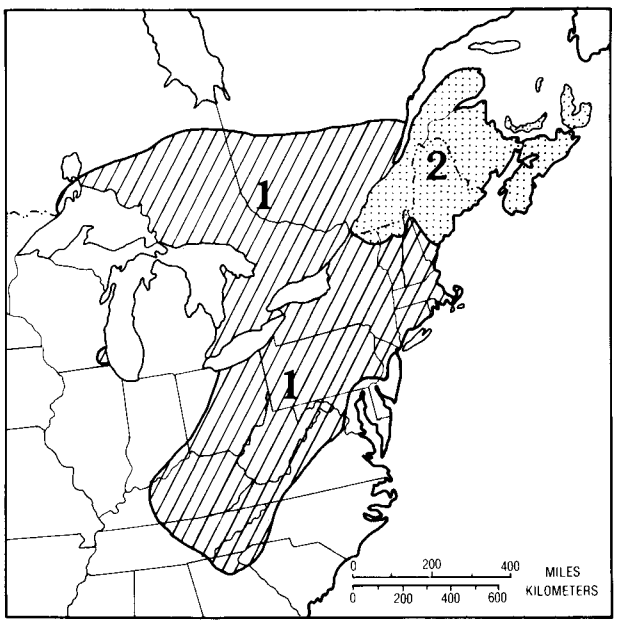

FIGURE 3. Current distribution of *Sorex fumeus* (adapted from Hall, 1981; Peterson, 1966): 1, *S. f. fumeus*; 2, *S. f. umbrosus*.

winter pelage on 3 May. The molt also was discussed by Connor (1960), Komarek and Komarek (1938), Miller (1895), and Smith (1940).

Within a given population many stages of the molt are evident over a considerable period of time (Hamilton, 1940), but an individual may complete the molt rapidly. Although Hamilton found that most smoky shrews lost hairs from the entire body, and thus did not exhibit a well-delineated molt line, he observed that the molt seemed to begin on the venter, progress to the shoulders and middorsum, and spread to the ears and rump.

Both sexes of *S. fumeus* possess side glands (Hamilton, 1940). Immature females may not manifest these glands but they are always evident in immature males. Glandular enlargement occurs in concert with reproductive maturity and in males produces an odorous secretion that may be a sex attractant (Hamilton, 1940). Descriptions and a photograph of the side glands were presented by Eadie (1938) and Hamilton (1940). When in reproductive condition, tails of both sexes may swell and a basal constriction may form (Goodwin, 1935; Hamilton and Whitaker, 1979; Snyder, 1942). In two subadults, Palmer (1947) described a bare triangular area on the skull roof.

Of the three pairs of inguinal teats, the first is the largest, extending from an area anterior to the thighs to near the sacral vertebrae (Hamilton, 1940). Hamilton provided a photograph of the mastology of a nursing smoky shrew. Palmer (1947) reported a postpartum female with both hind legs encircled by mammary glands.

The dentition of *S. fumeus* is: i 3/1, c 1/1, p 3/1, m 3/3, total 32 (Jackson, 1928).

The following discussion of the reproductive anatomy of *S. fumeus* was taken from Hamilton (1940). The testes of a sexually mature male were oval and measured 4 by 8 mm. The caput epididymis, often poorly defined, usually was infixed somewhat in yellow fatty tissue and the cauda epididymis was large. When visible through the walls of the epididymis the convoluted tubules always contained sperm and indicated that the specimen was in breeding condition. The proximal end of the vas deferens began as a narrow tube and gradually increased in size until its distal two-thirds was attained. At this point there was a conspicuous constriction. The distal section was greatly swollen and tapered gradually until reaching the urethra. Two large paired organs lying dorsal to the vasa deferentia and bladder were regarded as possible seminal vesicles. The bean-shaped Cowper's glands were about two-thirds the size of the testes and lay at the base of the tail. The penis, when retracted, was folded on itself with the tip lying over the proximal portion. The extended penis measured 16 to 18 mm and did not contain a baculum.

