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Arborimus pomo.

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Arborimus Johnson, 1968

Phenacomys True, 1890:303. Type locality "Marshfield [= Coos Bay], Coos Co., Oregon."

Arborimus Johnson, 1968:27. Elevation of the subgenus *Arborimus* to generic rank.

CONTENT AND CONTEXT. Order Rodentia, Suborder Myomorpha, Superfamily Muroidea, Family Muridae, Subfamily Arvicolinae, Tribe Microtini (Musser and Carleton, 1993). Following is a key to the three extant species of *Arborimus* recognized by Musser and Carleton (1993).

1 Reddish orange to cinnamon on dorsum; tail thick, well haired and not strongly bicolored; incisive foramina wide; upper incisors strongly recurved; a pronounced longitudinal depression between orbits 2

Dark brown on dorsum; tail slender, scantily haired and distinctly bicolored; incisive foramina narrow; upper incisors not strongly recurved; longitudinal depression between orbits not pronounced .... *Arborimus albipes*

2 Larger overall, nasals extend further posteriorly relative to the maxillaries, lacks an abductor digiti secundi muscle and lacks a full complement of lumbricales muscles; typically exhibits a diploid number (2n) = 52, with 22 pairs of acrocentric or subtelocentric autosomes, 3 pairs of small submetacentric autosomes, a large submetacentric X, and a small metacentric Y chromosomes; some individuals exhibit a diploid number (2n) = 48 in which four acrocentric pairs replace the two large metacentric pairs (Johnson and George, 1991); occurring in western forests of Oregon .... *A. longicaudus*

Smaller overall, nasals do not extend further posteriorly relative to the maxillaries, presence of an abductor digiti secundi muscle and a full complement of lumbricales muscles; exhibits a diploid number (2n) = 40 or 42 with 5 pairs of large metacentric autosomes, 1 pair of large submetacentric autosomes, 11 pairs of small acrocentric or subtelocentric autosomes, 2 pairs of small submetacentric autosomes, and a small subtelocentric Y chromosome; individuals with 42 chromosomes differ from those with 40 in having one less pair of large metacentric autosomes and two additional pairs of acrocentric or subtelocentric autosomes (Johnson and George, 1991); occurring in coastal forests of northwest California .... *A. pomo*

Arborimus pomo Johnson and George, 1991

Pomo Tree Vole

Phenacomys longicaudus True, 1890:303. Type locality Marshfield, Coos Co., Oregon.

Arborimus longicaudus Johnson, 1968:27. Elevation of the subgenus *Arborimus* to generic rank.

Arborimus pomo Johnson and George, 1991:12. Type locality 0.8 km north of Jenner, Sonoma County, California. Revision of California populations of *A. longicaudus*.

CONTENT AND CONTEXT. Order Rodentia, Suborder Myomorpha, Superfamily Muroidea, Family Muridae, Subfamily Arvicolinae, Tribe Microtini (Musser and Carleton, 1993). Musser and Carleton (1993) recognized three extant species in the genus *Arborimus*. No subspecies of *Arborimus pomo* are recognized (Johnson and George, 1991).

DIAGNOSIS. *A. pomo* (Fig. 1) and *A. longicaudus* can be distinguished from similar rodents by having a brownish-red dorsum with black-tipped hairs, a light gray venter often washed with reddish-orange, and a well-haired tail that is >50 mm long and >50% of length of head and body (Maser and Storm, 1970; Verts and Carraway, 1984). *A. pomo* differs from *A. longicaudus* by smaller overall body size, nasals that do not extend posteriorly beyond the maxillaries, presence of the abductor digiti secundi muscle and a complete set of lumbricales muscles, and differences in number and morphology of chromosomes (Johnson and George, 1991). Skulls of *Arborimus* can be distinguished from those of other arvicoline rodents by a combination of two characters: presence of three projections on the lingual side of the last upper molar; reentrant angles of the lower molars extend two-thirds of the way to the labial side on the lingual side and about one-third of the way to the lingual side on the labial side (Maser and Storm, 1970). Skulls of *A. pomo* (Fig. 2) and *A. longicaudus* can be differentiated from *A. albipes* by having a pronounced longitudinal depression between orbits bordered by a strong ridge on each side, wide incisive foramina, and strongly recurved upper incisors (Maser and Storm, 1970).

