Andrei Miljutin

THE PHENOMENON OF RAT

Mouse-like Body Structure in Mammals

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Abstract. This book introduces the most ancient and commonest mammalian life form, which is nonetheless largely overlooked – the muridoids, i.e., animals with mouse-like body structure. There are approximately two thousand mouse-like species, or about a third of all mammals, belonging to 9 different orders. The author explains the reason for the existence of mouse-like body structure, describes the taxonomic, morphological, ecological and ecomorphological diversity of mouse-like animals, and reveals the role of muridoids in the evolution of mammals.

Tonal drawings (except fig. 3) and the cover drawing are drawn by the author. Animal **silhouettes** are redrawn from the colour drawings by Toni Llobet in the *Handbook of the Mammals of the World* (Wilson, Mittermeier, 2015, 2018; Wilson et al., 2016, 2017), with the permission of Lynx Edicions.

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On the cover: the gray four-eyed opossum (*Philander opossum*)

Cover design and layout: Kalle Paalits

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Preface. DO RATS EXIST?

It may seem strange, but the answer to the question in the title: "Do rats exist?" is not at all obvious. On the one hand, there are undoubtedly the animals we call rats. Moreover, they can be found even in our pantry. There is also the zoological genus *Rattus*, all species of which are rats. On the other hand, many animals that do not belong to the genus *Rattus* are also called rats. Some of them belong to the same family of murids (*Muridae*) as true rats, others belong to other rodent families, for example, cane rats (*Thryonomys*), and still others are not rodents at all, such as the moonrat (*Echinosorex gymnura*) from the hedgehog family. The same applies with the name "mouse". In other words, there is no taxonomic group (taxon) that would unite **all** the animals called rats or mice in national languages. This is where the questions arise. If "rats" and "mice" are not taxonomic groups, then what they are? And is there a fundamental difference between "rats" and "mice"?

These questions may seem unimportant, but various animals are called rats and mice not by chance, rather as a consequence of their resemblance to true rats and mice. Is this similarity illusory, and the widespread use of these names the fruit of our ignorance and the paucity of language; or has folk nomenclature intuitively revealed an overlooked natural phenomenon? And if mammals of different origin really posses a common mouse-like body structure, then why?

Suppose that the similarity is illusory. Different species are similar only at first glance, but once you delve into the detail, then the similarity ultimately disappears. It could be all about the depth of our knowledge. This is exactly what I thought at first. I attributed my inability to distinguish between mouse-like mammals to my lack of knowledge and hoped to rid myself of it through years of studying the taxonomy and morphology of mammals, especially rodents. It did not help. Now I realise that mouse-like body structure is not a figment of our imagination; rather it is one of the most common mammalian life forms. If you don't believe it, you can check right now. Figure 1 shows mouse-like animals from 9 orders of mammals. Covering the caption with your hand, can you identify them at least up to the order? Or find the single rodent (that is, a true mouse or rat)? If you did not manage, don't worry: the animals really are very similar.

The phenomenon of similarity between unrelated species interested me so much that in 1991 I presented a report on mouse-like mammals at the Zoological Institute of the USSR Academy of Sciences (in the last year of the existence of the country). Before the talk began, I projected a slide onto the screen showing a pygmy possum (an Australian marsupial) jumping on a banksia flower. On entering the hall and seeing the slide, one very authoritative and really knowledgeable expert on mammals, exclaimed: "What a nice mouse!" In my heart I felt triumph. However, the report did not arouse much interest, or was not understood. Subsequently, I published an article based on this presentation (Miljutin, 1992a), and, as far as I know, that article remains the only publication on the subject.

Why did I return to the theme decades later? First, because virtually nothing has changed: ideas about life forms, so commonplace in botany (consider, for example, the everyday terms trees, shrubs, herbs), have not taken root in zoology. Secondly, during years of studying the ecomorphology of mammals, my understanding of the

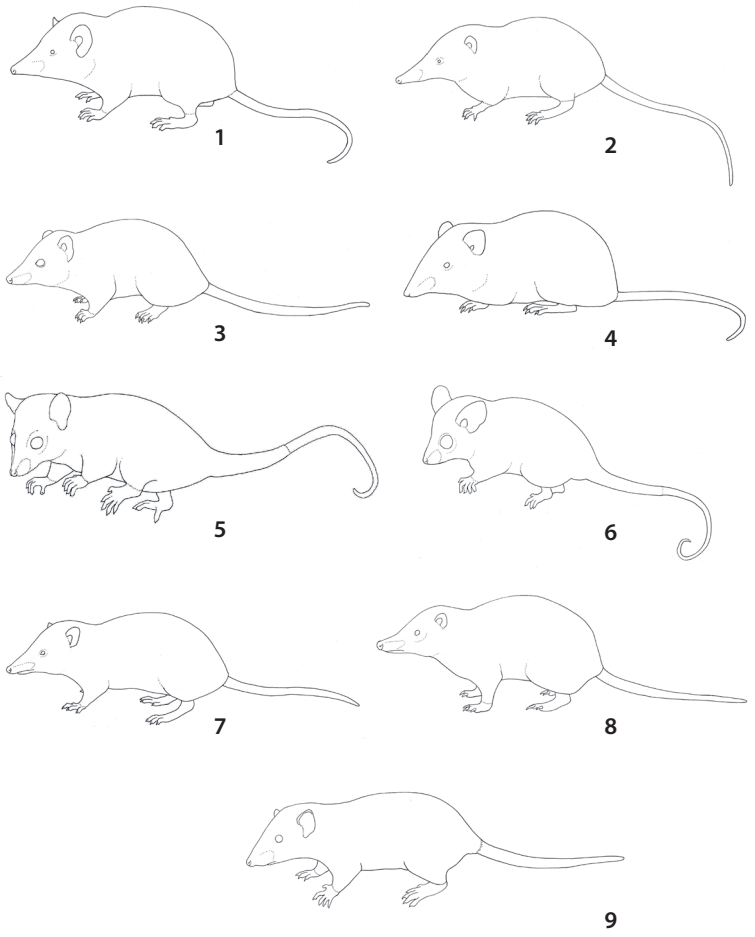


Fig. 1. All the animals in this picture have a mouse-like appearance, but they belong to nine different orders. Which one is the rodent?
1 – Paucituberculata (*Lestoros inca*); 2 – Afrosoricida (*Microgale gymnorhyncha*); 3 – Dasyuromorphia (*Antechinus arctos*); 4 – Rodentia (*Oxymycterus rufus*); 5. Microbiotheria (*Dromiciops gliroides*); 6 – Diprotodontia (*Cercartetus lepidus*); 7 – Eulipotyphla (*Echinosorex gymnurus*); 8 – Peramelemorphia (*Microperoryctes papuensis*); 9 – Didelphimorphia (*Monodelphis adusta*).

meaning and significance of mouse-like body structure in mammals has deepened, and a desire to share my thoughts has emerged. The following is an essay that does not claim to be either a complete study or an exhaustive review of the literature.

Besides preface and conclusions, the book contains five chapters. The first chapter explains the essence of mouse-like body structure in mammals and provides definitions for the terms "muridoid" and "life form". The second chapter provides an overview of mouse-like mammals. This material is summarized in the third chapter. At the beginning of the fourth, main, chapter, the principles of identifying life forms, methods for describing ecological strategies, and terminology used in the following text are explained. After that, follows an analysis of the ecomorphological diversity of mouse-like mammals. The fifth and final chapter discusses the role of mouse-like body structure in the adaptive evolution of mammals.

1. THE ESSENCE OF MOUSE-LIKE BODY STRUCTURE

1.1. What are rats and mice? The concept of the muridoid

When using the terms mice and rats, we usually mean small animals with a long scaly tail. These names are applied mainly to rodents, but not exclusively. In various languages, shrews are also called mice (e.g. German *Spitzmäuse*), as are bats and some marsupials (marsupial mice). Even one carnivore, the Egyptian mongoose (*Herpestes ichneumon*), is also called Waoh's rat.