The ovaries of immature and anestrous adults were oval and about 1 mm or less in length. In breeding animals the ovaries were considerably larger with follicles and two to five corpora lutea appearing above the surface. The ovaries were invested by a prominent periovarian sac. The oviduct was well differentiated from the uterine cornu and was bent into an S-shaped configuration. The vagina was bent back upon itself with the distal portion lying dorsal to the proximal portion so that the vagina joined with the uterine horns near the bladder. The lower part of the vagina joined the urogenital sinus near the urethral opening. The clitoris was poorly marked.

Wimsatt and Wislocki (1947) discussed the morphology of the placenta and fetal membranes in *S. fumeus*. The first indication of pregnancy in *S. fumeus* was the appearance of several spheroidal enlargements in each cornu involving the lateral and antimesometrial walls of the horn. A dilation of the antimesometrial half of the cornual lumen produced a swelling about the enlarging blastocyst. Although embryonic swellings might occur in the corpus uteri, they usually were regularly spaced along the uterine cornua. As the implantation chambers enlarged, the cylindrical segments of the cornua between them were gradually incorporated into the chamber walls. Thus, the cylindrical segments, at first well marked, became relatively shallow constrictions separating adjacent implantation sites. The progressive enlargement of the implantation chambers mainly involved the lateral and antimesometrial walls of the cornua, the mesometrial wall being only slightly affected. This caused the uterine horns to be bent sharply toward the mesometrium and twisted.

The uterine site of implantation comprised a larger darker swelling located mesometrially, and a smaller paler mass superimposed on it. The embryo was contained in the darker mesometrial swelling that enlarged rapidly as the fetus grew. The discoidal placenta constituted the paler mass and increased in size less rapidly. The boundary between these structures was marked by a shallow constriction on the uterine surface.

Unlike *Blarina brevicauda*, *S. fumeus* had a thin but conspicuous diaphragmal fold of uterine mucosa that partially separated the placenta from the remainder of the gestation chamber. This conspicuous membrane began to form in the first half of pregnancy and grew from the uterine wall at the edge of the placenta from which it projected into the uterine cavity. It thus lay between the trophoblastic annulus and the fetal surface of the placenta. The umbilical cord, the rim of the invaginated yolk-sac, and the upper half of the trophoblastic annulus passed through its central opening. Both sides of the diaphragm were covered by hypertrophied uterine epithelium.

Sorex fumeus also differed from *B. brevicauda* in that there was no appreciable thickening of the syncytiotrophoblast at the tips of the chorionic villi. The syncytium remained almost as thin at the ends of the villi as at the maternal capillaries within the labyrinth. In an older specimen most of the crypts were destroyed totally, but occasional groups of epithelial cells were clustered about the maternal vessels in the base of the placenta between the tips of the fetal villi. The connective tissue of the basal layer of the mucosa was in direct contact with the tips of the fetal villi, many of which apparently extended to the muscularis of the uterine wall. A thin lamina of syncytiotrophoblast usually lay over the tip of each villus. There was an hypertrophy of the mesenchymal cells comprising the cores of the chorio-alantoic villi.

In late stages of pregnancy, remnants of an entodermal allantois remained. An allantoic stalk extended through the umbilical cord of *S. fumeus* to the fetal surface of the placenta. The allantoic diverticulum was composed of a thin solid strand of epithelioid cells, and eventually became discontinuous.

The chorio-allantoic labyrinth of *S. fumeus* is endotheliochorial rather than hemochorial. Wimsatt and Wislocki (1947) presented several photographic figures of the placentation of *S. fumeus*.