GENERAL CHARACTERS. Pelage of *A. pomo* is reddish brown on the dorsum and gray with rusty-brown tinged hairs on the venter. Tail is thick, well-haired, dusky-brown above, somewhat paler below (Johnson and George, 1991). Body mass is 20–45 g. Ears are small (10–12 mm) and almost hairless. Externally, *A. pomo* is almost identical to *A. longicaudus*, although *A. pomo* is slightly smaller in overall body size (Johnson and George, 1991). Females are usually larger than males. Four inguinal mammary glands are present (Howell, 1926; Johnson, 1973; Taylor, 1915). Six well-developed tubercles are on the hind feet and five are on the forefeet (Hooper and Hart, 1962; Taylor, 1915), and the claw on digit I on the front foot is modified to a nail (Kesner, 1986). Minimum and maximum mean external measurements (in mm) of *A. pomo* from five geographic samples for 56 males and two geographic samples for 121 females (Johnson and George, 1991) are as follows: length of head and body, male 95–98, female 101–103; tail length, male 64–68, female 66–73; and hind foot, male 19–20, female 19–20.

Lumbar transverse processes of *A. pomo* are large and flaring, and cervical vertebrae are short and close together (Johnson, 1973). Acromion process of the scapula is narrow, sacral foramina are large, and sternum is wide (Johnson, 1973).

Skull of *A. pomo* is heavy and moderately angular. Dental formula is i 1/1, c 0/0, p 0/0, m 3/3, total 16. Molar teeth are rootless in juveniles and become rooted with age (Hooper and Hart, 1962; Howell, 1926).

FIG. 1. Adult *Arborimus pomo* from Humboldt County, California. Photograph by Lowell Diller.

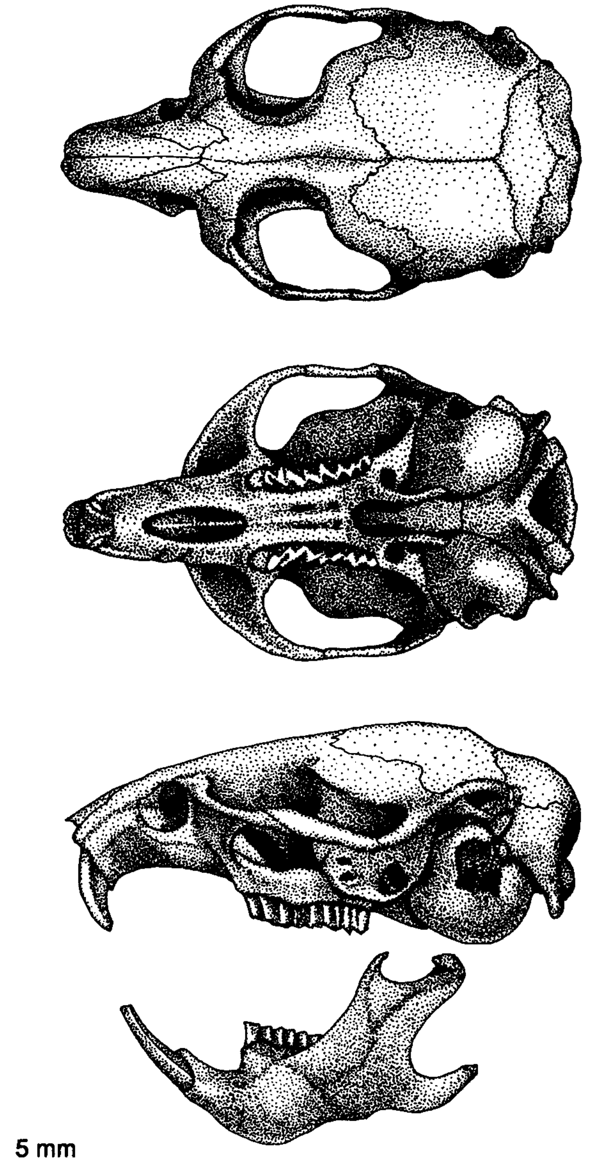

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Arborimus pomo* from 0.5 mi S of Occidental, Sonoma Co., California (Oregon State University Department of Fisheries and Wildlife mammal collection no. 6458). Drawing by G. Bracher. Greatest length of the skull is 22.5 mm.

