

Sorex granarius.

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Sorex granarius Miller, 1910

Iberian Shrew

Sorex araneus granarius Miller, 1910:458. Type locality "La Granja, Segovia, Spain."

Sorex granarius Hausser et al., 1975:249. Elevation of subspecies to species rank.

CONTEXT AND CONTENT. Order Insectivora, Family Soricidae, Subfamily Soricinae (11 recent genera). The genus *Sorex* contains 69 extant species (Hutterer, 1993). Currently, no subspecies have been described for this species. *Sorex granarius* was originally described as a subspecies of *S. araneus*, but based on karyological and morphological characters, Hausser et al. (1975) raised it to species rank. It was also erroneously assigned to *S. caecutiens* by Ellerman and Morrison-Scott (1955).

DIAGNOSIS. *Sorex granarius* (Fig. 1) is the smallest of the European *araneus* group (as defined by Hausser et al., 1985), which includes *S. araneus*, *S. coronatus*, and *S. granarius*. Ranges of length of head and body (in mm) and body mass (in g) for these species, respectively, are: 65-84, 6-15; 50-81, 4.6-13.5; 50-72, 4.5-8.

Compared with that of the closely-related *S. araneus* and *S. coronatus*, the skull of *S. granarius* has a relatively short rostrum, with the palate enlarged anteriorly (Fig. 2). The dorsal profile is straight, usually without evident concavity in the interorbital region. The coronoid process of the mandible is relatively short, and the angular process is slender. The internal temporal fossa is triangular, with the apex of the triangle pointing anteriorly (Hausser et al., 1975; Miller, 1912). The upper incisors are rather lightly pigmented, with the medial tines small to very small and not surpassing the lower half of the pigmented area; unpigmented hypocones appear on M1-M2 (Dannelid, 1989).

In León province (northwestern Spain), the Iberian shrew is sympatric with *S. coronatus* (Brunet-Lecomte and Delibes, 1988). Since the latter decreases in size from east to west (López-Fuster and Ventura, 1987), size cannot be used to differentiate *S. granarius* and *S. coronatus* in this region. However, mandibular measurements, when subjected to discriminant function analyses, can be used to separate the species. Variables included in the discriminant function are mainly related to the size and position of articular process, coronoid process, and temporal fossa (Brunet-Lecomte and Delibes, 1988).

GENERAL CHARACTERS. *Sorex granarius* is a medium-sized shrew, as determined by comparing its size with average values reported by Innes (1994:132, table 1) for the genus. Body measurements (in mm or g, means followed by ranges and sample sizes in parentheses) are: length of head and body, 63.2 (50-72, $n = 24$); length of tail, 40.4 (36-46, $n = 24$); length of hind foot, 11.8 (11-12.5, $n = 24$); length of ear, 6.7 (5.3-7.4, $n = 12$); body mass, 6.3 (4.5-8, $n = 17$ —Cabrera, 1914; Gisbert et al., 1988; Hausser, 1990; Miller, 1912). In adults, pelage is generally tricolor, ranging from sepia to dark brown dorsally, lighter on the flanks, and yellowish-gray ventrally. Juveniles are paler and lack noticeable contrast between dorsal and lateral color. The tail is bicolored (sepia above and dark ochre below) and feet are dirty ochre (Cabrera, 1914; Madureira and Ramalinho, 1981).

Iberian shrews show marked craniometric homogeneity, although there is a tendency for mandible size to decrease from north to south (Gisbert et al., 1988). Skull measurements (in mm, means followed by ranges and sample sizes in parentheses) of specimens from Galicia (northwestern Spain) are: condyloincisor length, 18.2 (18.1-18.3, $n = 2$); condylobasal length, 17.7 (17.5-17.8, $n = 4$); rostral length, 7.5 (7.2-7.8, $n = 23$); length of braincase, 10.2 (9.9-10.4, $n = 5$); staphylion-basion (distance between posteriormost bor-