Wislocki and Wimsatt (1947) discussed the chemical cytology of the gravid uterus, placenta, and fetal membranes in *S. fumeus*. *S. fumeus* has a chorio-allantoic and a yolk sac placenta. The epithelial cells of the uterine glands contained small quantities of glycogen and iron and showed cytoplasmic basophilia. Minute lipoidal droplets were demonstrated in the epithelium of the lining of the uterine glands and in the uterine surface epithelium. The epithelium and lumens of the uterine glands were rich in phosphatase. This enzyme also was demonstrated in the surface epithelium and in the uterine crypts at the sites of implantation.

Phosphatase, glycogen, and products giving the Turnbull blue reaction for iron occurred in the uterine lumen. This cavity also received secretions from the uterine glands and contained brown and green pigmented material, extravasates of maternal blood, and cellular debris derived from the endometrium. Combined, these substances formed a pabulum that bathed the chorionic membrane. The cells of the chorionic membrane, especially the columnar ones, composed the trophoblastic annulus and were phagocytic. They gave intense reactions for phosphatase, iron, and variably for glycogen.

The vascularized visceral layer of the yolk sac, together with the bilaminar omphalopleure, formed the yolk sac placenta. It appeared that the chorionic epithelium absorbed material in the uterine lumen, including iron compounds, erythrocytes, phosphatase, and possibly glycogen. Chorionic products passed through Reichert's membrane into the yolk sac and were absorbed by the cells lining its visceral wall. Iron and phosphatase occurred in the secretion filling the yolk sac.

The chorionic epithelium contained many large birefringent fat droplets, exhibited green fluorescence, and gave a positive Schiff's plasma reaction. Because of these properties it was conjectured to be the location of steroid hormone production. Reichert's membrane was composed of collagen and was regarded as a possible product of the chorionic epithelium. This membrane exhibited reactions for iron and phosphatase. The visceral layer of the yolk sac was lined with large entodermal cells giving the Turnbull blue reaction for iron, glycogen, phosphatase, and basophilic substance.

Strong cytoplasmic basophilia were exhibited by the trophoblast but declined as gestation proceeded. As the placental labyrinth aged phosphatase appeared in increasing amounts. This enzyme occurred mainly in the fetal elements of the endotheliochorial trabeculae. Wislocki and Wimsatt (1947) presented several micrographs of the placental cytology of *S. fumeus*.

Christian (1963) reported that the adrenal gland of *S. fumeus* was characterized by a relatively large medulla and a narrow cortex only a few cells in thickness. Cortical thinness was marked especially in adult males and suggested to Christian (1963) that a relationship existed between adrenocortical mass, metabolic rate, and body size.

Pearson (1950) sectioned the submaxillary gland of *S. fumeus* and found that the tubules contained grandular segments similar to, but not as enlarged as, those in *Blarina brevicauda* and *Neomys fodiens*. The staining reaction in the tubules of *S. fumeus* was similar to that of *B. brevicauda*. The nuclei of the granule-filled cells in *S. fumeus* were relatively large and spherical, and usually were not flattened or situated near the bottom of the cell as in *B. brevicauda*.

Sealander (1964) measured several characteristics of the blood of *S. fumeus*. An adult male that weighed 7.3 g had a mean hemoglobin blood concentration of 18.1 g/100 ml, a mean corpuscular hemoglobin concentration of 34.6%, and a hematocrit ratio of 52.3. He found *S. fumeus* to have a mean dry erythrocyte diameter of 5.5 microns (range 4.8 to 6.1). Kendeigh (1945) reported the body temperature of a female *S. fumeus* to be 37.8°C. However, this temperature may have been in error as the animal was very excited and died soon after the temperature was taken. *S. fumeus* may use vision to some extent but the sense of smell appears to be weak (Hamilton, 1940). Tactile sensation, mediated through the vibrissae may be an important sense in searching (Hamilton, 1940). Hamilton observed that captive smoky shrews drank little water, suggesting that most of their water might be obtained from food.