Minimum and maximum mean values (in mm) of 14 cranial measurements for 121 females from five geographic samples and 56 males from two geographic samples (Johnson and George, 1991) are as follows: greatest length of skull, male 24.03–24.15, female 24.49–24.92; zygomatic breadth, male 13.63–13.70, female 13.99–14.18; least interorbital width, male 3.28–3.33, female 3.12–3.47; mastoid breadth, male 8.36–8.69, female 8.50–8.77; length of nasals, male 6.29–6.43, female 6.42–6.72; depth of braincase, male 7.08–7.19, female 7.13–7.26; width of interparietal, male 8.14–8.31, female 8.15–8.44; length of interparietal, male 3.31–3.54, female 3.52–3.72; length of diastema, male 6.45–6.76, female 6.67–6.83; nasal-maxillary distance, male 0.86–0.89, female 0.82–1.11; length of palatal foramen, male 4.40–4.61, female 4.47–4.71; length of maxillary toothrow, male 5.41–5.43, female 5.33–5.49; M2-M2 width, male 5.39–5.52, female 5.38–5.53; and width of upper M2, male 1.22–1.23, female 1.20–1.23.

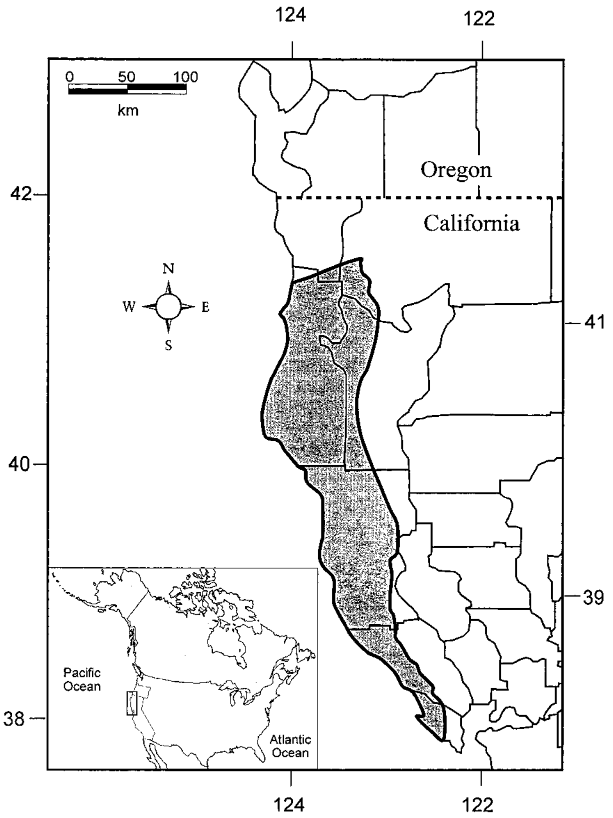

FIG. 3. Distribution of *Arborimus pomo* (modified from Hall, 1981).

DISTRIBUTION. *Arborimus pomo* is restricted to coniferous forests in northwestern California from the Klamath Mountains to Somoma County, north of San Francisco (Fig. 3; Huff et al., 1992; Johnson and George, 1991; Meiselman and Doyle, 1996; Murray, 1995). Johnson and George (1991) hypothesized that the Klamath Mountains are a geographical barrier between *A. pomo* and *A. longicaudus*. However, Murray (1995) proposed that specimens from northwest California (Del Norte County) be assigned to *A. longicaudus*. Precise limits of the range of *A. pomo* are unknown. In particular, the northern boundary of *A. pomo* and the southern boundary of *A. longicaudus* are uncertain (Hayes, 1996), in part due to the limited morphologic and genetic data for individuals in this area. *Arborimus pomo* most frequently occurs in forests consisting predominantly of Douglas-fir *(Pseudotsuga menziesii)* that may include other tree species such as western hemlock *(Tsuga heterophylla)*, western red cedar *(Thuja plicata)*, Sitka spruce *(Picea sitchensis)*, grand fir *(Abies grandis)*, and redwood (*Sequoia sempervirens*—Maser, 1965*a*; Meiselman and Doyle, 1996; Walker, 1930). Fossils of *A. pomo* are not known.

