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Microtus canicaudus.

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Microtus canicaudus Miller, 1897

Gray-tailed Vole

Microtus canicaudus Miller, 1897:67. Type locality McCoy, Willamette Valley, Polk Co., Oregon.

CONTEXT AND CONTENT. Order Rodentia, Family Muridae, Subfamily Arvicolinae, Genus *Microtus*, Subgenus *Microtus*, (Carleton and Musser, 1984; Hall, 1981; Hooper and Hart, 1962). No subspecies are recognized currently (Hall, 1981).

DIAGNOSIS. *Microtus canicaudus* (Fig. 1) can be distinguished from sympatric *M. townsendii* by a shorter tail (both relatively and absolutely) that is light gray beneath and brownish or blackish above, a V-shaped rather than squarish or U-shaped posterior margin of the palate, and a lighter yellowish-brown or yellowish-gray dorsal pelage (Hall, 1981; Maser and Storm, 1970). It is more robust than sympatric *M. oregoni* and is distinguishable from that species by relatively large eyes (>4 mm in diameter), six plantar tubercles, and M3 with four loops of enamel on the lingual side (Hall, 1981), and it may be distinguished from *M. montanus* (of which it formerly was considered a geographic race; Hall and Kelson, 1951) by incisive foramina that are not markedly constricted posteriorly (Maser and Storm, 1970). *M. canicaudus* and *M. montanus* are allopatric but not parapatric, have distinctive karyotypes (Hsu and Johnson, 1970), and different globulin and hemoglobin banding patterns (Johnson, 1968).

GENERAL CHARACTERS. In summer, the dorsal pelage of adult *M. canicaudus* is yellowish brown or yellowish gray; in winter, black-tipped hairs darken the dorsum. The venter is grayish white, the feet gray, and the tail gray with a brownish dorsal stripe (Maser and Storm, 1970). Juveniles are gray to grayish brown both dorsally and ventrally, the feet are gray, and the tail is gray with a black dorsal stripe (Maser and Storm, 1970). Most published descriptions of *M. canicaudus* are made in comparison with features of *M. montanus nanus* (Bailey, 1900, 1936; Hall, 1981; Miller, 1897) which it resembles in size and general appearance except that its dorsum is more yellowish, the tail grayer, and overall the pelage less grizzled.

In body dimensions, *M. canicaudus* is similar to *M. oregoni* (Hall, 1981; Maser and Storm, 1970), averaging about 145 mm in total length; however, its body mass may exceed 50 g, double that of *M. oregoni.* Means and ranges (in parentheses) of body dimensions (in mm) for 38 gray-tailed voles from the northern part of the Willamette Valley, Oregon (Anderson, 1959) are: total length, 149.7 (140 to 168); length of tail, 37.9 (32 to 45); length of hind foot, 19.6 (18 to 21). The same measurements for 23 specimens from the central part of the valley were: 146.9 (140 to 160); 36.9 (30 to 42); 19.9 (15 to 22).

The skull (Fig. 2) is "high, smooth, and well arched, with scarcely a trace of superciliary ridges" (Bailey, 1900:32). The bullae are relatively large and rounded, the interparietal is "lozenge-shaped," and the lateral pits in the palate exceptionally shallow (Bailey, 1900; Miller, 1897). The incisors protrude only slightly beyond the nasals in dorsal view and the incisive foramina are usually less than 5 mm long (Verts and Carraway, 1984). Means and ranges (in parentheses) of cranial dimensions (in mm) for 16 *M. canicaudus* (Anderson, 1959) are: condylobasal length, 25.1 (24.0 to 26.2); zygomatic breadth, 15.3 (14.2 to 16.7); interorbital breadth, 3.5 (3.2 to 3.8); prelambdoidal breadth, 9.4 (9.1 to 9.7); lambdoidal breadth, 12.5 (11.6 to 13.3); depth of braincase, 7.8 (7.4 to 8.0); length of upper molar row, 6.4 (5.9 to 6.8). The dental formula is i 1/1, c 0/0, p 0/0, m 3/3, total 16.