ONTOGENY AND REPRODUCTION. The reproductive season of *S. fumeus* appears to extend from late March to early October. In New York, Hamilton (1940) found males and females taken in January and February to be sexually immature. Males had undeveloped, aspermatic testes. In late March, Hamilton (1940) took specimens with mature, descended testes containing many sperm. All males collected by Hamilton (1940) from early April to early June possessed enlarged vasa deferentia, seminal vesicles, and testes. Connor (1960) collected a male in New York on 24 February that was approaching reproductive maturity. Roberts and Early (1952) reported males from southeastern Pennsylvania in breeding condition during early March. Grimm and Whitebread (1952) found that most males from northeastern Pennsylvania in April were in breeding condition. Males seem to maintain sexual activity through August and September (Hamilton, 1940). Komarek and Komarek (1938) and Conner (1960) took males during late August and mid-September, respectively, with enlarged testes. Connor (1960) and Hamilton (1940) discussed testicular differences between immature and sexually mature *S. fumeus*.

The maturation of reproductive organs of females may begin later than that of males (Hamilton, 1940). Of four females he captured in late March only one was in estrus; however, its vagina contained no sperm nor were there corpora lutea present. Hamilton (1940) suggested that in New York earliest pregnancies occurred in mid-April. Connor (1960) took a female with enlarged reproductive structures in New York in March but found no indications of sexual activity in three other females collected in late March. All females taken by Connor (1960, 1966) during April were in breeding or near breeding condition. Pregnant females were collected by Linzey and Linzey (1968) during March and early April from the Great Smoky Mountains National Park of North Carolina and Tennessee and by Whitaker et al. (1975) during April from North Carolina. On the basis of two subadults taken on 6 June, Palmer (1947) estimated that the breeding season began in late April or early May in Maine.

Reproduction may extend into late summer and early autumn. Lactating or recently lactating females were collected from late September to 12 October by Connor (1966), Green (1930), Grimm and Whitebread (1952), Hamilton (1940), and Komarek and Komarek (1938).

Smoky shrews do not breed in the year of birth but overwinter as immatures; they lose weight during winter and mortality may be high. In early spring, they quickly gain weight and become

sexually mature (Hamilton, 1940). Hamilton (1940) estimated the maximum life span of *S. fumeus* at about 14 to 17 months.

Postpartum estrus was reported by Hamilton (1940), who found nursing pregnant females. Hamilton estimated the gestation period to be about 3 weeks or less. Barbour and Davis (1974), Hamilton and Whitaker (1979), Jackson (1961), and Wrigley (1969) postulated that two and sometimes three litters were produced in a year.

Based on numbers of embryos and placental scars in 42 females, Hamilton (1940) estimated that the average female produced 5.5 embryos (range 2 to 8). A female taken by Linzey and Linzey (1968) had four embryos (crown-rump length = 5.5 mm); another contained 6 embryos (crown-rump length = 4.5 mm). Numbers of embryos also were reported by Connor (1960, 1966) and Whitaker et al. (1975). In Pennsylvania, pregnant females were taken from 13 April to 3 September, with a mean embryo count of 5.1 (Gifford and Whitebread, 1951; Grimm and Whitebread, 1952; Richmond and Grimm, 1950; Richmond and Roslund, 1949).

One-month-old *S. fumeus* weighed about 4 g (Hamilton, 1940). Among adult smoky shrews collected from March to August, 29 males averaged 8.9 g and 24 females averaged 7.4 g.