FORM AND FUNCTION. *Arborimus pomo* is similar in morphology to *A. longicaudus*. Due to the recency of the taxonomic reclassification of *A. pomo* (Johnson and George, 1991), much of the current literature describing the morphology of red tree voles has not distinguished between *A. pomo* and *A. longicaudus*. Origin of specimens used in several studies of morphology (Dearden, 1958; Kesner, 1980, 1986) were unknown or not provided; Hayes (1996) reviewed these studies.

The cecum of *A. pomo* differs from that of other microtines by the presence of a postcecal spiral consisting of 3–4 closely applied coils. Long cecal villi (up to 11 mm) are present in *A. pomo* both in the cecum proper and in the ampulla caicalis coli. Cecal villi differ from those in the ileum villi in having larger size, more elaborate structure, glandular inpocketings, an absence of goblet cells, and taller epithelial cells (Voge and Bern, 1949). The cecum of *A. longicaudus* may have similar characteristics.

Arborimus pomo possesses the full complement of lumbricales muscles to digits three through five plus a slip to digit two (Kesner, 1986). In addition, *A. pomo* possesses the adductor digiti secundi, which is absent in *A. longicaudus*. Kesner (1986) provided no locality information for specimens examined, and assignment to *A.*

pomo and *A. longicaudus* is based on comments in Johnson and George (1991).

ONTOGENY AND REPRODUCTION. The estrous cycle in *A. pomo* is irregular and variable. Duration of vaginal cornification of individuals kept in captivity ranged from 1 to 21 days, with a mean of 5.9 days. Periods between cornification ranged from 1 to 62 days. Mean proportion of time that four females had vaginal cornification was 13%, ranging from 5 to 17%. Pomo tree voles exhibit postpartum estrus and effective postpartum mating in the wild (Hamilton, 1962).

Ovulation in captive *A. pomo* is induced by copulation. Prior to copulation, individuals typically exhibit a brief initial contact through a frontal approach. This is generally followed by both assuming a naso-anal position and the pair spinning in a small circle. Subsequently the male generally overtakes and mounts the female. While mounted, males vibrate the hindquarters multiple times and remain in this position for <4 seconds (Hamilton, 1962). In captivity, a male will mount a female 6–133 times consecutively if permitted by the female. Time between copulations varies from less than one to several seconds. Following copulation the male frequently sits and licks his genital area (Hamilton, 1962). *Arborimus pomo* sometimes exhibits delayed implantation. Gestation ranges from 27 to 48 days, averaging 31 days (Hamilton, 1962).

Under laboratory conditions, females give birth during daylight hours. Litter size is typically 2, but varies from 1 to 5. Average weight of 35 newborns was inversely proportional to litter size and varied from 1.98 to 2.8 g. At birth eyes are covered by skin, and eye slits form between 18 h and 3 days. Prior to opening their eyes, young receive all of their nourishment from nursing. Absolute weight gain increases at about the same rate until eyes open. Of 17 animals raised in captivity, eyes opened 18–23 days after birth, with a mean of 20.8 days. Body weight of individuals at time of eye opening ranged from 7.5 to 10.4 g. After opening their eyes, young begin to eat foliage and gain weight rapidly (Hamilton, 1962).

Amount of time spent nursing decreases from the time young begin eating solid food until they are weaned. Time of weaning varies among litters. Litters in captivity were weaned as early as 25 days and as late as 46 days (Hamilton, 1962).

ECOLOGY AND BEHAVIOR. Pomo tree voles may occur in higher densities in older forests than in younger forests (Huff et al., 1992; Meiselman and Doyle, 1996), but evidence to strongly support this hypothesis is minimal. However, microclimatic conditions in old forests, such as thermal stability and protection from precipitation (Franklin et al., 1981), may provide suitable habitat conditions for this species.

Diet of *A. pomo* consists almost exclusively of needles of conifers, although occasionally the inner bark of twigs is eaten. Douglas-fir needles are most commonly consumed, but other conifer species, including grand fir and Sitka spruce, are also eaten (Benson and Borell, 1931). Captive Pomo tree voles eat foods other than needles of conifers, but have survived in captivity only when supplied with fresh, moist needles of conifers (Benson and Borell, 1931; Hamilton, 1962). Free water is obtained from dew that accumulates on needles (Taylor, 1915). Water may limit the eastern distribution of *A. pomo* (Hamilton, 1962) and the abundant forage and moist forest conditions of the humid coastal belt of California provide optimal habitat for Pomo tree voles.