DISTRIBUTION. *Microtus canicaudus* occurs in suitable habitats at lower elevations throughout the Willamette Valley, Oregon, and at least at two localities (Anderson, 1959) north of the Columbia River in Clark Co., Washington (Fig. 3). Specimens identified as *M. canicaudus* from east of the Cascade Mountains (Bailey, 1936; Hall and Kelson, 1951) subsequently were assigned to other taxa (Anderson, 1959; Hall and Kelson, 1951). There is no fossil record.

FORM AND FUNCTION. Because selenium is deficient in diets of livestock throughout the Willamette Valley, gray-tailed voles have been used as laboratory animals to investigate restrictions in dietary selenium and vitamin E in species native to the region. In voles, selenium, in the absence of vitamin E, reduces the incidence of abnormal sperm; it is concentrated in the nucleus and mitochondria of the sperm (Whitfield, 1978). Body mass, testis mass, and liver mass (the latter as a percent of body mass) increased significantly with selenium concentration in the diet to 1.0 ppm but not to 5.0 ppm. Concentrations of selenium were highest in kidneys, liver, testes, heart, and brain (in that order) among voles fed selenium, but brain, kidney, and heart masses were not related to concentration of dietary selenium (Pond, 1977). Voles fed diets with no selenium and no vitamin E exhibited diarrhea, rectal distension, swollen eyes, and liver necrosis (Pond, 1977).

Gray-tailed voles also were used as test animals to ascertain the feasibility of enhancing the nutritional quality of residues of annual ryegrass (*Lolium multiforum*) for animal feed by fermentation with *Candida utilis* (Han et al., 1978). Although in vitro and in vivo digestibility, soluble matter, and crude protein were increased by fermentation, voles fed diets containing fermented ryegrass straw gained less weight than voles fed diets without ryegrass straw and with untreated straw. Also, voles fed fermented ryegrass straw became lethargic and unkempt; Han et al. (1978) believed that some of the products of fermentation were toxic to voles.

Lei (1977) fed sprouted-wheat clippings containing 2.72×10^4 disintegrations g^{-1} min^{-1} (dpm/g) cesium-134 to captive gray-tailed voles. Voles attained body burdens of approximately 2,000 dpm/g within 1 day and maintained an "equilibrium" between about 1,500 and 4,000 dpm/g for 53 days with continuous feeding of the contaminated sprouts. Levels of contamination by cesium-134 in voles fell below the detectable level within 21 days after withdrawing the sprouts from the diet.

Among *M. canicaudus* fed greens (sprouted wheat), more females exhibited the estrous condition and singly-housed males had significantly heavier testes. However, stimulation of reproduction by dietary greens was not as great in *M. canicaudus* as in *M. montanus* (Gilston, 1976). Adrenal mass was greater among female gray-tailed voles than among males and was not affected greatly

FIG. 1. Photograph of an adult male *Microtus canicaudus* (OSUFW 7253) from 2.5 mi N Corvallis, Benton Co., Oregon.