ECOLOGY AND BEHAVIOR. *Sorex fumeus* inhabits primarily the cool, shaded floors of deciduous and coniferous forests. Microhabitats of *S. fumeus* commonly include thick leaf mold over friable soils, damp mossy-covered rocks, and old decaying logs and brush (Bole, 1935; Bole and Moultrop, 1942; Burt, 1957; Caldwell et al., 1982; Conner, 1960; Gifford and Whitebread, 1951; Goodwin, 1929; Grimm and Whitebread, 1952; Hamilton, 1940; Kellogg, 1939; Kirkland, 1974; Rand, 1933; Richmond and Roslund, 1949; Wrigley, 1969). Populations of *S. fumeus* also occupy a variety of other communities. In Canada, smoky shrews were reported from bogs and swamps (Brown and Lanning, 1954; Clark, 1938; Saunders, 1910, 1929), grassy areas (Snyder, 1930), and talus slopes (Snyder, 1942; Wrigley, 1969). In the United States, *S. fumeus* is known to occupy bogs and swamps (Christian, 1951; Copeland, 1912; Green, 1943; Grimm and Whitebread, 1952; Kellogg, 1937; Odum, 1949; Osgood, 1938; Rhoads, 1903), talus slopes (Caldwell et al., 1982; Connor, 1960; Harper, 1929; Harper and Harper, 1929; Roberts and Early, 1952; Werner, 1956), stream banks (Barbour, 1951*b*; Christian, 1951; Connor, 1960; Kellogg, 1937; Gifford and Whitebread, 1951), and grassy areas (Connor, 1960; Gifford and Whitebread, 1951; Odum, 1949; Roslund, 1951). Caldwell and Bryan (1982) found that smoky shrews were abundant in forest above the 5-year flood plain of the Kentucky river in northern Franklin County, Kentucky, but that these shrews seldom moved into the annually-inundated riparian forest. Hamilton and Whitaker (1979) noted that smoky shrews did not occur in coastal marshes.

Microhabitats of *S. fumeus* provide some protection from temperature extremes. Hamilton (1940) found that in August, in New York, the ambient temperature in open areas was 31.1°C, whereas in the shaded interior of the woods the temperature was 27.2°C, and beneath the leaf mold, in galleries used by smoky shrews, the temperature was only 20.6°C. During winter, in the absence of snow cover, temperatures in the galleries of *S. fumeus* ranged from −6.7°C to −0.6°C when the temperature of the open forest floor was −13.3°C.

Smoky shrews are reported to be less common in dry areas (Hamilton and Whitaker, 1979; Handley and Patton, 1947; Rand, 1933; Roberts and Early, 1952; Warburton, 1949). However, Hamilton (1940) noted that, although moist situations may be preferred, *S. fumeus* was collected in relatively dry situations. Barbour (1951*b*) took *S. fumeus* from dry deciduous woods in Kentucky, as did Howell and Conaway (1952) in Tennessee. Caldwell et al. (1982) reported *S. fumeus* from mesic to dry-mesic north-facing upland situations in Indiana.

Local distributions of smoky shrews appear to be clumped, suggesting the possibility of colonial habits. Hamilton (1940) observed that *S. fumeus* occurred in abundance in certain forest localities but was relatively scarce in others. Cameron and Orkin (1950), Goodwin (1929), Saunders (1929), and Snyder (1942) reported an uneven ecological distribution in Canada as did Barbour and Davis (1974), Goodwin (1935), Kirkland and Griffin (1974), Miller (1899), and Richens (1974) in the United States.

Sorex fumeus is active throughout the year (Connor, 1960; Hamilton, 1940; Hamilton and Whitaker, 1979), and is tolerant of low winter temperatures. Connor (1960) collected specimens on the surface of snow in subzero weather. Whitaker (Hamilton and Whitaker, 1979) collected *S. fumeus* in −35°C weather.

Hamilton (1940) and Godin (1977) listed the predators of *S. fumeus* as bobcats (*Felis lynx*), foxes (*Vulpes vulpes* and *Urocyon cinereoargenteus*), hawks (Accipiteridae and Falconidae), owls (Tytonidae and Strigidae), and weasels (*Mustela* spp.). Skull fragments of *S. fumeus* were discovered by Hamilton (1940) in the pellets of long-eared owls (*Asio otus*).

