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Synaptomys cooperi.

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Synaptomys Baird, 1858

Synaptomys Baird, 1858:558. Type species *Synaptomys cooperi* Baird.

Mictomys True, 1894:242. Type species *Mictomys innuitus* True (= *Synaptomys borealis innuitus*).

CONTEXT AND CONTENT. Order Rodentia, Suborder Myomorpha, Family Cricetidae (considered Muridae by some authors), Subfamily Microtinae. *Synaptomys* contains two living species in two subgenera. A key to the species follows (adapted from Blair et al., 1968, and Hall, 1981).

Mammae six; mandibular molars with closed triangles on labial (outer) side; mandibular incisors heavy; palate ending posteriorly with a broad blunt median projection .... (subgenus *Synaptomys*) *S. cooperi*

Mammae eight; mandibular molars without closed triangles on labial (outer) side; mandibular incisors relatively slender; palate ending posteriorly with a sharply pointed median projection .... (subgenus *Mictomys*) *S. borealis*

Synaptomys cooperi Baird, 1858

Southern Bog Lemming

Synaptomys cooperi Baird, 1858:558. Type locality fixed by Bole and Moulthrop (1942) at Jackson, Carroll County, New Hampshire.

CONTEXT AND CONTENT. Context given in generic summary above. Seven subspecies are recognized:

S. c. cooperi Baird, 1858:558, see above.

S. c. gossii (Coues, 1877:235). Type locality Neosho Falls, Woodson County, Kansas (*saturatus* Bole and Moulthrop is a synonym).

S. c. helaletes Merriam, 1896:59. Type locality "Dismal Swamp, Norfolk Co., Virginia."

S. c. kentucki Barbour, 1956:414. Type locality "Sadieville, Scott County, Kentucky."

S. c. paludis Hibbard and Rinker, 1942:26. Type locality "Meade County State Park, fourteen miles southwest of Meade, Meade County, Kansas."

S. c. relictus Jones, 1958:387. Type locality "Rock Creek State Fish Hatchery, 5 mi. N, 2 mi. W Parks, Dundy County, Nebraska."

S. c. stonei Rhoads, 1893:53. Type locality May's Landing (Egg River), Atlantic County, New Jersey.

DIAGNOSIS. Diagnostic features of the genus *Synaptomys* include a short tail (slightly longer than the hindfoot), short rostrum (less than 25% of total skull length), and broad, longitudinally grooved upper incisors (Hall, 1981; Howell, 1927). This combination of characteristics distinguishes *S. cooperi* from all sympatric microtine species except *S. borealis*. Differences between *S. cooperi* and *S. borealis* are given in the key above. As noted, the lower incisors of *S. cooperi* are broad and blunt in contrast with the slender, sharply pointed incisors of *S. borealis*. The result is that each upper incisor of *S. borealis* is unworn at the outer edge, producing a splinter of enamel, but the upper incisors of *S. cooperi* are evenly worn across their width. Except for the subspecies *cooperi*, skulls and incisors of *S. cooperi* are more massive than those of *S. borealis*. Conversely, *S. cooperi* tends to have smaller auditory bullae, shorter incisive foramina, and a relatively shorter rostrum.

GENERAL CHARACTERISTICS. *Synaptomys cooperi* is a comparatively small vole with small eyes and ears, and a short tail (Fig. 1). The head appears large relative to overall body size. Facial hairs can be erected to form a "facial disk" around the snout. Dorsal color ranges from bright chestnut to dark grizzled brown, whereas the venter is silver to light gray. Juvenal pelage is dark gray-brown and is replaced by subadult pelage that resembles the adult pelage, but is darker and duller (Connor, 1959). Bole and Moulthrop (1942) noted that fresh winter pelage of *S. c. cooperi* was longer, softer, and paler than the dark brown summer pelage. Howell (1927) also commented that the winter coat was longer and more dense.

Among the subspecies, *S. c. kentucki* and *S. c. cooperi* are smallest in overall body size, whereas *S. c. paludis* and *S. c. relictus* are largest (Barbour, 1956; Jones, 1958; Wetzel, 1955). Ranges of measurements (in mm) are: total length, 94 to 154; length of tail, 13 to 24; length of hindfoot, 16 to 24; length of ear from notch, 8 to 14. Mass ranges from 21.4 to 50 g. Wetzel (1955) noted that the sexes did not differ significantly in size.