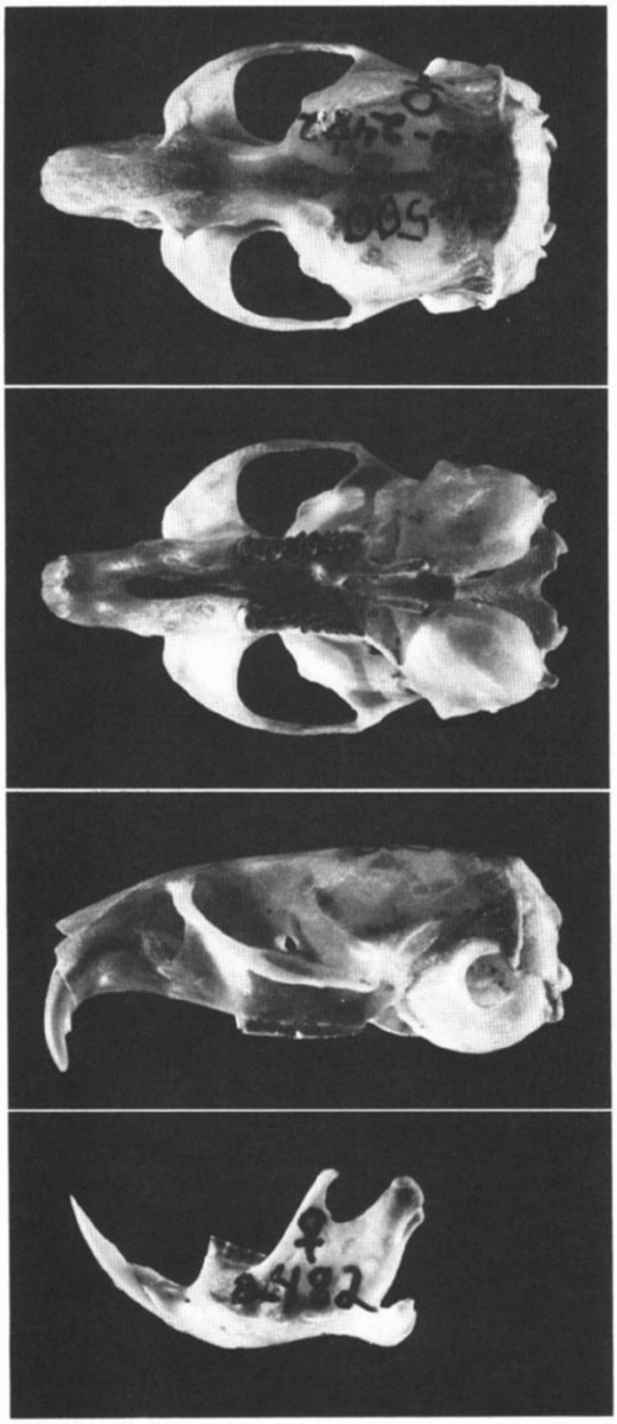

FIG. 2. Dorsal, ventral, and lateral views of the skull and lateral view of the mandible of an adult female *Microtus canicaudus* (OSUFW 2482) from 1 mi N, 1.5 mi E Monmouth, Polk Co., Oregon. Occipitonasal length 26.1 mm.

either by numbers of individuals housed together or by presence of greens in the diet (Gilston, 1976). Males produced more total adrenocortical steroids than females regardless of diet or housing, but group-housed males produced more total steroids, corticosterone, and progesterone than males housed singly (Gilston, 1976).

ONTOGENY AND REPRODUCTION. Essentially nothing is published regarding reproduction among gray-tailed voles in the wild. In the laboratory, female *M. canicaudus* as young as 18 days of age and weighing only 12.5 g are capable of mating and subsequently producing viable offspring (Hagen and Forslund, 1979). Within this age class, mean size of first litters (5.2±0.3) was significantly larger, mean mass of offspring at birth (2.4±0.03 g) significantly less, and offspring survival to 18 days (22/73) significantly lower than among females first mated at 28 days (mean litter size = 4.8±0.3; mean mass of offspring at birth = 2.5±0.04 g; survival = 50/58 to 18 days; Hagen and Forslund, 1979). To 70 days of age, litter size declined inversely with age at which females were first mated; no animals older than 70 days were tested. Lower mean mass at birth was attributed, in part, to greater litter size. Postpartum matings were relatively infrequent among females first mated at 18 days, thus, despite the greater mean litter size, total production of young in 12 weeks by females in this group was less than among females first mated at 28 days or older (Hagen and Forslund, 1979).