Short-tailed shrews, *Blarina brevicauda*, often occur in substantial numbers in the same habitats as *S. fumeus*, and Connor (1960) and Jameson (1949) noted an inverse relationship between population densities of *Blarina* and *S. fumeus*. Documentation of predation by *Blarina* was provided by Hamilton (1940), who found the remains of *S. fumeus* in the stomach of a *B. brevicauda*. The possibility that *S. fumeus* may engage in intraspecific aggression is suggested by Goodwin (1935) and Hamilton and Whitaker (1979). Hamilton (1940) postulated that the canopy of leaf mold may afford *S. fumeus* some degree of protection from predation.

Kirkland and van Deusen (1979) noted the morphological similarity between *S. fumeus* and *S. dispar*. They emphasized that these two shrews foraged through the same galleries beneath the leaf mold and were often caught in the same traplines. On the basis of both morphological and ecological similarities, they suggested that *S. fumeus* and *S. dispar* were competitors. Jameson (1949) observed that in the presence of *S. cinereus*, *S. fumeus* was less common and suggested the possibility of interspecific intolerance.

The food of *S. fumeus* consists of a wide variety of invertebrates. Small quantities of plant material are taken, but animal matter is by far the largest component of the diet (Linzey and Linzey, 1968; Whitaker et al., 1975). Whitaker et al. (1975) presented the following analysis, by volume, of food contained in the stomachs of 10 *S. fumeus* collected in North Carolina: Chilopoda, 36.5%; earthworms, 19.0%; adult Lepidoptera, 19.5%; adult Scarabaeidae, 10.0%; unidentified insect larvae, 8.5%; lepidopterous larvae, 5.0%; *Chauliognathus* (Cantheridae) larvae, 1.5%; sowbugs, 1.5%; Phalangida, 1.5%; unidentified Coleoptera larvae, 1.5%; spider, 1.5%; internal organs of insects, 1.0%; vegetation, 0.5%; unidentified Coleoptera, 0.5%; dipterous larvae, 0.5%; and chironomid larvae, 0.5%. Hamilton (1940) listed an analysis of the stomach contents of 168 *S. fumeus* taken throughout the year in New York. The fungus *Endogone* was reported in the diet of the smoky shrew by Whitaker (1962) and Linzey and Linzey (1973). Data on the food habits of *S. fumeus* also were presented by Connor (1966), Hamilton (1930), Hamilton and Hamilton (1953), and Richmond and Roslund (1949).

Hamilton (1940) maintained *S. fumeus* in captivity on a diet of small snails, beetles, small earthworms, mouse flesh, centipedes, spiders, and sowbugs. Contrary to common belief, captive shrews never consumed more than about one-half of their own weight daily. Hamilton (1940) found that this varied diet was better for the shrews than one restricted to mealworms or cockroaches. Much chitinous material was undigested. Intermittent eating occurred throughout the daily cycle. When consuming small prey, captive *S. fumeus* simply bit and swallowed. Pieces were bitten from larger food as it was held down with the forepaws. Small plethodontid salamanders were held down and killed with a bite severing the spinal cord. After eating the viscera, feet, and head, the remaining parts were often left for other food. Hamilton doubted that *S. fumeus* could kill small rodents. He once placed a 14 g *Peromyscus* sp. and a 10 g smoky shrew together in the same cage. After unsuccessfully trying to take the mouse several times, the shrew stopped attacking.

Weight, tooth wear, and degree of hairiness of the tail were used by Hamilton (1940) to separate adult from immature *S. fumeus*. With these criteria, he determined that *S. fumeus* underwent an annual population turnover. He also found that subsequent to the breeding season the adult population died and that most shrews caught in fall and winter were immatures.