Arborimus pomo feed on Douglas-fir needles in a meticulous manner. A needle is bitten off at the base and held in one or both forefeet. Sides of the needle and resin ducts are split off and the remainder eaten (Benson and Borell, 1931; Hamilton, 1962; Taylor, 1915). Occasionally young needles are consumed entirely (Benson and Borell, 1931).

Nests of *A. pomo* are typically located in Douglas-fir trees, although grand fir, Sitka spruce, western hemlock, redwood, and Pacific madrone (*Arbutus menziesii*) are also used (Meiselman and Doyle, 1996; Vrieze, 1980; Zentner, 1977). Nests occur 1.5–35 m above ground (Taylor, 1915) and are often located near the lowest branches with green leaves (Meiselman and Doyle, 1996; Vrieze, 1980). Location of nests varies depending on size of tree. In smaller trees, nests are typically located near the top next to the bole, but in larger trees, nests can be farther out on branches and large trees may have more than one nest (Benson and Borell, 1931; Howell, 1926; Taylor, 1915). Location of a nest probably depends on location of structural supports and proximity to green leaves. Nests are most frequently located on the south side of a tree (Howell, 1926; Meiselman and Doyle, 1996).

Pomo tree voles probably initiate construction of nests using a number of discarded twigs and needles established in a structurally secure location. Size of nest increases with accumulation of discarded resin ducts, branchlets, and feces. Nests can reach over one meter in diameter depending on length of occupation, materials used for construction, and location in the tree. Several generations of voles may use the same nest. Externally, nests of *A. pomo* are somewhat spherical in shape, have a flattened top, and consist of small diameter twigs and branchlets. One or more entrance holes are often located near the bottom of the nest. Internally, nests have a series of tunnels leading to individual chambers, which tend to be near the top of the nest even as the nest increases in size with age (Howell, 1926). Inside, the nest is typically lined with resin ducts, moss or lichen, and bits of bark. Feces occur throughout the nest, although some chambers are more frequently used for latrines than others. Green needles, cut branchlets, resin ducts, and fresh feces typically occur on top of an active nest. Discarded resin ducts and cut green twigs are sometimes found at the base of trees with active nests. Although *A. pomo* probably constructs most of its own nests, it sometimes uses nests of other arboreal species, including those constructed by northern flying squirrels (*Glaucomys sabrinus*), Douglas squirrels (*Tamiasciurus douglasii*), western gray squirrels (*Sciurus griseus*), woodrats (*Neotoma fuscipes*), deer mice (*Peromyscus maniculatus*), or birds (Benson and Borell, 1931; Howell, 1926; Taylor, 1915).

During wet periods, feces, discarded twigs, and resin ducts in the lower portion of the nest may become moist and compact. Salamanders and numerous species of invertebrates may inhabit the lower portion of nests (Benson and Borell, 1931; Howell, 1926).

Adult males and females occupy separate nests, except when the female is sexually receptive. Nests of females may be larger than those of males and subadult females, although this pattern is inconsistent (Howell, 1926; Taylor, 1915). *A. pomo* is primarily arboreal and nocturnal (Howell, 1926). Most activity of *A. pomo* may be restricted to trees in which it lives, although Pomo tree voles sometimes occur on the ground (Raphael, 1988); the frequency and function of non-arboreal activity are unknown. Male *A. pomo* may use subterranean nests (Howell, 1926), but this has not been confirmed since originally reported.

Abandoned nests often occur in the immediate vicinity of active nests. Reasons for abandonment are unknown, but *A. longicaudus* in Oregon deserted a nest when disturbed (Maser, 1965*a*).

Nests of *A. pomo* are often distributed in a clumped manner, leading to speculation that *A. pomo* is loosely colonial (Howell, 1926; Taylor, 1915; Zentner, 1977). Whether clumped distribution of nests results from coloniality, dispersal abilities, parasitism, use of multiple nests by individuals, or presence of favorable conditions in a specific area is unknown.