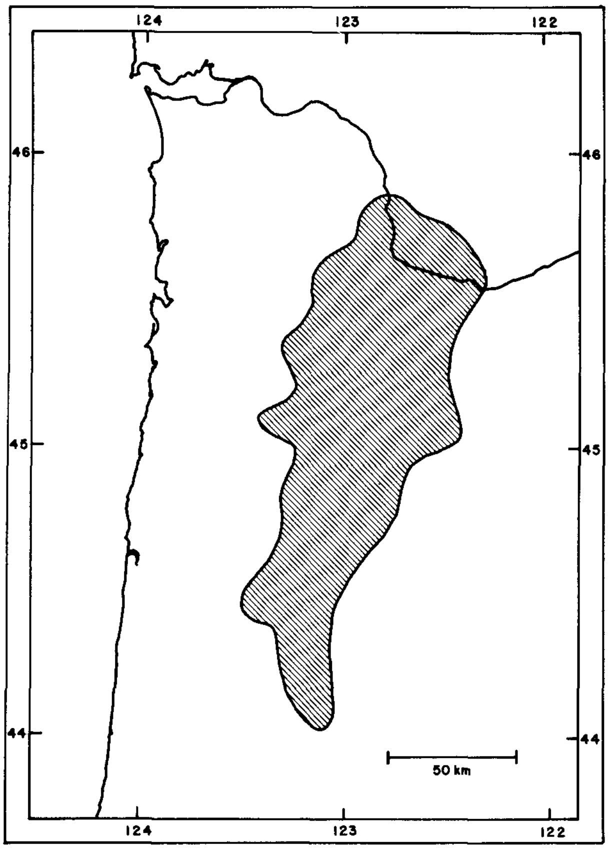

FIG. 3. Distribution of *Microtus canicaudus*; entire geographic range of the species is in Washington and Oregon. Map based largely on locality records provided by Anderson (1959) and Hall (1981).

When paired in other laboratory experiments, individual gray-tailed voles familiar with one another, whether related or not, produced fewer litters than unfamiliar individuals, but litter size and viability of offspring were not affected by parents being related (Boyd and Blaustein, 1985). Because individual familiarity, reproductive behavior, population density, and dispersal seem related, Boyd and Blaustein (1985) postulated that familiarity and inbreeding avoidance may be involved in population cycles of voles.

Gestation is approximately 21 to 23 days (Hagen and Forslund, 1979), most commonly 21 days (Tyser, 1975).

Captive gray-tailed voles fed restricted diets weighed significantly less than those fed the same diets ad libitum, but did not produce offspring with sex ratios biased toward females (Goldenberg, 1980) as hypothesized for mammals in poorer physical condition (Trivers and Willard, 1973).

The incidence of pregnancy in interspecific matings of *M. canicaudus* and *M. montanus* was similar to that of intraspecific matings of *M. montanus* and greater than that of intraspecific matings of *M. canicaudus*. However, mean litter size and survival of hybrid progeny was significantly less than for progeny of intraspecific matings (Tyser, 1975).

Growth, as indicated by changes in total length and body mass, is more rapid and more extended in males than in females (Tyser, 1975). Total length (in mm) and body mass (in g; in parentheses) for samples ($n = 25$ to 40) of males and females (Tyser, 1975), respectively, for weeks 1 through 8 were: 68.7±1.1 (6.0±0.2), 66.0±0.8 (5.5±0.1); 97.5±1.4 (11.0±0.3), 92.2±0.9 (10.3±0.2); 117±0.8 (16.5±0.4), 114.8±0.7 (15.2±0.3); 129.5±0.7 (21.0±0.4), 124.1±0.5 (19.3±0.3); 136.9±1.0 (24.6±0.6), 129.0±0.7 (21.3±0.3); 140.9±1.3 (26.1±0.7), 131.1±0.7 (22.2±0.4); 144.8±1.2 (27.6±0.9), 132.6±0.8 (22.1±0.4); 146.9±1.4 (28.8±1.0), 134.3±0.8 (22.8±0.5).

ECOLOGY. Presently, gray-tailed voles are associated almost exclusively with agricultural lands, especially grasses grown for seed, small grains, and permanent pastures of legumes and grasses (Bailey, 1936; Goertz, 1964). Presumably, the species was associated with the ". . . extensive prairies maintained by annual fires set by Indians" in the Willamette Valley for centuries before settlement by Caucasians (Johannessen et al., 1971:286). Gray-tailed voles seemingly have invaded formerly forested lands converted to agriculture in Coast Range valleys adjoining the Willamette Valley; hence, the species is thought to have benefited by at least some agricultural practices (Goertz, 1964; Maser and Storm, 1970). In such valleys we have captured *M. canicaudus* along grassy railroad and highway rights-of-way, but not off of the valley floor.

Although densities of populations of gray-tailed voles are known to fluctuate, sometimes attaining levels requiring control measures (Goertz, 1964), little quantitative information regarding numbers is available for the species. From our casual observations, we are confident that fluctuation of numbers is cyclic. Pearson (1972) estimated the density of a population in the central Willamette Valley at 141±62/ha, but his methods were obscure.

Owls (Tytonidae, Strigidae), hawks (Falconidae), foxes (*Vulpes vulpes*, *Urocyon cinereoargenteus*), skunks (*Mephitis mephitis*), and domestic and feral cats (*Felis catus*) are common predators of gray-tailed voles (Maser and Storm, 1970). In Benton Co., Oregon, 104 regurgitated pellets of long-eared owls (*Asio otus*) contained remains of 51 gray-tailed voles (Reynolds, 1970) and 28 pellets of saw-whet owls (*Aegolius acadicus*) contained remains of 14 gray-tailed voles (Forsman and Maser, 1970).