DISTRIBUTION. The southern bog lemming occurs in eastern North America from southeastern Canada west to western Minnesota; south to southwestern Kansas, northeastern Arkansas, southeastern Tennessee, and northeastern North Carolina (Fig. 2). Within this general range, populations may be localized and distribution may change with time. Two subspecies (*S. c. helaletes* and *S. c. relictus*) have disjunct distributions, and two subspecies (*S. c. paludis* and *S. c. relictus*) are known only from their type localities. The Dismal Swamp subspecies (*S. c. helaletes*) was recently "rediscovered" after a hiatus of 83 years between collections (Rose, 1981). *Synaptomys c. stonei* is restricted to higher elevations in the southern portion of its range.

FOSSIL RECORD. The late Pleistocene range of *Synaptomys cooperi* extended much further southward than the present range. Cushing (1945) removed several mandibles from surface level deposits of San Josecito Cave (elevation 2,256 m), near the town of Aramberri, southern Nuevo Leon, Mexico. Remains of this species were identified from several sites across eastern Texas, and from fluviatile deposits near Dallas (Dalquest, 1965; Patton, 1963). During the Pleistocene, much of the current range of *S. cooperi* was occupied by *S. borealis*, as fossil remains of the boreal species were found as far south as Tennessee and Kansas (Guilday et al., 1978; Hibbard, 1954). Remains of *S. borealis* outnumber those of *S. cooperi* at sites in Pennsylvania and Virginia but are rare in Tennessee cave deposits (Guilday et al., 1978). Guilday et al. (1977) recovered both species from a Pennsylvania cave, where a stratigraphic shift in relative numbers indicated that *S. cooperi* replaced *S. borealis* about 11,000 years ago. However, except for late

FIGURE 1. Adult female *Synaptomys cooperi stonei* from Montgomery County, Virginia. Photo by A. V. Linzey.

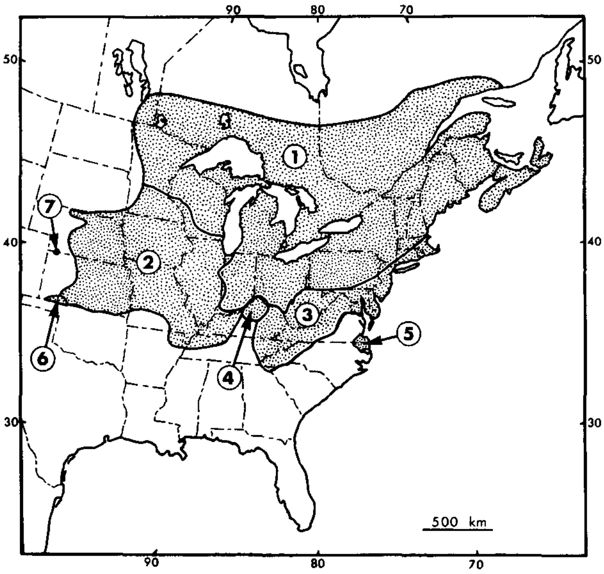

FIGURE 2. Geographic range of *Synaptomys cooperi*. Subspecies are: 1, *S. c. cooperi*; 2, *S. c. gossii*; 3, *S. c. stonei*; 4, *S. c. kentucki*; 5, *S. c. helaletes*; 6, *S. c. paludis*; 7, *S. c. relictus*. Map modified from Hall, 1981.

Wisconsinan sites in Tennessee, *S. cooperi* fossils constituted a small percentage of vole remains in Pennsylvania and Virginia, leading Guilday et al. (1978) to suggest that southern bog lemmings were uncommon even in precolonial times.

Wilson (1933) found remains of *Synaptomys vetus* in late Pliocene deposits in southern Idaho, whereas Hibbard (1941) assigned to this species remains found in the oldest interglacial fauna of Kansas. Other *Synaptomys* fossils found in Kansas Pleistocene deposits include *S. borealis*, *S. bunkeri*, and *S. landesi* (Hibbard, 1939, 1954).

Simpson (1928) described *S. australis* from Saber-tooth Cave, Citrus County, Florida. Remains of this species were reported from several caves in northern Florida and from southwestern Kansas (Hibbard, 1955; Olsen, 1958). Olsen (1958), citing minute differences between *S. cooperi* and *S. australis*, questioned whether *S. australis* warranted specific designation. Fossil material from Pennsylvania, Virginia, and Tennessee examined by Guilday et al. (1978) indicated that *S. cooperi* increased in size with decreasing latitude during Pleistocene. These authors suggested that there was a size continuum between *S. cooperi* and the larger *S. australis*, but indicated a need for specimens from Alabama and Georgia.