First of all, it would be useful to figure out which of them are "mice" and which are "rats". Actually, there is no fundamental difference between mice and rats: a rat is a big mouse, and a mouse is a small rat. As we will see below, most murid rodents are intermediate in size and are called rats or mice arbitrarily.

In order avoid repeating the words "mice and rats" every time, we can introduce a general term covering all size variants: **muridoid** (Miljutin, 1992a, 2010). It is derived from the Latin name for the murid family, *Muridae*, and the suffix "-oid", indicating similarity.

A brief definition of the term is as follows: **A muridoid is an animal that has a mouse-like body structure.** This definition will, of course, remain incomprehensible and useless, if we do not specify what kind of body structure can be considered "mouse-like". This should be the body structure that most murids have, for example, the well-known human companions – the house mouse and the

brown rat. On the other hand, the features characteristic of this structure should also be present in the most phylogenetically distant forms that we associate with mice and rats, such as the least specialized opossum species, like *Monodelphis*. Identifying external features common to true mice and opossums that are also characteristic of other mouse-like mammals, led me to develop the following definition.

Muridoids are four-legged, morphologically plantigrade animals, without protective armour or flying membrane; their hind legs are longer than their front legs, and the digits of all limbs are mostly unfused and not shortened, and usually end with claws; their tails are oval in cross section, are equal to or exceed half the head and body length, and are covered either with bare skin (with or without scales) or short fur without a tuft at the tip.

This definition refers to animals, but may be the muridoid structure is found only in mammals? At the present time this is true, but in the Mesozoic it could have been and obviously was otherwise.

It should be explained that by *morphologically* plantigrade condition I mean extension of the soles of the feet to the wrist and heel, but not necessarily that the animals move on a full sole. Thus, the brown rat, for example, rests on full soles when stationary, but when moving rests on the soles of the forefeet and only on the digits of the hind feet. Such locomotion is also characteristic of other muridoids. In a functional sense, they are *palm-digitigrade* animals (Kuznetsov, 1999).

One characteristic feature of the general appearance of a muridoid is associated with its plantigrade morphology – its body is close the ground. It appears that the animal is short-legged; however, this is only true of the forelimbs. The relative length of the hind limb in a brown rat and in a dog (fox terrier) is approximately the same (60– 65% of the head and body length), but in a rat the heel is pressed to the ground when stationary, while in the dog it is held well off the ground.

Another characteristic feature of muridoids is the distribution of hair on the body. Among muridoids, fur on the body does not

usually extend to the ears, tail and feet. These body parts are usually either naked or have only short, sparse hairs. The tail, and in some species the feet, are often "scaly", that is, covered with keratinized skin, separated by a network of grooves.

Based on the definition, fish-like, winged, and bipedal mammals are not muridoids. Nor are short-tailed, flat-tailed, or bushy-tailed species (such as the marmot, beaver, or squirrel), or species with limbs approximately equal in length (such as hedgehogs, dogs, or horses). Ungulates, as well as species predominantly without claws (primates), are not muridoids. Species with shortened or fused digits, such as cats or otters, also do not fit this definition. At the same time, the number of digits in muridoids may vary. Thus, for example, in all murids (*Muridae*) the inner digits on the forefeet are reduced. The relative length of the muzzle, vibrissae, ears, and the size of eyes also vary, so these characters are not included in the definition.

Characteristic muridoids usually have an elongated muzzle, medium or long vibrissae, and normally developed but not very large eyes and ears. Muridoids are also characterized, but not exclusively, by a hunched back in a natural position, due to the unequal length of the fore and hind limbs (fig. 2). A more detailed morphological description will be given below.

Fig. 2. The brown rat (*Rattus norvegicus*) is a typical muridoid.

1.2. Why do they look like this?

Above, I presented a set of features that are generally associated with mouse-like appearance and are characteristic not only of murids, but also of other mouse-like mammals, for example, opossums. What do these features tell us?

First, almost all of the characteristics listed in the definition of muridoids are **primitive** (ancestral) among mammals. That is, these characteristics were present among the most ancient mammals and even among their reptilian ancestors. During the course of evolution, all other features – for example, bipedalism, digitigrade gait, protective armour, nails – developed from these characteristics. Therefore, **muridoid body structure consists of a set of primitive characters.**

A second conclusion, which is less immediately obvious but perhaps more important, is that all features that characterise muridoids are related, directly or indirectly, to **locomotion.** This suggests that all muridoids have a common type of locomotion, which is indeed the case. This gait is called the **bound** by Howell (1944) and Hildebrand (1977) and the **primitive ricochet** by Gambaryan, because it was probably the most ancient asymmetric fast gait in mammals (Gambaryan, 1972). I use here a clearer synonym of the latter term – the **quadrupedal** or **four-legged ricochet** (in contrast to bipedal ricochet). The peculiarity of the four-legged ricochet is that, unlike to the gallop, the hind and forelimbs have different functions: the hind limbs are propulsive (they push off), while the front legs are used only for landing. This explains why animals that move with a four-legged ricochet have hind limbs that are much longer than their front ones. Furthermore, this gait requires a balancer in the form of a long tail. This ratio of limbs and tail leads to a mouse-like body structure.

Thus, mouse-like body structure is not only real, but also easily explained by the type of locomotion used by the animals possessing it, as well as by the ancient origin of their morphological traits.

1.3. The antiquity of mouse-like body structure

The primitive structure and locomotion of muridoids indicate the antiquity of mouse-like body structure and its possible primacy among mammals. The antiquity of the structure is also supported by the fact that forms with a mouse-like appearance are found among nine orders of recent mammals: among insectivores, afrosoricids, rodents and in six orders of marsupials. It is parsimonious to assume that their common ancestor also exhibited mouse-like body structure. If so, then muridoids existed before the divergence of placental mammals and marsupials.

Let us consider the evidence provided by paleontology. The most ancient mammals in the traditional sense, or mammaliforms in cladistic terminology, are known from the Late Triassic; that is, they appeared about 200 million years ago. It is customary to say that the first mammals resembled shrews in size, appearance and way of life (e.g. Carroll, 1988); however, it seems to me that it is more correct to compare the earliest mammals with small opossums, since most shrews are highly specialized animals. Nonetheless, both comparisons imply a mouse-like body structure among the first mammals, and this is borne out by close examination of fossil evidence.

The *Morganucodontidae* (fig. 3) were among the most ancient mammals (mammaliforms), and we are fortunate to have not only fossilised teeth and skulls, but also the bones of the postcranial skeleton, making it possible to reconstruct the complete skeleton of a morganucodontid (Jenkins & Parrington, 1976; the drawing of the skeleton is reproduced in Carroll, 1988). The head and body length of the animal is about 10 cm. The skull and teeth resemble those of the opossum, although, of course, they differ in details. The head is relatively large – about 3 cm. The neck is shorter than the head, but not shortened. The trunk is of medium length or slightly long (about three times as long as the dorsal-ventral depth of the thorax). The length of the tail is about half the length of the body. The hind limbs are about 1.5 times longer than the forelimbs; therefore, when

stationary, the hind leg was positioned at an angle (not vertically). The relative lengths of the limb segments are in the following order: shank > thigh > foot and forearm > arm = forefoot. The limbs are plantigrade, with five normally developed digits, and the inner digits are shortened. This ratio of body parts corresponds to the structure of extant mouse-like mammals, which allows us to assert that muridoids were present among the most ancient mammaliforms.

Fig. 3. Morganucodons, one of the oldest mammaliformes, probably had a muridoid body structure (*Morganucodon oehleri*, reconstructed by FunkMonk (Michael B. H), distributed under a CC-BY 2.0 license).

But perhaps the immediate reptilian ancestors of mammaliforms were also muridoids? The direct ancestors of mammaliforms may have included several groups of cynodonts (+ *Cynodontia*). It is noteworthy that late cynodonts had long tails: not the thick tails weighed down by powerful muscles that are characteristic of recent reptiles; rather thin like a rat's tail (Carroll, 1988). In many modern long-tailed mammals, such as rats, the tail serves as a balancer when jumping. Therefore, it is possible that the small, long-tailed cynodonts that lived in the Mesozoic moved with a four-legged ricochet and were the first muridoids.