Estimates of population densities of *S. fumeus* vary considerably with different investigators and ecological situations. Bole (1935) estimated a population of 143/ha during a peak year, but, in habitats other than climax forest, he regarded less than 2/ha to be typical. Hamilton (1940) estimated densities of *S. fumeus* at 62 to 124/ha in good habitat in New York, but added that this was exceptionally high. In a beech forest near Ithaca, New York, *S. fumeus* populations of 22 to 35/ha were estimated by Hamilton

(1940). He also suggested that populations in some areas of western New York did not exceed 12 to 15/ha. Townsend (1935) estimated that combined populations of *S. fumeus* and *S. cinereus* varied from 0 to 156/ha in central New York. However, Bole (1939), Burt (1940), and Blair (1940) criticized the procedure used by Townsend. At a study area in northwestern Maine, Richens (1974) collected 0.92 *S. fumeus*/100 trap nights in 1969 but only 0.10/100 trap nights in 1970.

Hamilton (1940) noted the following small mammals associated with *S. fumeus* in New York: *Blarina brevicauda, Napaeozapus insignis, Peromyscus leucopus, Synaptomys cooperi, Zapus hudsonius, Microtus pennsylvanicus, Clethrionomys gapperi, Microtus pinetorum,* and *Parascalops breweri.* In Indiana, Caldwell et al. (1982) collected *S. fumeus* in association with *B. brevicauda, Cryptotis parva, M. pinetorum,* and *P. leucopus.* In upland situations in western Kentucky, *S. fumeus* was trapped in association with *S. longirostris* and *Microsorex hoyi* (Caldwell et al., 1982). Caldwell and Bryan (1982) captured five species of shrews (*S. fumeus, S. dispar, S. cinereus, M. hoyi,* and *B. brevicauda*) at Bad Branch Falls, Letcher County, Kentucky.

In favorable situations, the smoky shrew may constitute a significant portion of the small mammal population. Hamilton (1940) reported that, in good shrew habitats in New York, 11.8 to 20.2% of the small mammals captured were *S. fumeus.* Hamilton found that at three different study sites smoky shrews averaged 18.3% of the small mammals captured. Werner (1956) noted that *S. fumeus* was the most common mammal captured on a talus slope in hardwood forest in northern New York. Caldwell and Bryan (1982) reported that *S. fumeus* was the most common long-tailed shrew in the Eastern Coal Field of Kentucky. In rich mesic forest of Kentucky, they took as many as 15 specimens in two pitfall cans left in place for 15 days.

Smoky shrews may not construct their own runways and tunnels, but they often use those made by other small mammals. Smoky shrews were captured from runways of *Cleithrionomys gapperi* (Hamilton, 1940; Smith, 1940), *Microtus* sp. (Conner, 1960; Kellogg, 1937; Odum, 1949), *Synaptomys cooperi* (Hamilton, 1941; Odum, 1949; Roslund, 1951), *Condylura cristata* (Rand, 1933), and *Parascalops breweri* (Hamilton, 1939). When Hamilton (1939) disturbed runways used by smoky shrews they did not repair them. Hamilton (1940) observed that captive smoky shrews did not excavate the friable soil on the floor of their cage.

Hamilton (1940:478) described the voice of *S. fumeus* as follows: "When alarmed . . . the smoky shrew utters a high-pitched grating note, not unlike that of the smaller bats. If greatly disturbed, it will throw itself on its back, and with spread and waving legs, repeatedly utter these squeaking staccato notes. When foraging for food these little shrews utter an almost indiscernible twitter. I have twice seen these little forest mammals rooting through the leaf mold or appearing on the forest litter about rotted logs, the twitching nose and vibrissae held aloft, and this faint, almost inaudible twittering was kept up continually."

The nest of the smoky shrew is nearly spherical and about 23 cm in circumference (Hamilton, 1940). Hamilton found nests in hollow logs, within tunnels, or beneath forest floor debris, usually from 10.2 to 22.9 cm under the surface. Animal fur and plant matter may be used for nest material (Hamilton, 1940).