FORM AND FUNCTION. The literature contains few references to morphology and physiology of *Synaptomys*.

Developmental molts showed a definite sequence of hair replacement, but adult seasonal pelage replacement progressed from irregularly-located centers of growth (Hall, 1981; Howell, 1927).

Howell (1927) and Hall (1981) described the skull of *Synaptomys cooperi* as characteristically massive in appearance and with robust incisor teeth (Fig. 3). Upper incisors are prominently grooved. Mandibular molars have closed triangles on the labial side and well-developed outer reentrant angles. Molars are hypsodont, but not as high crowned as in most microtine genera. The palate has a poorly developed posterior spinous process. Wetzel (1955) examined skulls of adult *S. cooperi* from throughout its range. Five of 13 skull characteristics measured were useful in distinguishing the five subspecies studied: (1) width of upper incisors; (2) width of nasal bone; (3) condylobasilar length; (4) zygomatic width; and (5) height of skull. A regular increase in measurements of these dimensions occurred among the five subspecies as follows (arranged from smallest to largest)—*cooperi*, *stonei*, *helaletes*, *gossii*, and *paludis*. Cranial measurements of the more recently described subspecies *relictus* (Jones, 1958) and *kentucki* (Barbour, 1956) indicate that *relictus* is closest in size to *paludis*, whereas *kentucki* is most similar to *cooperi*.

Hamilton (1946) described the baculum of *S. c. cooperi* as follows: "The stalk has a broad, somewhat rounded base, a long narrow shaft, and an expanded, knob-like distal portion . . . digital processes are all small and may be closely appressed or widely separated." The baculum of *S. c. paludis*, illustrated by Hibbard and Rinker (1942), lacks lateral digital processes, but it may have been damaged during preparation. Hamilton (1946) concluded that, based on the baculum, *Synaptomys* is related more closely to *Dicrostonyx* than to *Lemmus*. Guilday (1951) described sexual dimorphism in the pelvic girdle of *Microtus pennsylvanicus* and commented that cursory examination of *Synaptomys* revealed the same characteristics. He noted that the postacetabular portion of the innominate is oval in males, but triangular in females. Furthermore, males have a heavier pelvic bone than females.

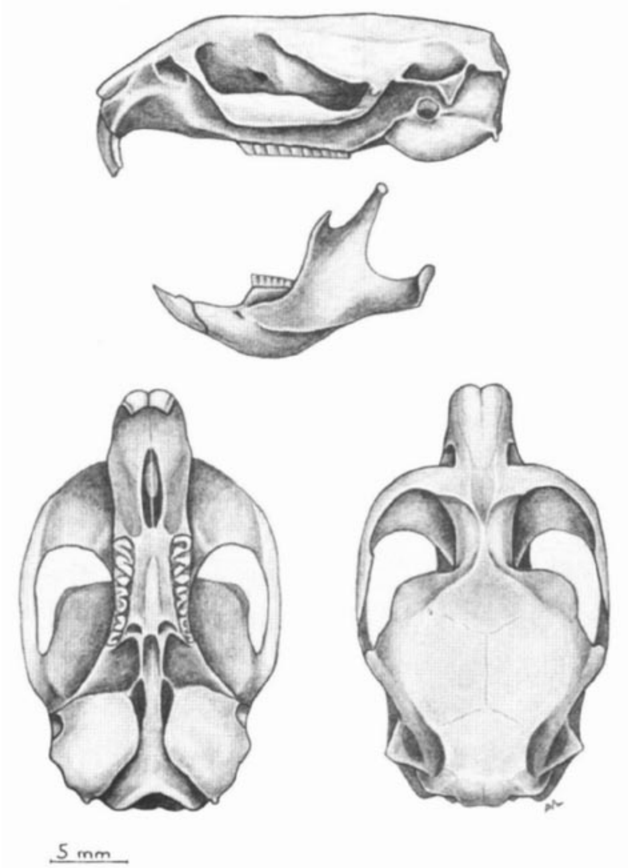

FIGURE 3. Dorsal, ventral, and lateral views of cranium and lateral view of lower jaw of *Synaptomys cooperi stonei* (AVL 469, male) from Spruce Knob, Pocahontas County, West Virginia. Illustration by A. V. Linzey.