der of palate and anteriormost border of foramen magnum), 8.0 (7.6-8.3, $n = 5$); interorbital breadth, 3.8 (3.5-4.1, $n = 22$); zygomatic breadth, 5.3 (5.1-5.4, $n = 13$); breadth of braincase, 8.7 (8.3-9.0, $n = 3$); length of upper tooth row, 7.7 (7.3-7.9, $n = 10$); length of P4-M3, 4.3 (4.1-4.5, $n = 19$ —Gisbert et al., 1988). Mandible measurements of specimens from Sierra de Gredos (central Spain) are: labial length, 6.3 (5.8-6.6, $n = 73$); length of articular process 1.1, (0.9-1.3, $n = 73$); inclination of coronoid process, 1.9 (1.5-2.3, $n = 73$); mandibular foramen, 0.2 (0.0-0.4, $n = 73$); length of incisor-angle, 11.4 (10.9-12.0, $n = 60$); mandibular length, 9.5 (9.1-10.1, $n = 64$); length of internal temporal fossa, 1.0 (0.8-1.2, $n = 73$); length of lower tooth row, 6.9 (6.3-7.2, $n = 58$); length of m1-m3, 3.6 (3.4-3.9, $n = 62$); maximum length of m3, 1.0 (0.9-1.1, $n = 55$); articular length of mandible, 9.1 (8.6-9.5, $n = 71$); coronoid height, 4.2 (3.9-4.6, $n = 73$ —Gisbert et al., 1988). Skull and mandible measurements of 12 juveniles from Candelario and Rascafría (Sistema Central) are given in Hausser (1990).

DISTRIBUTION. *Sorex granarius* is endemic to the Iberian Peninsula (Fig. 3). It is distributed along Sistema Central, from Sierra de Ayllón (Spain) to Serra da Estrela (Portugal), and extends northward from the Tajo River to Galicia in northwestern Spain (Gisbert et al., 1988; C. Nores, pers. comm.). Several specimens from northcentral Spain have been assigned to this species, although some authors consider these to be *S. coronatus* (see Remarks). Because individuals of this species are difficult to identify based on cranial features, there are no fossil records assigned to this species.

FORM AND FUNCTION. The dental formula is $i\ 3/1, c\ 1/1, p\ 3/1, m\ 3/3$, total 32 (Miller, 1912). All four cusps of the lower incisor are usually included in a continuous pigmented area. The first lower unicuspid sometimes shows a prominent posterior ridge. The mental foramen below the trigonid of m1 is relatively centrally placed (Dannelid, 1989).

The curly overhairs of this species exhibit two grooved sides with central ridges and are similar in structure to those of other Soricinae (Ducommun et al., 1994). The structure allows the pelage to shed water and seems to be related to a preference for humid, temperate to cold habitats.

ONTOGENY AND REPRODUCTION. A pregnant female with six embryos was captured at Laguna de El Barco, Avila (Sistema Central, Spain) on 23 June 1984 (Gisbert et al., 1988). Another pregnant female with four embryos was captured in April in Galicia, Spain (unpublished data).

ECOLOGY. Areas occupied by *S. granarius* are characterized by average annual temperatures of 3-15°C, with cold to extremely cold winters, and average annual rainfall >600 mm (Gisbert et al., 1988). In Sistema Central, Iberian shrews are found at elevations ranging from 500 to 2000 m, usually in forests of *Fagus sylvatica*, *Pinus silvestris*, *Quercus pyrenaica*, *Q. rotundifolia*, *Fraxinus* or *Betula*. They also occur where native forests have been replaced by cultivated lands, such as vegetable gardens or forests of *Castanea sativa* or *P. pinaster* (Gisbert and García-Perea, 1988). Above timberline, this species can be found on granite screes adjacent to grasslands of *Nardus stricta*. In winter, *S. granarius* is the most specialized of the small mammal community in habitat preference, occurring only in forests of *Quercus pyrenaica* (Alcántara, 1992).

West and north of Sistema Central, *S. granarius* occurs at progressively lower altitudes, reaching the western coast of the Iberian Peninsula (Gisbert et al., 1988). In Portugal, Iberian shrews are present in almost all bushy habitats, but are more abundant in relatively humid areas of dense vegetation (Madureira and Ramalinho, 1981). In northern Portugal and northwestern Spain, *S.*



FIG. 1. *Sorex granarius* from Peñalara Natural Park, Madrid, Central Spain. Photograph by J. Latova and J. Gisbert.

granarius penetrates the Eurosiberian region, where it appears in forests of *Q. pyrenaica* and in plantations of *Eucalyptus* and *P. pinaster* that have replaced native forests (Gisbert et al., 1988). In this area, *S. granarius* is absent in places where annual rainfall is <500 mm (C. Nores, pers. comm.)

Reported predators of this species are the barn owl (*Tyto alba*—Campos, 1978; Dueñas and Peris, 1985; Gisbert et al., 1988; Veiga, 1980), European wild cat (*Felis silvestris*—Aymerich et al., 1980), and domestic cats (*F. catus*—Madureira and Ramalhinho, 1981). We have captured Iberian shrews with crossbow traps and live traps (Sherman and Hyware traps) baited with oily bread or a mixture of wheat flower and sardine oil.