Among extant mammals, the most reptilian morphology is exhibited by monotremes (*Monotremata*), which are now represented by echidnas and platypus. These highly specialized animals are nothing like rats. However, their ancestors may have resembled morganucodontids (Carroll, 1988), that is, they may have had a mouse-like body structure. While we lack palaeontological evidence about the most ancient monotremes, the mouse-like appearance of the most ancient marsupials and placental mammals, as well as their common ancestors, is confirmed by paleontological data (Kemp, 2005; Carroll, 1988).

1.4. Are muridoids a life form? The concept of life form

Many species of mammal exhibit the same mouse-like body structure. However, they have diverse origins, which is why they are not a common group in the phylogenetic sense, i.e., they are not a distinct taxon. If muridoids are not a taxon, then what they are? Maybe a life form? But what is a life form?

Since the emergence of the term "life form" (Warming, 1884), it has been used with very different meanings (reviewed in Aleyev, 1986; Miljutin, 1992b). Available life form definitions are usually very vague, except for the extreme opinions: 1) each species represents an independent life form; or 2) there are no life forms at all. Nevertheless, a constructive definition of the life form was provided in 1980 by Yuri Aleyev, who developed the theme later in his book "Ecomorphology" (Aleyev, 1980, 1986). Instead of the rather ambiguous expression "life form", Aleyev and Burdak (1984) introduced the term "**ecomorph**". Both terms are used synonymously hereafter.

According to Aleyev (1980), "ecomorph is an integral system of ecological and morphological adaptations that determines the general structure of the body of an organism in accordance with a specific direction of evolution of a species in a particular biotope." Aleyev compares an ecomorph with a casting mold that makes it possible to cast the same sculpture from different materials (Aleyev, 1986: 182).

It means that the same life form may evolve among phylogenetically different taxa. Here, I take the liberty of shortening Aleyev's definition somewhat, in the hope of making it more understandable and operational: **the life form (ecomorph) is a system of morphological adaptations that determines the general structure of an organism's body.**

It is important to note that the life FORM (ecoMORPH) can be identified solely on the basis of morphological features. Ecological groups, for example, "aquatic animals" are not life forms, because aquatic animals may have very different structure, that is, they are represented by different life forms: think of a coral, a jellyfish, and a dolphin. The mixture of ecological and morphological approaches, so common in the scientific literature, gives rise to meaningless life form classifications.

For the sake of fairness, it should be noted that the term "ecomorph" was proposed before Aleyev and Burdak by Ernst Williams (Williams, 1972), albeit with a slightly different meaning, as "*species with the same structural habitat/niche, similar in morphology and behavior, but not necessarily close phyletically*". Unlike in Aleyev's definition, ecology (habitat) and morphology are mixed in this definition. In fact, one and the same ecomorph (if morphologically defined) can be found in different habitats.

So, do muridoids fit the definition of a life form adopted here? Yes. Muridoids have a similar general body structure associated with a common type of locomotion, that is, they have a common set of adaptations for locomotion. At the same time, it is important to recognise that ecomorphs, like taxa, have different hierarchical levels. Among hundreds of muridoid species, there are many variants of the body structure, which are due to differences in the ecological strategy of the species. The presence of certain combinations of ecologically significant morphological features makes it possible to single out ecomorphs of a lower rank within muridoids. The ecomorphological diversity of muridoids will be considered in the Chapter 4.

2. MURIDOIDS AMONG MAMMALS

How many mammal species have a mouse-like body structure? How are they distributed among higher taxa – families and orders – and what are their features? The answer to these questions requires the use of a classification that is both up-to-date and likely to remain more or less stable in the future. The choice of such a classification in the current period of unrestrained species splitting and revision of higher taxa is not an easy task. As a compromise, I chose the classification of the multi-volume *Handbook of the Mammals of the World* (Wilson, Mittermeier, 2015, 2018: Wilson et al., 2016, 2017). The number of taxa is intentionally not corrected for the somewhat updated classification in Burgin et al., 2020, since in the context of the study of muridoids, these updates are insignificant and do not affect the course of the analysis and conclusions drawn here. In addition, during a period of species splitting, it is wise to be somewhat conservative.

The main sources of data on the distribution, morphology and ecology of mammals were the above-mentioned *Handbook*, along with Nowak, 1991, 2018; Wilson, Reeder, 2005 and Miljutin, 2019. In addition, I used numerous taxonomic revisions and faunistic reports, references to which are given at the relevant places in the text, as well as the results of my own research.

As it transpired, species corresponding to the definition of a muridoid adopted here are found in nine orders of recent mammals: among opossums, caenolestids, microbiotheres, carnivorous marsupials (dasyuromorphs), bandicoots, diprotodonts, insectivores, afrosoricids and rodents. The muridoid representatives of these orders are discussed below.

2.1. Muridoids among marsupials

Species with a mouse-like body structure are found in six of the seven orders of marsupials: among opossums, caenolestids, microbiotheres, carnivorous marsupials, bandicoots, and diprotodonts, with the first four orders consisting entirely or predominantly of muridoids. There are 173 species of muridoid marsupials belonging to 35 genera and 8 families.

2.1.1. Opossums – order *Didelphimorphia*

The order *Didelphimorphia* includes one **family *Didelphidae*** (opossums) containing 18 genera and 103 species. Most of these species have a mouse-like body structure (fig. 4:1): 98 species (95%) in 15 genera (*Caluromys philander*, *Didelphis*, *Gracilinanus*, *Hyladelphys*, *Lestodelphys*, *Lutreolina*, *Marmosa*, *Marmosops*, *Metachirus*, *Micoureus*, *Monodelphis*, *Philander*, *Thylamys*, *Tlacuatzin*). Only 5 species do not meet the definition of muridoid: a water opossum (*Chironectes minimus*) with webbed hind feet, and most species in the subfamily *Caluromyinae*, which have largely bushy tails (*Caluromys derbianus*, *C. lanatus*, *Caluromysiops irrupta* and *Glironia venusta*).

The distribution of muridoid opossums coincides with the range of the family as a whole. They are found in South, Central and North America from Canada (Virginian opossum, *Didelphis virginiana*) to Patagonia (*Lestodelphys*, *Thylamys pallidior*). Most species live in tropical South America.

The head and body length and weight of muridoid opossums vary from 7 cm and 10 g to 50 cm and 5 kg. The smallest species

is apparently the Chaco pygmy opossum (*Chacodelphys formosa*); the largest species is the Virginian opossum. In most species the pelage is soft. Common opossums (*Didelphis*) have long guide hairs protruding from their fur. The colour of the upperparts varies from white to black, but is usually greyish, yellowish, reddish, or brown. The ventral part of the body is usually lighter, sometimes white. Many species have dark longitudinal stripes or spots on the head, back and legs. Some have light spots above the eyes and elsewhere.

Most muridoid opossums have an elongated and pointed muzzle. The eyes and ears are normally developed in most species, but relatively small in some (e.g., *Lutreolina*). All have prehensile tails. Opossums use their tails not only for climbing, but also for carrying nesting material. The tail is covered with scales or short hairs. In some species (*Lestodelphys*, *Thylamys*), fat reserves are deposited in the tail, which gives the tail a conical shape. The number of digits is 5/5 (forefoot/hind foot). In all species, the inner digits of the hind feet (hallux) have a nail and are, at least to some extent, opposable. Dental formula: (I5/4, C1/1, P3/3, M4/4) × 2 = 50. The canines are well developed; looking from the side of the masticatory surface, the molars are triangular with sharp cusps.