Fecal pellets of *Synaptomys* are bright green in contrast with the brown or black droppings of *Microtus* (Burt, 1928; Cockrum, 1952; Connor, 1959; Linzey, 1981) suggesting inherent differences in digestive physiology. Knopf (1978) reported that caloric efficiency of *S. cooperi* was extremely low (4.85%) and that daily energy budget in winter was about 12.67 Kcal/animal^{-1} day^{-1}. Although digestive efficiency of *Synaptomys* probably is relatively low, the average value obtained by Knopf (1978) seems questionable because it was based on preserved specimens; seven of 21 had material with higher caloric content in the colon than in the stomach.

ONTOGENY AND REPRODUCTION. The gestation period for four litters of *Synaptomys* born in captivity ranged from 23 to "not more than 26 days," with conception occurring during postpartum estrus (Connor, 1959).

A synthesis of data on litter size (number of embryos, number of young at birth) indicates a range of one to eight young per litter, with three most common (Barbour, 1956; Burt, 1928; Connor, 1959; Coventry, 1937; Doutt et al., 1973; Fisher, 1945; Gottschang, 1965; Hall and Cockrum, 1952; Howell, 1927; Lindsay, 1960; Linsdale, 1927; Linzey, unpubl.; Oehler, 1942; Stegeman, 1930). Breeding occurs in all seasons, although the frequency of winter breeding seems to differ from place to place and from year to year. In Kansas, Gaines et al. (1977) reported that most young were born during "summer" (March to October), although later studies in the immediate area indicated that the percentage of adult females in breeding condition was approximately equal in "summer" (March to October) and "winter" (November to February) (Gaines et al., 1979). The frequency of breeding in eastern United States is extremely low between November and February. Connor (1959) noted a marked regression in testis size between October and November, with recrudescence occurring by April (no data for January through March). Fragmentary data from numerous other sources support these observations (Barbour, 1951, 1956; Doutt et al., 1973; Gottschang, 1965; Hamilton, 1941*a*; Howell, 1927; Komarek and Komarek, 1938; Lindsay, 1960; Linzey, unpubl.; Manville, 1960; Oehler, 1942; Stegeman, 1930; Stewart, 1943).

The only *Synaptomys* known to have bred in captivity is a female that gave birth to six litters (22 young) during a 26-week period (Connor, 1959). Available information on growth and development is based primarily on observations of these young, plus two additional wild-born litters (six young). Stegeman (1930) also reported on early development of two wild-conceived young. Neonates are pink except for light gray pigmentation of the dorsum. In addition to mystacial vibrissae, hair is present on the head and dorsum. Eyes are closed, ear pinnae are folded over, but claws are present on the toes. Average and extreme measurements (in mm) of 11 neonates (Connor, 1959) were: tail, 5.7 (5.0 to 6.5); hindfoot, 7.9 (7.5 to 8.5). Average mass was 3.9 (3.1 to 4.3) g. Increase in mass is rapid up to about 3 weeks, when growth nearly ceases. Wild-born young weigh considerably less than laboratory raised young at a comparable stage of development. Individuals are well furred by 7 days, and attain juvenal appearance by 2 weeks. Replacement of juvenal pelage begins at about 4 weeks and is completed in 10 days. Young are nursed regularly until 16 days of age and weaning is complete by the end of the third week. Eyes open at 10 to 11 days of age, and ear pinnae unfold by the second day. Lower incisors erupt between 6 and 8 days.

Connor (1959) reported that three of 12 wild individuals marked in October 1954 were recaptured during the following May, thus surviving at least 7 to 8 months. In captivity, a mated pair kept by Connor (1959) was at least a year old when killed. I maintained several *Synaptomys* for periods exceeding a year; the oldest was a female captured as an adult that lived an additional 2 years, 5 months.