Several *A. pomo* individuals were infested with the mite *Atricholaelaps californicus* (Benson and Borell, 1931). Other ectoparasites, primarily mites, ticks, and fleas, common on or in nests of *A. longicaudus* from Oregon (Hayes, 1996) may be associated with *A. pomo*. Unidentified nematodes, probably in the Order Filaroidea, infested one individual *A. pomo* (Benson and Borell, 1931).

A primary predator of *A. pomo* is probably the northern spotted owl (*Strix occidentalis caurina*—Miller, 1933). *A. longicaudus* comprise nearly 50% of the prey items consumed by spotted owls in Oregon (Forsman et al., 1984); spotted owls may also consume large numbers of *A. pomo* in California. Other birds, documented as potential predators of *A. longicaudus* in Oregon, include great horned owls (*Bubo virginianus*—Maser, 1965*b*), long-eared owls (*Asio otus*—Reynolds, 1970), and northern saw-whet owls (*Aegolius acadicus*—Forsman and Maser, 1970), may also prey upon *A. pomo* in California. Mammals, including raccoons (*Procyon lotor*), martens (*Martes americana*), and fishers (*M. pennanti*), probably prey on *A. longicaudus* (Maser, 1965*a*), and may also prey on *A. pomo*.

Arborimus pomo is difficult to capture. Studies conducted in California have had limited success capturing *A. pomo* (Ralph et al., 1991; Raphael, 1988). The most successful method appears to be catching voles by hand as a nest is pulled apart (Carey et al., 1991).

Logging activities may result in declines and extinctions of some populations of *A. pomo* (Benson and Borell, 1931; Huff et al., 1992;

Zentner, 1977). Pomo tree voles may have limited dispersal capabilities (Howell, 1926) and may be vulnerable to habitat loss or fragmentation (Huff et al., 1992).

GENETICS. *Arborimus pomo* has a diploid number of 40 or 42 with 5 pairs of large metacentric autosomes, 1 pair of large submetacentric autosomes, 11 pairs of small acrocentric or subtelocentric autosomes, 2 pairs of small submetacentric autosomes, and a small subtelocentric Y chromosome. In addition, two morphologically distinct X chromosomes are present. One is a large submetacentric and the other is a large subtelocentric. Individuals with 42 chromosomes differed from those with 40 in having one less pair of large metacentric autosomes and two additional pairs of acrocentric or subtelocentric autosomes (Johnson and George, 1991).

Johnson and George (1991) reported karyotypic analyses for four *A. longicaudus* × *A. pomo* hybrid individuals bred in captivity. F_1 individuals had 6 large metacentrics, 1 large submetacentric, 35 acrocentric or subtelocentric chromosomes, and 4 small metacentric or submetacentric chromosomes.

Murray (1995) summarized mtDNA variability among seven microtine species in the genera *Arborimus, Clethrionomys, Microtus,* and *Phenacomys,* including 21 specimens of *Arborimus* from four locations in California and two locations in Oregon. Cladistic and phenetic analyses of mtDNA restriction sites supported the hypothesis that *A. pomo* is a distinct species and that *Arborimus* is a distinct genus. Tree voles collected from Del Norte County in northwestern California clustered with *A. longicaudus* in Oregon, while the remaining tree voles from Sonoma, Mendocino, and Humbolt counties clustered together with *A. pomo,* thus defining more precisely the distribution of the two species (Murray, 1995).

REMARKS. Taxonomy of *Arborimus* remains controversial. Some argued that it should be included in the genus *Phenacomys* (Hall, 1981; Jones et al., 1992; Verts and Carraway, 1995). Hayes (1996) recognized *Arborimus* based on recent karyotypic, mtDNA, and morphologic evidence (Johnson, 1973; Johnson and Maser, 1982; Murray, 1995). Similarly, the findings of Johnson and George (1991) and Murray (1995) support the specific status of *A. pomo.* Johnson and George (1991) hypothesized that both species are allopatric and reproductively isolated. Reproductive success of captive-bred males from Oregon and females from California was significantly lower than in reciprocal crosses, suggesting a barrier to reproduction between the two populations. Unknown limits of the distribution of *A. pomo,* along with uncertainty of locality records of specimens identified as *A. longicaudus* leaves much of the current information subject to debate.

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