Endoparasites of *S. fumeus* were reported by Lankester and Anderson (1966), who found lungworm larvae (Metastrongyloidea) encapsulated in the liver. They considered the smoky shrew to be a paratenic host for this worm. Hamilton (1940) reported that nematodes, *Porrocaecum* sp., were found coiled in a sheath among muscles, the external walls of the stomach, and attached to the viscera generally. Heavy infestations of this sizeable roundworm (measuring 40 mm in length) consisted of about 10 or 12 individuals (Hamilton, 1940). Wrigley (1969) reported a nematode coiled in the fascia between the scapulae in a smoky shrew from South Bolton, Quebec. Soloman and Handley (1971) reported the nematode, *Capillaria hepatica,* from the liver of *S. fumeus* at Mountain Lake, Virginia.

The following ectoparasites and other associates were reported from *S. fumeus*: mites—*Myobia, Haemogamasus, Protomyobia* (Hamilton, 1940), *Xenoryctes nudus* (Fain and Whitaker, 1975; Whitaker et al., 1975), *Myonyssus jamesoni* nymphs (Jameson, 1950), *Haemolaelaps glasgowi* (Strandtmann, 1949), *Euhaemogamasus liponyssoides* (Keegan, 1951), *Hirstionyssus talpae* (Whitaker et al., 1975; Herrin, 1970), *H. blarinae* (Herrin, 1970), *Protomyobia brevisetosa* (Jameson, 1948; Whitaker et al., 1975), *P. claparedei* (Jameson, 1948; Ewing, 1938), *Androlaelaps fahrenholzi, Orycteroxenus soricis, Haemogamasus ambulans, H. liponyssoides, Ornithonyssus bacoti, Pygmephorus horridus, P. equitrichosus,* Anoetidae (unidentified), ?*Hypoaspis* sp. (Smiley and Whitaker, 1979; Whitaker et al., 1975); chiggers—*Euschongastia blarinae* (Jameson, 1950), *Euschongastia jonesi, Neotrombicula cavicola, Cheladonta ouachitensis* (Whitaker et al., 1975); ticks—*Ixodes angustus* (Whitaker et al., 1975); fleas—*Doratopsylla blarinae* (Hamilton, 1940; Jameson, 1950; Benton and Kelly, 1975), *Protomyobia brevisetosa* (Jameson, 1948), *Corrodopsylla curvata* (Whitaker et al., 1975), *Ctenopthalmus pseudagyrtes* (Hamilton, 1940; Miller and Benton, 1973; Benton and Kelly, 1975; Whitaker et al., 1975), *Epitedia wenmanni* (Benton and Kelly, 1975), *Nearctopsylla genalis* (Benton and Kelly, 1975). Nests of *S. fumeus* examined by Hamilton (1940) were found to be free of parasites.

GENETICS. Meylan (1968) reported a diploid chromosome number of 66; the fundamental number (FN) was 98, and included autosomal arms and arms of the sex chromosomes of the female.

REMARKS. Opinion differs regarding the subgeneric position of *S. fumeus.* Jackson (1928) and Findley (1955) placed *S. fumeus* in the subgenus *Sorex* but Junge and Hoffmann (1981) stated that *S. fumeus* seemed to be an *Otisorex.* The subgenus *Otisorex* is characterized by a lingual pigmented ridge running from the apex to the cingulum of each unicuspid and by the absence of a post-mandibular foramen (Diersing and Hoffmeister, 1977; Findley, 1955; Hoffmann and Peterson, 1967; Junge and Hoffmann, 1981). Junge and Hoffmann (1981) noted that in *S. fumeus* the pigmentation on this ridge may be faint or absent. Additionally, although some *Otisorex* have a post-mandibular foramen, this character occurs more often in one or both rami in *S. fumeus* than is typical of the subgenus *Otisorex* (Findley, 1955; Junge and Hoffmann, 1981). Thus, some *S. fumeus* may be confused with shrews of the subgenus *Sorex* (Junge and Hoffmann, 1981). Fortunately, the distribution of *S. fumeus* is allopatric to that of all species of the subgenus *Sorex* except *S. articus,* with which it overlaps slightly (Junge and Hoffmann, 1981).

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