ECOLOGY. Although the vernacular name "bog lemming" implies that *Synaptomys cooperi* is a bog-dwelling species, it occupies a wide range of habitats in addition to sphagnum (*Sphagnum* sp.) bogs. In the Midwestern prairie region and Great Lakes States, *Synaptomys* inhabits grassland (Burt, 1928; Easterla, 1970; Fisher, 1945; Getz, 1960; Lindsay, 1960; Linsdale, 1927; Mumford and Handley, 1956; Oehler, 1942; Stegeman, 1930), although some authors allude to the presence of shrubs in areas where *Synaptomys* occurs (Gaines et al., 1977; Getz, 1961; Rose and Spevak, 1978). Elsewhere, the habitat is considerably more diverse. Kirkland and Schmidt (1982) trapped six *Synaptomys cooperi* in mixed deciduous/coniferous forest in Nova Scotia and New Brunswick. However, most captures in southern Canada, New York State, and along the east coast of the United States are associated with sphagnum bogs or heavily forested areas (Buckner, 1957; Connor, 1953; Coventry, 1942; Goodwin, 1932; Hamilton, 1941*a*; Manville, 1960; Poole, 1943; Rose, 1981; Tuttle, 1968). Connor (1959) noted that *Synaptomys* numbers surpassed those of *Microtus* only in sphagnum bogs with shrub cover. In the southern Appalachians (Pennsylvania to Tennessee), where sphagnum bogs are rare, *Synaptomys* also is found in wet meadows, dry broomsedge (*Andropogon scoparius*) fields, pastures, grassy openings in woods, power-line rights-of-way, clearcuttings, and among mossy boulders in spruce (*Picea* sp.) forests (Barbour, 1951, 1956; Doutt et al., 1973; Hooper and Cady, 1941; Kirkland, 1977; Linzey, 1981; Odum, 1948, 1949; Smyth, 1946; Stewart, 1943; Welter and Sollberger, 1939). This bewildering array of habitats led Doutt et al. (1973) to suggest that the major feature common to *Synaptomys* habitats was that they were marginal for *Microtus*. This suggestion was supported by recent research that documented competitive exclusion of *Synaptomys* by *Microtus* in southwestern Virginia (Linzey, 1981).

Population density is probably low in forested areas of eastern United States. However, poor trapping success in situations where runways are not produced precludes reliable estimation of density. When patches of habitat with heavier ground cover are colonized by *Synaptomys*, signs of their presence (runways, droppings, cuttings) aid in trap placement and enhance trap success. Local, temporary concentrations (up to 24/ha, Linzey, 1981) cannot be used as estimates of area-wide densities. Connor's (1959) estimate of 4 to 12/ha probably is more representative of habitats where *Synaptomys* is a permanent resident. Considerably higher densities have been reported in other regions. For example, Stegeman (1930) recorded 34/ha in Michigan and Gaines et al. (1977, 1979) found densities up to 51/ha in Kansas. Demographic studies of the Kansas populations indicated that one population exhibited annual cycles of abundance, whereas two other populations underwent multiannual cycles (Gaines et al., 1977). They attributed the absence of a long-term cycle in the single population to lower reproduction and juvenile survival.

The home range of a single individual in sphagnum bog habitat in eastern Manitoba was 0.32 ha (determined by exclusive boundary-strip method; Buckner, 1957). Getz (1960) calculated home ranges for seven individuals in a grass-sedge marsh by the same method; average for females was 0.06 ha and for males 0.04 ha. Connor (1959) calculated minimum-area home ranges for nine individuals in sphagnum bog habitat in the New Jersey pine barrens between 0.04 ha and 0.20 ha with males ranging more widely than females.

The food of *Synaptomys* consists almost exclusively of vegetation. The diet is composed primarily of grasses and sedges, but also includes mosses, fruits, fungi, bark, and roots (Connor, 1959; Knopf, 1978). Stomach analyses of 86 specimens trapped throughout the year by Connor (1959) revealed that most of the diet (by volume) consisted of green vegetation (66%) and fruits of huckleberries and blueberries (14%). Primary food items of *Synaptomys* in Kentucky during winter and spring were fescue (*Festuca* sp.), bluegrass (*Poa* sp.), panic grass (*Panicum*) and manna grass (*Glyceria striata*) (Knopf, 1978). In southwestern Virginia, major foods were broomsedge in summer and mosses in winter (Linzey, 1981). The fungus *Endogone* was reported from *Synaptomys* stomachs on several occasions (Burt, 1928; Hamilton, 1941*a*, 1941*b*; Linzey and Linzey, 1973).