Muridoid opossums live in a variety of habitats, from deserts and alpine meadows to tropical rainforests. Most species inhabit forests, but some also live in open areas or near water bodies. Most species are scansorial, and even terrestrial forms can climb well. Nests are built in tree hollows, on branches, in rock crevices, under logs or in burrows – mostly abandoned, more rarely dug by themselves. Among opossums there are animalivorous, omnivorous and frugivorous species. They feed on invertebrates, small vertebrates and carrion, as well as fruit and seeds. Opossums are mainly active at night. In cold weather, Virginian opossums may remain in their dens for several days, relying on fat reserves. Opossums are mostly solitary. Litters have from one to 21 young. In captivity, opossums live 3–7 years, depending on the species.

2.1.2. Shrew opossums – order *Paucituberculata*

The order *Paucituberculata* includes one **family *Caenolestidae*** (shrew opossums or caenolestids) containing 3 genera and 7 species. All species have a mouse-like body structure. Shrew opossums are found in the western part of South America from Colombia to southern Chile.

Shrew opossums (fig. 4:2) are the size of a mouse or a small rat. Externally they resemble shrews. The head and body length is 9–14 cm, and the weight is 20–53 g. The fur is short, dense and soft. The upperparts are dark brown, grey or black. The underparts are the same colour or lighter.

The muzzles of shrew opossums are long and pointed. The eyes are small, and the ears are normally developed. The tail in *Rhyncholestes raphanurus* is moderately long (about 70% of the head and body length); in other species it is longer: 90–115%. The tail is non-prehensile and covered with short hairs. The tail of *Rhyncholestes raphanurus* may be thickened due to fat deposits. The number of digits is 5/5 (forefoot/hind foot). The hind feet are of medium length or somewhat elongated (18–21%). Unlike true opossums, the hallux of cenolestids is small. The digits are not opposable.

The middle incisors of the lower jaw are larger than the other teeth and point forward (as in shrews and many Australian marsupials). Dental formula: (I4/3–4, C1/1, P3/3, M4/4) × 2 = 46–48. The molars have sharp-tipped cusps.

Shrew opossums live in the cool and humid climates of highlands or coastal areas. They inhabit alpine meadows, shrublands, and forests, where they prefer dense herbaceous vegetation into which surface runways are laid. They use natural shelters, such as cavities among tree roots. Shrew opossums are able to climb but move mainly on the ground. They feed predominantly on invertebrates and to a lesser extent on small vertebrates and fruit. They are active in the dark and at dusk.

2.1.3. Microbiotheres – order *Microbiotheria*

The order *Microbiotheria* includes one **family *Microbiotheriidae*** with only one extant species, the monito del monte (*Dromiciops gliridoides*), that has a mouse-like body structure. The monito del monte lives in the south-western part of South America, in Chile and Argentina.

The monito del monte is a mouse-sized animal that looks like a small arboreal opossum (fig. 4:3). The head and body length is 8.5–13 cm, and the weight is 15–30 g. The fur is short, thick, and silky. The head and sides are brownish. The back, forelegs and thighs are dark grey. The underparts are white. There are dark rings

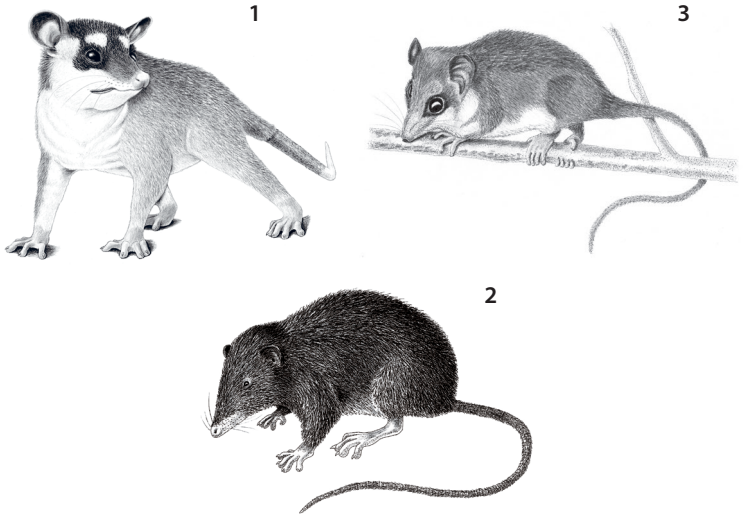


Fig. 4 Muridoids among New World marsupials: 1– gray four-eyed opossum (*Philander opossum*; Didelphidae: 98 muridoid species); 2 – Andean shrew opossum (*Caenolestes condorensis*; Caenolestidae: all 7 species are muridoids); 3 – monito del monte (*Dromiciops gliroides*; Microbiotheriidae: the only species in the family).

around the eyes. The tail is long – approximately equal to or slightly exceeding the length of the head and body – and to a certain extent prehensile. The tail is densely covered with short hairs, except for a bare strip on the lower surface of the terminal section. The base of the tail may be thickened due to fat deposits. The number of digits is 5/5 (forefoot/hind foot). The hallux is opposable. The dental formula is identical to that of true opossums (I5/4, C1/1, P3/3, M4/4) × 2 50), but the canines are smaller and the molar cusps are less sharp.

The monito del monte inhabits dense, moist forests in the temperate zone, especially bamboo thickets. It climbs well and builds a round nest from twigs and leaves in tree hollows or on branches. The diet includes insects and other invertebrates, as well as small vertebrates and fruit. The monito del monte is nocturnal. In autumn, fat reserves accumulate in the tail, and when cold weather sets in, the animal hibernates. It produces 2–4 young in a litter. Captive animals live for approximately two years.

2.1.4. Carnivorous marsupials – order *Dasyuromorphia*

Together with the marsupial wolf, which died out in the 20th century, the order *Dasyuromorphia* (dasyuromorphs) includes 3 families, 19 genera and 76 species. Species with a mouse-like body structure are represented in **the family *Dasyuridae*** (dasyurids). This family includes 3 subfamilies (*Dasyurinae*, *Phascogalinae* and *Sminthopsinae*), 17 genera and 74 species, of which most have a mouse-like body structure: 56 species (76%) in 11 genera and all three subfamilies. About half of the species (12) in the subfamily *Dasyurinae* are muridoids (*Dasykaluta*, *Parantechinus*, *Myoictis wavicus*, *Pseudantechinus*, *Neophascogale*, *Phascolosorex*). In the subfamilies *Phascogalinae* and *Sminthopsinae*, the vast majority of species have mouse-like body structure; the exceptions being the phascogales (*Phascogale*, all 3 species), the kultarr (*Antechinomys laniger*) and the greater long-tailed dunnart (*Sminthopsis longicaudata*).

Non-muridoid dasyurids differ from muridoids in exhibiting 1) a tufted tail (in desert-dwelling genera *Dasycercus* and *Dasyuroides*, arboreal genus *Phascogale* and in rock-dwelling species *Sminthopsis longicaudata*); 2) a tufted tail and elongated limbs (kultarr); 3) a bushy tail (part of the genus *Myoictis*); and 4) a bushy tail and different limb structure (the genera *Dasyurus* and *Sarcophilus*).

Muridoid dasyurids are widely distributed in New Guinea, Australia, and nearby islands, including Tasmania.

The head and body length of muridoid dasyurids is 5–27 cm, and the weight is 4–134 g. The smallest are the planigales (*Planigale*); the largest is *Murexia longicaudata*. In many species, males are larger than females. In most species, the fur is thick and soft, but colouration varies somewhat between species. The upperparts are predominantly yellowish, greyish or brownish. The underparts are lighter, up to cream or white. Some species have one or three black stripes along the back. A dark stripe or spot may also be present on the head. In some species, the eyes are surrounded by a dark or light ring.

The muzzle is of medium length or long, and in most cases is thin and pointed. The eyes and ears are normally developed, but in some species are small or large. The relative length of the tail varies from 64% in *Dasykaluta rosamondae* up to 129% in *Murexia habbema*; however, in most species, it is approximately the length of the head and body. The tail is non-prehensile and is covered with scales or short hairs. In some desert species of *Pseudantechinus* and *Sminthopsis*, as well as in *Dasykaluta rosamondae*, fat reserves are deposited in the tail, due to which it takes on a conical shape. The number of digits is 5/5 (forefoot/hind foot). In most species, the hind feet are of medium length, while in *Sminthopsis* they are elongated due to lengthening of the tarsus and metatarsus, while the digits are somewhat shortened. In many species, the inner digits of the hind feet (hallux) are short and lacks claws, while other digits have claws. Dental formula: (I4/3, C1/1, P2–3/2–3, M4/4) × 2 = 42–46.