GENETICS. *Sorex granarius* is one of the European representatives of the Holarctic *araneus-arcticus* group, which is characterized by the male chromosome complex XY,Y₂ (Fedyk and Ivanitskaya, 1972; Meylan and Hausser, 1973). *S. granarius* has a diploid number of 36–37 chromosomes (FN = 38–40), and its chromosomes are homologous to those of *S. araneus* (Hausser et al., 1985; Volobouev and Dutrillaux, 1991; Wojcik and Searle, 1988). In two G-banded karyotypes (one male and one female) studied by Wojcik and Searle (1988), all autosomes were acrocentric, except for one pair that was polymorphic (one metacentric and one acrocentric chromosome) in the female. The male was homozygous for acrocentric chromosomes. Hausser et al. (1985) had previously reported this polymorphism and illustrated a heterozygous male. Similar results with R-banding techniques on two females (both heterozygous) have been reported by Volobouev (1989).

Study of electrophoretic variation in 22 allozyme loci (Catzeflis et al., 1982) confirms that this species is closely related to *S. araneus*, showing differences in only two alleles. Genetic distances between *S. granarius*, *S. araneus*, and *S. coronatus* (0.055 ± 0.028) are similar to those generally observed in mammals for intermediate stages of the speciation process (Catzeflis et al., 1982). According to Hausser et al. (1985), *S. granarius* likely differentiated from *S. araneus* by geographic isolation earlier than *S. coronatus*. *S. granarius* retained the primitive karyotype, while subsequent modifications occurred in the other species. Genetic differentiation eventually made fertile hybridization almost impossible.

Wojcik and Searle (1988) consider the karyotype of *S. granarius* to be the ancestral acrocentric karyotype of *S. araneus*. This opinion is consistent with that of Volobouev and Catzeflis (1989), who hypothesized that the ancestor of *S. araneus*, *S. coronatus*, and *S. granarius* had a karyotype similar to that of present-day *S. granarius*. The karyotypes of *S. araneus*, *S. coronatus*, and *S. arcticus* could have derived from that of *S. granarius* by means of three types of chromosomal rearrangements: Robertsonian translocations, telomere-centromere translocations, and centromic shifts (Volobouev, 1989). Speciation processes leading to the present species of the *araneus-arcticus* group are rather recent, placing the origin of these species in the Pleistocene (Volobouev and Catzeflis, 1989).

REMARKS. The generic name of this species is from the Latin *Sorex*, meaning "shrew mouse." The specific term *granarius* is from the Latin *granarium*, meaning "granary." Spanish and Portuguese vernacular names for this species are "musaraña ibérica" and "morganho" or "musaranho," respectively.