Although *Synaptomys* undoubtedly is preyed upon by a variety of carnivores, records of specific predation are sparse. Cook (1939) found a dead, but still warm, *Synaptomys* with tooth marks fitting the dentition of a weasel (*Mustela erminea*). Skulls of *Synaptomys* were recovered from owl pellets collected in southwestern Virginia (Linzey, unpubl. data), Indiana (Mumford and Handley, 1956) and Pennsylvania (Richmond and Rosland, 1949). French (pers. comm.) recovered a half-eaten *Synaptomys* from a road-killed short-eared owl (*Asio flammeus*).

Wassel et al. (1978) examined 65 southern bog lemmings for ectoparasites; 95.4% of animals were infested. The most common parasites were the louse, *Hoplopleura acanthopus*, the mites *Listrophorus synaptomys*, *Dermacarus hypudaei*, *Laelaps alaskensis*, and *Euschoengastia peromysci*, and the tick, *Dermacentor variabilis*. There was significant seasonal variation in parasite load. *Listrophorus synaptomys* was most abundant in summer and fall; *Hoplopleura acanthopus* was abundant in fall and winter; and *Laelaps alaskensis*, *Dermacarus hypudaei*, and *Euschoengastia peromysci* were most abundant in spring and winter. These authors found that chiggers (*Euschoengastia peromysci* and *E. ohioensis*) were significantly more common on females than on males.

Parasites recorded from *Synaptomys* are:

Acarina
- *Androlaelaps glasgowi* (Linzey and Linzey, 1968)
- *A. fahrenholzi* (Wassel et al., 1978)
- *Bakerdania* sp. (Wassel et al., 1978)
- *Dermacarus hypudaei* (Wassel et al., 1978)
- *Dermacentor variabilis* (Wassel et al., 1978)
- *Euschoengastia peromysci* (Wassel et al., 1978)
- *E. ohioensis* (Wassel et al., 1978)
- *E. setosa* (Wassel et al., 1978)
- *Euryparasitus* sp. (Wassel et al., 1978)
- *Eutrombicula alfreddugesi* (Wassel et al., 1978)
- *Haemogamasus liponyssoides* (Wassel et al., 1978)
- *Ixodes muris* (Wassel et al., 1978)
- *I. dentatus* (Wassel et al., 1978)
- *Laelaps alaskensis* (Wassel et al., 1978; Whitaker and Wilson, 1968; Wilson, 1957)
- *L. kochi* (Wassel et al., 1978)
- *L. stupkai* (Linzey and Crossley, 1971)
- *Listrophorus synaptomys* (Fain et al., 1974; Wassel et al., 1978)
- *Myocoptes japonensis* (Wassel et al., 1978)
- *Ornithonyssus bacoti* (Wassel et al., 1978)
- *Proctolaelaps* sp. (Wassel et al., 1978)
- *Pygmephorus mustelae* (Wassel et al., 1978)
- *P. scalopi* (Wassel et al., 1978)
- *Pygmephorus* sp. (Wassel et al., 1978)
- *Quasilistrophorus microticolus* (Fain et al., 1978)
- *Radfordia lemnina* (Wassel et al., 1978)
- *Xenoryctes latiporus* (Wassel et al., 1978)
- Oribatidae (Wassel et al., 1978)
- Anoetidae (Wassel et al., 1978)

Siphonaptera
- *Ctenophthalmus pseudogyrtes* (Wassel et al., 1978)
- *Epitedia wenmanni* (Wilson, 1961, *in* Wassel et al., 1978)
- *Megabothris asio* (Wassel et al., 1978)
- *Rhadinopsylla orama* (Wilson, 1961, *in* Wassel et al., 1978)

Anopleura
- *Hoplopleura acanthopus* (Wassel et al., 1978)

Trematoda
- *Quinqueserialis hassalli* (Whitaker and Adalis, 1971)

Cestoda
- *Andrya* sp. (Erickson, 1938)

BEHAVIOR. Burt (1928) and Connor (1959) commented on extreme nervousness of *Synaptomys* in captivity, but also noted that captives were docile and easily handled. Connor (1959) reported that pregnant females constructed nests for the young 1 to 2 days before parturition and the same nest was used for a subsequent litter. Females carried young by grasping the ventral surface in the mouth and were never observed to leave the nest with young attached to the teats. Connor (1959) noted several types of calls; he categorized them as associated with aggression, courtship, or communication between mothers and young.