The canines are well developed, and the molars have sharp-tipped cusps.

Muridoid dasyurids inhabit a variety of habitats, from tropical rainforests to deserts. They are mainly active on the ground, but many are good climbers. They build nests in burrows dug by themselves or by other animals, in cracks in the ground, among rocks and in tree hollows. Their diet mainly consists of insects and other invertebrates, small vertebrates and, to a lesser extent, fruit. They are mainly active at night, but many bask in the sun during the day. When food is scarce, some species fall into a torpor; others rely on fat reserves in the tail. They are mostly solitary, producing litters of 2–12 young. Many live in nature only 1.5 years.

2.1.5. Bandicoots – order *Peramelemorphia*

Including the pig-footed bandicoots (*Chaeropus*) and lesser bilby (*Macrotis leucura*), which went extinct during the 20th century, the order *Peramelemorphia* includes 3 families, 8 genera and 24 species. Muridoids are represented in **the family *Peramelidae*** (bandicoots), which consists of 6 genera and 20 species. Bandicoots with a mouse-like body structure are represented in the genus *Microperoryctes* (mouse bandicoots), which includes 4 species (20% of *Peramelidae*). Other bandicoot species are relatively short-tailed. Mouse bandicoots inhabit New Guinea.

Mouse bandicoots (fig. 5:2) are approximately the size of a rat, with head and body length and weight varing from 14 cm and less than 100 g in *Microperoryctes aplini* up to 30 cm and 670 g in *M. longicauda*. Their fur is short and soft (reminiscent of shrews), and brown or grey in colour, though the underparts are lighter. All species except the darkly-coloured *M. murina* have a dark "mask" on the muzzle and longitudinal dark stripes on the back. *M. aplini* has one stripe, *M. longicauda* three, and *M. papuensis* one stripe along the middle of the back and two incomplete stripes on the sides of the rump.

The snout is long and pointed. The eyes are small. The ears are of medium length or short. The tail is relatively longer than in other bandicoots, but shorter than the head and body. The relative length of the tail varies from 64% in *M. murina* up to 85% in *M. longicauda*. The tail is non-prehensile. The feet have a characteristic bandicoot structure. There are 5 digits on the **forefeet**, but the extreme digits (1 and 5) are shortened and without claws, while the 2nd and 3rd digits are longer than the others and are equipped with long, slightly curved claws. The 4th digit is much shorter, with a shorter claw. The **hind feet** are slightly elongated: 20–23% of the head and body length (Helgen and Flannery, 2004; Dickman, 2015). Its 4th digit is much larger than the others and has a long claw, the 2nd and 3rd digits are fused, the 5th digit is normally developed, and the 1st digit is small and without a claw. Animals use the claws of fused digits as a comb. The number of teeth is 48: (I5/3, C 1/1, P 3/3, M 4/4) × 2.

The habits of mouse bandicoots are poorly understood. They live mainly in rainforests, but also in gardens, sugarcane thickets and alpine meadows. In mountains, they occur up to altitudes of 4000 m. Mouse bandicoots are terrestrial. They shelter in shallow burrows, in tussocks, under tree roots and in forest litter. Their diet includes insects, worms, and other invertebrates, fallen fruit, and possibly also small vertebrates. Food is apparently obtained by digging in litter and soil on the forest floor. They are active mainly in the dark and at dusk. They produce 1–4 young in a litter (in *M. longicauda*).

2.1.6. Diprotodonts – order *Diprotodontia*

The order *Diprotodontia* includes 11 families, 40 genera and 142 species. Species with a mouse-like body structure are represented in three families: *Burramyidae* (pygmy possums) – all 5 species, *Tarsipedidae* (honey possums) – the only species, and *Hypsiprymnodontidae* (musky kangaroos) – the only species. Thus, all three families in the order consist entirely of muridoid species: in total 7 species belonging to 4 genera. The non-muridoid diprotodonts are

exceptionally diverse in morphology and habits. Mouse-like diprotodonts are found in New Guinea, Australia, and nearby islands, including Tasmania.

2.1.6.1. Pygmy possums – family *Burramyidae*

The family *Burramyidae* includes 2 genera (*Burramys*, *Cercartetus*) and 5 species. All of them have mouse-like body structure. Pygmy possums are found in New Guinea, Australia, and nearby islands, including Tasmania.

The pygmy possums externally resemble mice (fig. 5:3). The head and body length of pygmy possums is 5–12 cm, and the weight is 6–80 g. The pelage is thick and soft, with the upperparts brownish or greyish and the underparts light grey, yellowish or white. Some species have black stripes between the nose and ear, or dark rings around the eyes.

The muzzle is pointed, and the eyes and ears are comparatively large. The tail is long or very long – up to 140% of the head and body length in the long-tailed pygmy possum (*Cercartetus caudatus*). The tail is prehensile, and almost naked, except for a hairy base. The number of digits is 5/5, but on the hind feet the 2nd and 3rd digits are fused. The hallux is opposable. The claws are short, and the digital pads are large. Dental formula: (I3/1–3, C1/0, P2–3/2–3, M3–4/3–4) × 2 = 30–42. The middle incisors are enlarged. In the mountain pygmy possum (*Burramys parvus*), the last premolar tooth has the form of a sharp vertical plate. The molars are cuspidate. In *Cercartetus*, the elongated papillae of the tongue tip create a "brush", which is used to collect nectar and pollen.

Pygmy possums inhabit forests and shrubland. They nest in tree hollows, cracks in bark, in cavities in the ground, in rotten stumps, in dense vegetation, under stones or in abandoned bird nests. Pygmy possums are very adept at climbing and jumping. Their diet includes fruit, seeds, nectar, pollen, insects, and other small animals. The mountain pygmy possum caches seeds and berries

for the winter. Pygmy possums are nocturnal. In cold weather some species may fall into a torpor for several days; the mountain pygmy possum, apparently, hibernates. Pygmy possums are probably solitary, but may spend winter in conspecific groups. They produce litters of up to 6 young. In captivity, pygmy possums live for 4–8 years, depending on the species.

2.1.6.2. Honey possums – family *Tarsipedidae*

The family *Tarsipedidae* contains one species, the honey possum (*Tarsipes rostratus*), which is found in south-western Australia.

The honey possum (fig. 5:4) is a very small animal: its head and body length is 7–9 cm, its weight is 7–16 g. Its pelage is short and coarse. Three longitudinal dark stripes run along its greyish-brown back. The underparts are pale yellow to white. The snout is long and pointed, the eyes are small, and the ears are of medium length.

The honey possum's tail is about 17% longer than its head and body length and exhibits some degree of grasping ability. The number of digits is 5/5, but the 2nd and 3rd digits are fused. On the fused digits, the claws are normally developed, while the other digits have nails. The claws do not protrude beyond the tips of the digits. The digits are long, with enlarged tips, while the plantar pads are not enlarged. The hallux is enlarged and opposable. Dental formula: (I2/1, C1/0, P1/0, M3/3) × 2 = 22. Except for the incisors, the teeth are very small. The tongue is long, with a brush-like tip.

The honey possum inhabits dense scrub and herbaceous thickets. It shelters in tree hollows, in cracks in tree bark or in abandoned bird nests. It is a good climber and jumper. It feeds exclusively on nectar and pollen. The honey possum is the only flightless mammal that is a specialized nectar feeder. It is active in the dark and at dusk. In bad weather, it will fall into a torpor. Honey possums live alone or in small groups. They produce 1–4 young in a litter (usually 2–3). New-born honey possums weigh less than 5 mg, the minimum weight for a new-born mammal. Honey possums live for around two years.