Ectoparasites reported to infest *M. canicaudus* include the fleas *Epitedia jordani* (Hubbard, 1940), *Micropsylla goodi* (Hubbard, 1941*a*), *Leptopsylla selenis*, *Catallagia chamberlini*, *C. charlottensis*, *Opisodasys keeni*, *Atyphlocereas multidentatus*, *Hystrochopsylla gigas dippiei* (Hubbard, 1941*b*), *Catallagia sculleni*, and *Orchopeas sexdentatus* (Easton, 1983). Faulkenberry and Robbins (1980) reported collecting 511 fleas of eight species (*Catallagia charlottensis*, *Atyphloceras multidentatus*, *Peromyscopsylla selenis*, *Monopsyllus wagneri*, *Hystrichopsylla occidentalis*, *Nosopsyllus fasciatus*, *Corrodopsylla curvata*, and *Rhadlinopsylla* sp.) from 377 *M. canicaudus*. Rates of infestation of voles and their nests by adult and larval fleas fluctuated seasonally; peaks occurred in spring and early winter with dramatic declines in summer and midwinter (Robbins, 1983). Temperature and humidity were considered the primary factors regulating flea populations infesting gray-tailed voles (Robbins, 1983). Frequency distributions of *Atyphloceras multidentatus*, *Catallagia charlottensis*, and all other species of fleas collected from 377 *M. canicaudus* caught near Corvallis, Benton Co., Oregon, fit negative binomial probability distributions indicating that the fleas were contagiously dispersed (Robbins and Faulkenberry, 1982). Easton and Goulding (1974) found larvae, nymphs, and adult males of the tick *Ixodes angustus* in nesting material of *M. canicaudus*; however, they did not indicate the basis for distinguishing the nesting material of *M. canicaudus* from that of other local species of small mammals. In their comprehensive treatment of the mites infesting mammals in Oregon, Whitaker and Maser (1985) listed no species infesting *M. canicaudus* although other *Microtus* were infested by several species.

Mammalian associates of *M. canicaudus* and other terrestrial species of small mammals within its range include *Sorex vagrans*, *Scapanus townsendii*, *Sylvilagus bachmani*, *S. floridanus*, *Spermophilus beecheyi*, *Thomomys bulbivorus*, *Peromyscus maniculatus*, *Neotoma fuscipes*, *Microtus townsendii*, *M. oregoni*, *Zapus trinotatus*, *Mustela frenata*, and *Mephitis mephitis* (Hall, 1981; Maser and Storm, 1970).

Gile and Gillett (1979) included gray-tailed voles in laboratory ecosystems designed to test the dynamics and fate of the insecticide dieldrin; they claimed that the omnivorous nature of the diet of the species permitted it to forage on all components in their terraria except adult snails (*Helix pomata*) and microscopic organisms. They specifically included larval mealworms (*Tenebrio molitar*), gray house crickets (*Achetus domesticus*), and young of garden snails in the terraria for *M. canicaudus* to feed upon. However, they cited no reference in support of the implication that invertebrates contributed significantly to the diet of *M. canicaudus* and they provided no evidence that these invertebrates were preyed upon by voles in the terraria. Although all voles in terraria treated with dieldrin died, contained high levels of residues of dieldrin in their brains, and "released" plant productivity in the terraria at death, voles in untreated terraria survived, suggesting that components of the simple ecosystems that included alfalfa and ryegrass provided an adequate diet (Gile and Gillett, 1979). To our knowledge, food habits of wild or captive *M. canicaudus* have not been investigated, although Maser and Storm (1970) list grasses (Poaceae), clover (*Trifolium*), wild onion (*Allium amplectens*) and false dandelion (*Hypochoeris radicata*) as common items in the diet. Those that we have maintained in captivity thrived on white clover (*Trifolium repens*), apple, bluegrass (*Poa* sp.), and ryegrass.