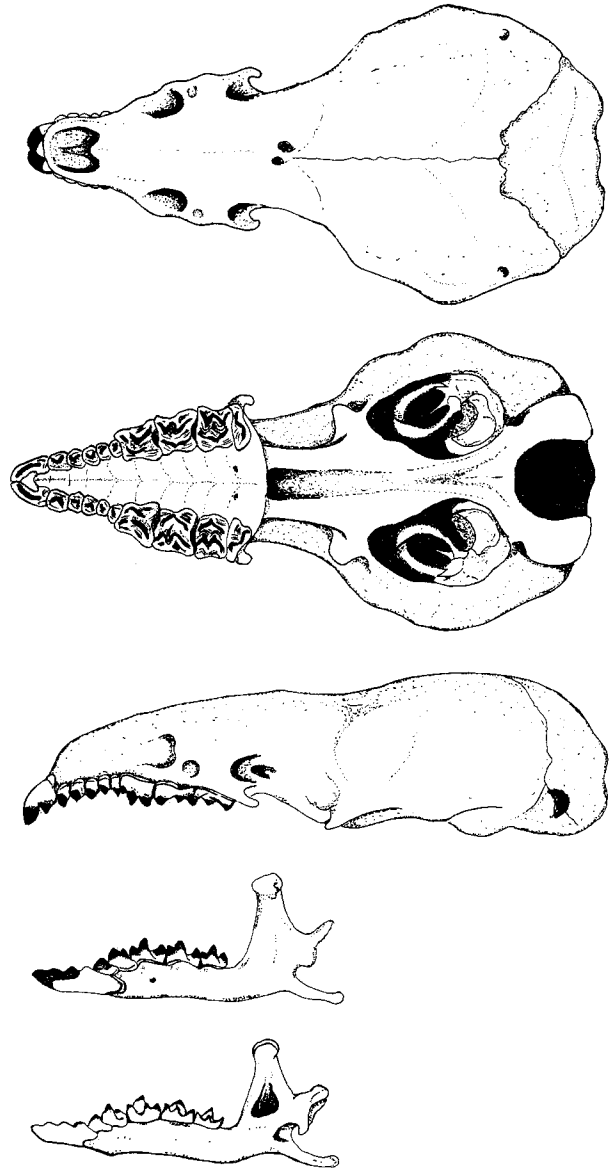


FIG. 2. Dorsal, ventral, and lateral views of cranium, and lateral and medial views of mandible of *Sorex granarius* from Peñalara Natural Park, Madrid, Central Spain (female, Universitat de Barcelona, Departament de Biologia Animal, 94.12.10.01). Greatest length of cranium is 18.1 mm. Illustration by J. Gisbert.

Representatives of the *araneus* group in north central Spain have been variously assigned either to *S. granarius* (Hausser, 1984; Niethammer, 1956) or to *S. coronatus* (Brunet-Lecomte and Delibes, 1988; Garzón-Heydt et al., 1971). In the distribution map offered by Hausser et al. (1985), the specific affiliation of these specimens is not clarified.

Chromosomal banding, biochemical, and paleontological data on six species of the *araneus-arcticus* species group have led to the following hypothesis on its evolutionary history (Volobouev, 1989; Volobouev and Dutrillaux, 1991). The ancestral karyotype of this group in Eurasia was similar to that of *S. tundrensis*. This ancestor led to a *granarius*-like form which spread over the whole Palearctic before the Riss period. One population split in north-eastern Asia, migrating to North America as the ancestor of *S. arcticus*. The Eurasian lineage of the *granarius*-like ancestral form reached the Iberian Peninsula to the west. The first centric fusion, a+f, arose in central Europe, and this form spread over most of Europe. The Iberian Peninsula became isolated during the Riss period, when it was inhabited by the *granarius*-like ancestor and a population of shrews with an a+f karyotype. The subsequent evolution of these two populations was independent: the *granarius*-

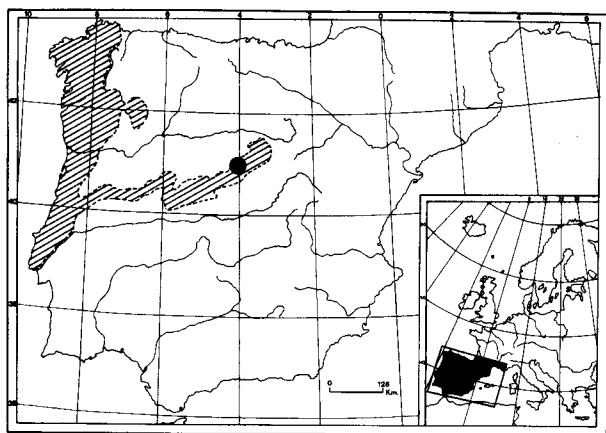


FIG. 3. Distribution of *Sorex granarius* (based on Gisbert et al., 1988). The symbol designates type locality.

like shrews became *S. granarius* without changes in the karyotype, and the other population acquired eight additional chromosomal rearrangements, and became *S. coronatus*. In Eastern Europe, an additional Robertsonian fusion occurred in shrews with a +f karyotype, spreading over central and eastern Europe, and leading to the modern *S. araneus* (Volobouev, 1989; Volobouev and Dutrillaux, 1991). The study of G-banded chromosomes in *S. daphaenodon* extends the distribution of shrews with an a+f karyotype to the eastern coast of Asia, posing the question about the origin of this fusion in Siberia, instead of central Europe (Zima, 1991).

A phylogenetic hypothesis involving different populations of the European species of the *araneus* group, inferred from mitochondrial DNA (cytochrome b gene), is not congruent with the one based on chromosomes (Taberlet et al., 1994). Whereas the tree inferred from karyological data indicates that *S. granarius* is the sister group of *S. coronatus*–*S. araneus*, and is consistent with the evolutionary history proposed by Volobouev and Dutrillaux (1991), the tree inferred from mtDNA proposes *S. coronatus* to be the sister group of *S. granarius*–*S. araneus*. This tree is consistent with the phenetic tree offered by Catzefflis (1984), although it places the origin of the common ancestor of the three species 1.0×10^6 years ago, while Catzefflis (1984) placed it 100,000 years ago. Results also suggest that mitochondrial changes could have occurred far earlier than chromosomal arrangements, and thus the chromosome polymorphism of the group could be considered as a phenomenon of recent acquisition (Taberlet et al., 1994).

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