2.1.6.3. Musky rat-kangaroos – family *Hypsiprymnodontidae*

The family *Hypsiprymnodontidae* includes one species, the musky rat-kangaroo (*Hypsiprymnodon moschatus*), which is found in north-eastern Australia.

The musky rat-kangaroo (fig. 5:5) is a rat-sized animal. The head and body length is 15–27 cm, and the weight is 360–680 g. The fur is thick and velvety, and red-brown in colour. The muzzle is conical and slightly elongated. The vibrissae are relatively short. The eyes and ears are of medium size. The tail is scaly and about 60% of the length of the head and body. It has a grasping ability, which is used by the animal when climbing and for carrying nesting material.

The musky rat-kangaroo walks on four legs. Its feet are pentadactyl (5/5), but on the hind feet the 2nd and 3rd digits are fused. The hallux is opposable, but not enlarged. The hind feet are narrow and long; however, they are much less elongated than in related bipedal species. In musky rat-kangaroos both the digits and the tarso-metatarsal parts of the hind feet are elongated, especially the 4th digit. Unlike in potoroos (*Potoroidae*) and true kangaroos (*Macropodidae*), the hind feet of the musky kangaroo retain a grasping ability. The plantar pads are not enlarged and the claws are of medium length and straightened.

Dental formula: (3/1, C 1/0, P1–2/1–2, M4/4) × 2 = 30–34 (adults have one premolar). The middle incisors are enlarged, the canines are small, the last premolars have the form of a vertical plate with a sharp edge, and the molars are cuspidate. Unlike other kangaroos, the musky rat-kangaroo has a one-chambered stomach.

Musky rat-kangaroos inhabit tropical rainforests. They are mainly terrestrial, but may climb fallen trees and lianas. The nest of leaves is arranged in dense vegetation, in log hollows, under stones or under tree roots. Musky rat-kangaroos feed mainly on the pulp of fallen fruit, as well as seeds, invertebrates, and fungi. They cache fruit and seeds in the forest floor. These animals are active mainly during the day and are solitary. They usually give birth to two young. Musky rat-kangaroos live 4–5 years.

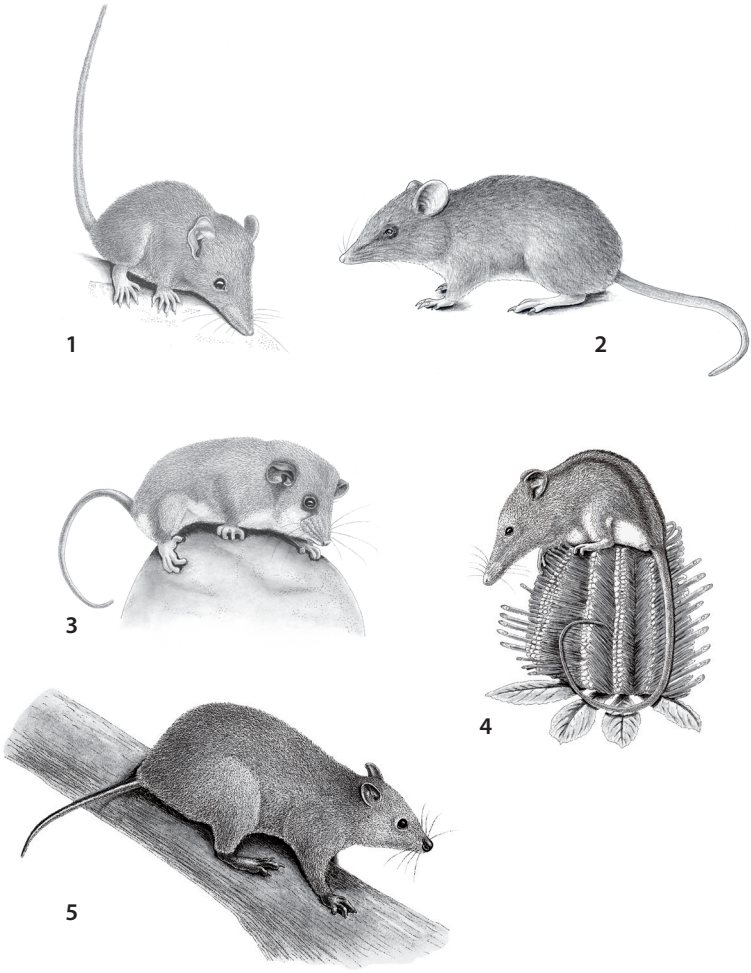


Fig. 5. Muridoids among Australian marsupials: 1– brown antechinus (*Antechinus stuartii*; Dasyuridae: 56 muridoid species); 2 – Arfak pygmy bandicoot (*Microperoryctes* aplini; Peramelidae: 4 muridoid species); 3 – mountain pygmy possum (*Burramys parvus*; Burramyidae: all 5 species are muridoids); 4 – honey possum (*Tarsipes rostratus*; Tarsipedidae: the only species in the family); 5 – musky rat-kangaroo (*Hypsiprymnodon moschatus*; Hypsiprymnodontidae: the only species in the family).

2.2. Muridoids among insectivores

The order *Eulipotyphla* (insectivores) includes 4 families, 56 genera and 530 species. Species with a mouse-like body structure are represented in all families and 27 genera, totally 389 species (73%). Non-muridoid species of insectivores have a short tail (some gymnures and shrews), a spiny covering (hedgehogs), or are morphologically adapted to digging (moles) or swimming (desmans).

Muridoid insectivores are widespread in Eurasia, North America, and Africa, as well as in the Antilles (solenodons). They also inhabit mainland Central America and the northern part of South America, but are represented there only by a small number of relatively short-tailed shrews of the genus *Cryptotis*.

2.2.1. Hedgehogs – family *Erinaceidae*

The family *Erinaceidae* (hedgehogs) includes 10 genera and 26 species. A mouse-like body structure occurs in 3 species (12%), which belong to the subfamily *Galericinae* (gymnures): the moonrat (*Echinosorex gymnure*), the long-eared gymnure (*Hylomys megalotis*), and the shrew gymnure (*Neotetracus sinensis*). The remaining gymnures have a shortened tail, and the true hedgehogs are short-tailed, have a spiny covering, and exhibit different limb structure. Mouse-like erinaceids occur in Southeast Asia.

The head and body length and weight of muridoid gymnures vary from 11 cm and 36 g in the shrew gymnure to 46 cm and 2 kg in the moonrat (fig. 6:1). Gymnures do not have spines and are instead covered with fur. The moonrat has coarse guard hair. Its head is usually light with a dark "mask". The body is almost black, but some individuals are almost white. In other gymnures, the hair is soft, greyish or brownish in colour.

The muzzle is pointed, with a proboscis. The eyes are small. The ears of small species are quite large (17% of the head and body length), but they only slightly protrude above the head. The moonrat has ears of medium length (11%). The relative length of the tail is 60–70%. The

number of digits is 5/5 (forefoot/hind foot). All digits are quite long and have claws, both on the fore and hind feet. Claws and plantar pads are of medium size. The hind feet in *Echinosorex* and *Hylomys megalotis* are fairly short (16%), while those of *Neotetracus* are long (24%). Dental formula: (I3/3, C1/1, P3–4/3–4, M3/3) × 2 = 40–44. The zygomatic arches are normally developed.

Muridoid gymnures inhabit tropical and subtropical forests, bamboo thickets, shrublands, plantations, and areas near water bodies (moonrat). They are predominantly terrestrial animals, but the moonrat partly forages in shallow water. All species are able to climb. They shelter among logs, in rock crevices or hollows under roots, or dig burrows. Gymnures deter enemies by producing an unpleasant smell. They feed mainly on invertebrates, but the moonrat also eats frogs and fish. Fruit and the belowground parts of plants also make up a small part of gymnure diet. Gymnures are nocturnal animals, but are sometimes active during the day. They are solitary and produce 1–7 young in a litter. In captivity, moonrats may live for more than 4 years.