BEHAVIOR. Gray-tailed voles construct "intricate and extensive" systems of runways and subterranean burrows; they sometimes use burrows of other species such as those of *Thomomys bulbivorus* (Maser and Storm, 1970:107). Middens at intersections of some runways range in size to 8 to 15 cm long by 3 to 5 cm wide by 8 to 10 cm deep (Maser and Storm, 1970). Nests are built underground or above ground under boards, bales, and debris scattered in fields. Throughout the range of *M. canicaudus*, heavy rains commonly flood fields for several days at a time during winter. Air trapped in subterranean nest cavities permits continued occupancy by voles even though they must swim through flooded tunnels to reach their nests; freshly cut grasses and fresh droppings may be found in the flooded tunnels (Maser and Storm, 1970). Gray-tailed voles retreat to unflooded areas when water rises into their nests. One of us (BJV) observed 20–30 voles clinging to a fence post at the border of a flooded field; when approached, the voles jumped into the water en masse and swam to a grassy roadside nearby.

Intraspecific encounters of laboratory-reared voles in a neutral arena were categorized as dominant-subordinate, mutual avoidance, fraternal, and "no decision" for 60, 21, 3, and 14% of 28 male-male pairings, 50, 31, 6, and 13% of 16 female-female pairings, and 50, 31, 0, and 13% of 16 male-female pairings (Weil, 1975). In interspecific encounters with both participants male, the same categorizations were made in 56, 28, 3, and 12% of 32 *M. canicaudus*-*M. oregoni* encounters and 43, 53, 0, and 3% of 32 *M. canicaudus*-*M. townsendii* encounters; when dominance was exhibited, *M. canicaudus* was invariably dominant to *M. townsendii* (all 14 encounters), but only half the time to *M. oregoni* (9 of 18 encounters). Among females, the same categorizations were made in 62, 0, 0, and 37% of 16 *M. canicaudus*-*M. oregoni* encounters and 50, 37, 0, and 13% of 16 *M. canicaudus*-*M. townsendii* encounters; more *M. canicaudus* were dominant to *M. townsendii* (six of eight encounters), but more *M. oregoni* were dominant to *M. canicaudus* (6 of 10 encounters). In interspecific encounters of participants of opposite sex, both male and female *M. oregoni* were dominant to *M. canicaudus*, but both male and female *M. canicaudus* were dominant to *M. townsendii* (Weil, 1975).

GENETICS. The karyotype of *M. canicaudus* consists of 22 (diploid number) biarmed autosomes, a nearly metacentric X, and a submetacentric Y (Hsu and Johnson, 1970). Seven pairs of autosomes are large metacentric or submetacentric (one pair especially large), one medium-sized pair is subtelocentric, and three small pairs are equal-sized and metacentric. The karyotype differs from that of *M. montanus* (with which *M. canicaudus* formerly was considered to be conspecific) in that one of the three small pairs is distinctly smaller than the other two and the sex chromosomes are acrocentric in the latter species (Hsu and Johnson, 1970).

On the basis of an electrophoretic study, Johnson (1968:26) reported that *M. canicaudus* and *M. montanus* exhibited ". . . a difference in secondary globulin banding, two bands being wider apart in *M. canicaudus* . . ." and that the hemoglobin molecule migrated more slowly in *M. canicaudus*.

No albino or melanistic individuals are reported in the literature. However, a juvenile male from Washington Co., Oregon, on deposit in the Oregon State University Department of Fisheries and Wildlife mammal collection (OSUFW 7260) is entirely white except for a light grayish triangular area from the nose to eyes, grayish ears and dorsal surface of the tail, and a sprinkling of grayish hairs in the dorsal midline from shoulders to the rump.

REMARKS. We suggest that the paucity of information on the biology of wild *Microtus canicaudus* is related to its extremely strong aversion to entering enclosed types of live traps (Maser, 1967), an attribute well known to researchers in the region. Live traps that give the illusion of not obstructing runways and that are set in a manner that voles moving rapidly along runways run directly into them produce the best results (Maser, 1967; Pearson, 1972). Also, it is unfortunate indeed that such a large proportion of information available for the species has not been published but is contained in unpublished theses and dissertations.

The generic name *Microtus* is from the Greek *mikros* meaning "small" and *otos* meaning "ear"; the specific name *canicaudus* is from the Latin *canens* meaning "gray" and *cauda* meaning "tail" (Jaeger, 1955).

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