Daily activity rhythms in *Synaptomys* have been reported as (1) chiefly nocturnal with some activity in the daytime (Burt, 1928); (2) exhibiting greatest activity in the afternoon and at night (Oehler, 1942); and (3) equally active day and night (Connor, 1959). Linzey (1981) found *Synaptomys* to be almost completely nocturnal regardless of season, with 86% of field captures throughout the year occurring between sunset and sunrise.

Studies of intraspecific (*Synaptomys* with *Synaptomys*, *Microtus* with *Microtus*) and interspecific (*Microtus* with *Synaptomys*) aggressive behavior in co-existing *Microtus ochrogaster* and *Synaptomys cooperi* populations indicate that *Synaptomys* shows more avoidance and less aggression as a species (intraspecific comparisons; Rose and Spevak, 1978). Furthermore, during interspecific encounters, *Microtus* more frequently dominates *Synaptomys* (Rose and Spevak, 1978). These results are supported by field observations that *Synaptomys* exhibits increased dispersal rates during rapid population increase by *Microtus* (Gaines et al., 1979).

Several authors have referred to *Synaptomys* as a "colonial" species (Barbour, 1951, 1956; Doutt et al., 1973; Hamilton, 1941*a*; Stegeman, 1930). Although *Synaptomys* is frequently highly local in distribution, there is presently no support for the notion that they are colonial in a social context.

GENETICS. The karyotype of *Synaptomys cooperi* exhibits a $2n = 50$, with $NF = 52$ (Hoffmann and Nadler, 1976). *S. cooperi* differs from *S. borealis*, as described by Matthey (1973), in having fewer chromosomes (*S. borealis* has $2n = 54$, $NF = 56$), a smaller X chromosome, and a different size relationship among the autosomes. These differences support the placement of *S. cooperi* and *S. borealis* in separate subgenera (Hoffmann and Nadler, 1976). Hoffmann and Nadler (1976) and Matthey (1973) suggested that *Synaptomys* represents an evolutionary link between voles and lemmings because the chromosome number of *Synaptomys* ($2n = 50$ or 54) is greater than that of other lemmings (*Dicrostonyx*, $2n = 30$ to 44; *Lemmus*, $2n = 50$; *Myopus*, $2n = 32$), but comparable to that of primitive vole genera (*Clethrionomys* and *Phenacomys*, $2n = 56$).

A completely albino *S. cooperi* was reported by Mannville (1955).

REMARKS. Wetzel (1955) suggested that the last glacial advance divided the subgenus *Synaptomys* into two populations: an ancestral *gossii* group in the southwest and ancestral *stonei* group in the southeast. Following glacial retreat, northward expansion occurred from these dispersal centers. Jones (1958) noted that *S. c. relictus* and *S. c. paludis* represented relict populations left behind as the southwestern range shifted northward. Similarly, *S. c. helaletes* appears to be a remnant of the southeastern dispersal center (Wetzel, 1955).

In the eastern portion of its range, *Synaptomys cooperi* long was regarded as a rare and elusive creature. Despite recent additions to our knowledge of this species, this assessment remains basically correct. *S. cooperi* occurs at low densities primarily in wooded areas, glades within forests, and ecotones. Association with these habitats is related partially to competitive exclusion by *Microtus pennsylvanicus* from areas with heavier ground cover. Clearing of eastern woodlands and replacement of native grasses with introduced species favors *Microtus*, thus precluding habitation by *Synaptomys* under most circumstances. Conversely, man-made clearings in places not readily colonized by *Microtus* (such as clearcuttings within extensive forested areas) favor *Synaptomys*. This general portrait of eastern populations contrasts sharply with that of midwestern populations in which *Synaptomys cooperi* coexists with *Microtus ochrogaster* (Gaines et al., 1977, 1979). If Wetzel's (1955) interpretation is correct, the species pair of *Synaptomys cooperi* and *Microtus ochrogaster* probably coevolved in isolation for an extended period and was subjected to different selection pressures than the *Synaptomys cooperi*-*Microtus pennsylvanicus* species pair.

I am indebted to Thomas W. French for providing data on a specimen of *Synaptomys cooperi* from along Interstate 24 in Montgomery County, Tennessee. This specimen is referred to *S. c. gossii* on the basis of geographic proximity. It extends the present range known for *Synaptomys* to include western Kentucky and northwestern Tennessee. I also thank reviewers Gordon L. Kirkland, Jr. and Margaret H. Schadler for their helpful criticisms.

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