2.2.2. Shrews – family *Soricidae*

The family *Soricidae* (shrews) includes 26 genera and 448 species. Most of them have a mouse-like body structure: approximately 377 species (84%) from 21 genera. The exceptions are the short-tailed *Blarina* (all 5 species), *Congosorex* (2 species), the Ussuri white-toothed shrew (*Crocidura lasiura*), most *Cryptotis* (approximately 45 species), *Myosorex* (6 species), *Notiosorex* (all 4 species), *Surdisorex* (all 3 species), as well as the mole-like *Anourosorex* (all 4 species) and the web-footed *Nectogale elegans*.

Muridoid shrews are widespread in Eurasia, North America, and Africa. They also occur in Central and northern South America, but are represented there only by a small number of relatively short-tailed *Cryptotis*, which are mostly non-muridoid or not quite muridoid in appearance.

Shrews (fig. 6:2) are small animals, mostly around the size of a mouse. The head and body length and weight of muridoid shrews, as well as shrews in general, vary from 4 cm and 2 g in the Etruscan shrew (*Suncus etruscus*) to 18 cm and 105 g in the Asian house shrew (*Suncus murinus*). Shrews have short, dense fur. The upperparts are greyish, brownish or black; the underparts are usually lighter, up to white. The piebald shrew (*Diplomesodon pulchellus*) has variegated grey-white coloration.

Shrews typically have a flat, narrow head, with a long, thin, and mobile proboscis. The eyes are small, the ears usually do not protrudee above the top of the head, many species have short ears. The tail is usually covered with short hairs or scales, while some shrews have vibrissae on the tail (e.g., white-toothed shrews – *Crocidura*), and semi-aquatic species have a keel of stiff hair on the underside of the tail (*Chimarrogale*, *Neomys*). Scales are also found on the feet. The number of digits is 5/5 (forefoot/hind foot). In muridoid semi-aquatic shrews, such as the water shrews (*Neomys*), the hind feet are bordered with stiff hairs. The number of teeth is 26–32. The middle incisors of the upper jaw are enlarged and have two tips. Together with the large, forward-pointing lower incisors, they form "tweezers" for catching prey. Shrews do not have zygomatic arches, which makes their already narrow heads even narrower and allows them to penetrate very small openings.

Shrews inhabit various biotopes. They are active mainly on the ground among dense vegetation, as well as in the forest litter and soil. Due to their small size, they are able to penetrate all sorts of cracks and holes. Some are semi-aquatic, while others are good climbers. Shrews feed mainly on invertebrates and rarely on small vertebrates. Plant foods, such as seeds, are eaten to a lesser extent. Shrews are active all year round. Some species are active at night and during the day, others mostly at night. Most species lead a solitary way of life. Shrews produce 2–10 young in a litter. Their life span is short, approximately 12–18 months.

2.2.3. Moles – family *Talpidae*

The family *Talpidae* (moles) includes 18 genera and 54 species. A mouse-like body structure occurs only in all 7 species of the genus *Uropsilus* – Chinese shrew moles. Among non-muridoid species, the body structure is modified for digging (moles) or swimming (desmans). Shrew moles live in Southeast China.

The shrew moles are the smallest moles and resemble shrews both in size and appearance (fig. 6:3). The head and body length is 7–8 cm, and the weight is 6–11 g. The fur is short and dense, with colouration ranging from brownish and greyish to almost black. The proboscis is long and mobile, with a scaly surface. It is formed by nostrils that are elongated into connected tubes, separated from above by a furrow. The eyes are very small. The ears are well developed, but do not protrude above the head.

The tail is long, though shorter than the head and body (75–96%), and is covered with scales and short hairs. The limbs are less specialized for digging than in other moles. The number of digits is 5/5 (forefoot/hind foot), and all digits possess a claw. The hind feet are of medium length (19–21%). Dental formula: (I2/1–2, C1/1, P3–4/3–4, M3/3) × 2 = 34–40. The zygomatic arches are normally developed.

The ecology of shrew moles is not well understood. They inhabit mountain forests and alpine meadows and forage mainly on the ground, but sometimes climb on the low branches of woody vegetation. Their nests are located in natural cavities. Their diet mainly includes invertebrates, but sometimes also fruit.

2.2.4. Solenodons – family *Solenodontidae*

The family *Solenodontidae* (solenodons) includes 2 genera and 2 species: the Cuban solenodon (*Atopogale cubana*) and the Hispaniolan solenodon (*Solenodon paradoxus*). Both species have a muridoid appearance. Solenodons are currently present only on two Caribbean islands, Cuba and Hispaniola, with one species on each.

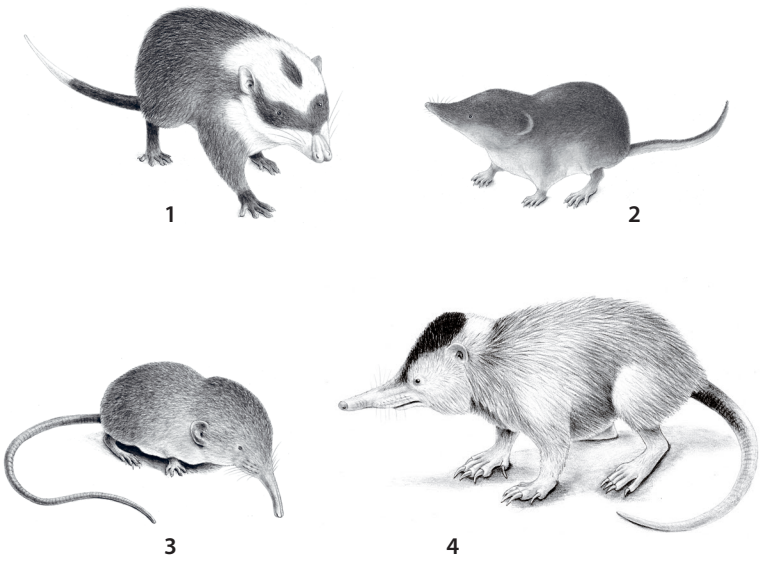


Fig. 6. Muridoids among insectivores: 1 – moonrat (*Echinosorex gymnura*; Erinaceidae: 3 muridoid species); 2 – common shrew (*Sorex araneus*; Soricidae: 377 muridoid species); 3 – shrew mole (*Uropsilus sp.*; Talpidae: 7 muridoid species); 4 – Hispaniolan solenodon (*Solenodon paradoxus*; Solenodontidae: both species are muridoids).

Solenodons (fig. 6:4) are the size of a very large rat. The head and body length is 20–46 cm, and the weight is 450–1170 g (Derbridge et al., 2015). Their fur is coarse and coloured black, yellowish, or brownish. The head is equipped with a long and mobile proboscis. The eyes are small, and the ears are normally developed (on average 9% of the head and body length in *S. paradoxus*).

The tail is long, though shorter than the head and body (72% in *S. paradoxus*), and covered with scales. The number of digits is 5/5 (forefoot/hind foot). The claws are large and curved; those on the front legs are considerably larger than those on the hind legs. The hind feet are of medium length (20% in *S. paradoxus*). Dental

formula: (I3/3, C1/1, P3/3, M3/3) × 2 = 40. The first upper incisors are enlarged. The second lower incisors have a deep slit through which flows a venomous saliva secreted by the submaxillary gland. The skull lacks zygomatic bones.

Solenodons inhabit mountain forests. They move mostly on the ground, but dig extensive burrows and can climb. They shelter in burrows, caves and tree hollows. Solenodons forage by rummaging in soil and rotten wood. They feed mainly on invertebrates and small vertebrates, but also on carrion and fruit. They are active mainly at night. Solenodons actively defend themselves from enemies, and their saliva is poisonous. They produce 1–3 young in a litter. In captivity, solenodons live for up to 11 years.

2.3. Muridoids among afrosoricids

The order *Afrosoricida* (afrosoricids) includes 3 families, 20 genera and 55 species. Species with a mouse-like body structure are represented in two families: among tenrecs and otter shrews. In total there are 24 muridoid species (i.e. 44% of afrosoricids), belonging to 4 genera. Non-muridoid afrosoricids are either short-tailed (rice tenrecs, *Oryzorictes*); have webbed hind feet (aquatic tenrec, *Microgale* (*Limnogale*) *mergulus*; Ruwenzori otter shrew, *Micropotamogale ruwenzorii*); a vertically flattened tail (giant otter shrew, *Potamogale velox*); have spiny covering and resemble hedgehogs (*Tenrecinae*) or are morphologically adapted to a subterranean way of life (*Chrysochloridae*).

Muridoid afrosoricids are found in equatorial West Africa (Nimba otter shrew, *Micropotamogale lamottei*) and in Madagascar (all other species).

2.3.1. Tenrecs – family *Tenrecidae*

The family *Tenrecidae* includes 8 genera and 31 species. A mouse-like body structure occurs in 23 species (74%), belonging to 3 genera: the large-eared tenrec (*Geogale aurita*) and shrew tenrecs of

the genera *Nesogale* and *Microgale*. Non-muridoid members of the family are either short-tailed (rice tenrecs, *Oryzorictes*), have webbed hind feet (aquatic tenrec, *Microgale (Limnogale) mergulus*) or have a spiny covering and resemble hedgehogs (all other genera). All tenrecs live on the island of Madagascar.

Muridoid tenrecs resemble shrews (fig. 7:1). The head and body length is 4–14 cm, and the weight is 2.5–49 g. The smallest species is the pygmy shrew tenrec (*Microgale parvula*); the largest species is Talazac's shrew tenrec (*Nesogale talazaci*; fig. 7:1). The fur is short, dense, and soft and coloured brownish or grey to almost black on the upperparts, and lighter, greyish or yellowish, on the underparts. Drouhard's shrew tenrec (*Microgale drouhardi*) has a dark brown stripe along its back.

The muzzle is long, thin, and pointed. In some species, it has the appearance of a bare proboscis (e.g. in the naked-nosed shrew tenrec, *Microgale gymnorhyncha*). The eyes are small or very small. The ears vary in size, but in all species they are normally developed (15–24% of the head and body length). The large-eared tenrec exhibits the longest ears. The tail is long or very long. In some species (*Microgale longicaudata*, *M. principula*) it is more than twice as long as the head and body length. The tail is covered with scales and sparse hairs. The longest-tailed tenrecs (*Microgale longicaudata*, *M. majori*, *M. principula*) have a prehensile tail tip with a bare dorsal (upper) surface and enlarged scales (Jenkins, 2018). The lesser long-tailed tenrec (*Microgale longicaudata*) has 47 caudal vertebrae, while the shorter-tailed *Microgale cowani* has only 20 (Nowak, 1991). In Dobson's shrew tenrec (*Nesogale dobsoni*), the tail thickens from fat reserves in the wet season and becomes thinner during the dry season. The limbs are pentadactyl (5/5), and each digit ends with a claw. Apparent climbing species (*Microgale longicaudata*, *M. majori*, *M. principula*) have long digits. Hind foot length varies from relatively short to long (15–26%).

The large-eared tenrec has 34 teeth: (I2/2, C1/1, P3/2, M3/3) × 2 = 34. Other muridoid tenrecs have 40 teeth: (I3/3, C1/1, P3/3,

M3/3) × 2 = 40. The large-eared tenrec and shrew-toothed shrew tenrec (*Microgale soricoides*) have enlarged first (middle) incisors, similar to those of shrews. In *Microgale gracilis* and M. *gymnorhyncha* the teeth are somewhat reduced and sparse. The zygomatic arch is incomplete due to the absence of the zygomatic bone.

Muridoid tenrecs live mainly in forests, both wet and dry. Among them there are species leading subterranean-terrestrial, terrestrial, and semi-arboreal ways of life. Nests are made in rotten trunks, under fallen trees, under tree roots or under stones. There is no information about burrowing in muridoid tenrecs. They feed mainly on invertebrates and, to a lesser extent, on small vertebrates (larger species) and fruit. The large-eared tenrec seems to be specialized in feeding on termites. Muridoid tenrecs are active mainly in the dark and at dusk. Dobson's shrew tenrec accumulates fat reserves in its tail, which allows it to survive unfavourable periods of the year in a state of torpor. The large-eared tenrec also falls into short-term and seasonal torpor, and the same is possibly true of other species as well. Muridoid tenrecs are solitary and produce 1–5 young in a litter. Species belongong to the genus *Nesogale* live in captivity for more than five years.

2.3.2. Otter shrews – family *Potamogalidae*

The family *Potamogalidae* (otter shrews) includes 2 genera and 3 species. Mouse-like body structure occurs in one of them – the Nimba otter shrew (*Micropotamogale lamottei*; fig. 7:2). Non-muridoid members of the family have special adaptations for swimming: membranes between the digits of the hind feet (Ruwenzori otter shrew, *Micropotamogale ruwenzorii*) or a vertically flattened tail (giant otter shrew, *Potamogale velox*). The Nimba otter shrew lives in equatorial West Africa.

The head and body length of the Nimba otter shrew is 12–15 cm, and the is weight 32–95 g. The fur is thick and soft, with grey-brown to black colouration. The muzzle is wide and flat (otter-like). The vibrissae are long, thick and hard. The eyes are very small, the ears are small (7% of the head and body length) and rounded. The tail is round in cross section (not flattened) and covered with sparse short

hairs. The relative length of the tail is 86%. The length of the hind foot is 14%. The number of digits is 5/5, but the 2nd and 3rd digits of the hindfeet are fused. Their claws are used for grooming. The animal has no webbing on its feet.

Dental formula: (I3/3, C1/1, P3/3, M3/3) × 2 = 40. The first (middle) upper incisors are enlarged and conical; the other upper incisors, canines and the first premolar are also conical, but flattened. The lower first incisors, like the upper ones, are enlarged, but chisel-shaped and tilted forward. The skull is flattened. The zygomatic arches are incomplete. The clavicle is missing.

The Nimba otter shrew inhabits equatorial rain forests, mainly along the banks of mountain streams. They shelter in burrows, and swim and dive well. When swimming, they use their hind feet for propulsion. Prey is caught mainly in the water. Their diet predominantly consists of crabs, but also insects, fish and, to a lesser extent, frogs. They are solitary and active at night. They produce 1–3 young in a litter.

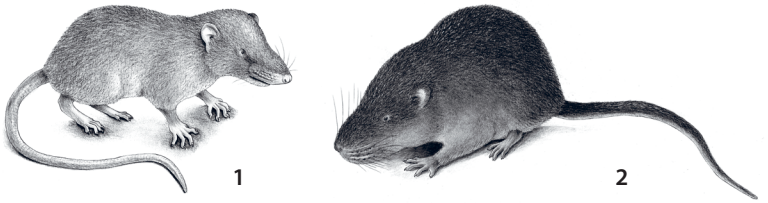


Fig. 7. Muridoids among afrosoricids: 1 – Talazac's shrew tenrec (*Nesogale talazaci*; Tenrecidae: 23 muridoid species); 2 – Nimba otter shrew (*Micropotamogale lamottei*; Potamogalidae: 1 muridoid species).

2.4. Muridoids among rodents

Rodents (*Rodentia*) are the most species-rich order of mammals. The order includes 34 families, 503 genera, and 2475 species (Wilson et al., 2016, 2017). Thus, rodents make up approximately 40% of

all mammalian species. Species with a mouse-like body structure are represented in 9 families: among murids (*Muridae*), cricetids (*Cricetidae*), nesomyids (*Nesomyidae*), birch mice (*Sminthidae*), jumping mice (*Zapodidae*), dormice (*Gliridae*), heteromyids (*Heteromyidae*), spiny rats (*Echimyidae*) and chinchilla rats (*Abrocomidae*). In total there are 1341 mouse-like species of rodents (54%) in 268 genera. Non-muridoid rodents are extremely ecomorphologically diverse. They exhibit morphological adaptations to semi-aquatic, subterranean, terrestrial, and arboreal ways of life and include spiny, gliding, and bipedal species.

The natural distribution of muridoid rodents covers the whole world, except for the polar regions, but the house mouse and brown rat have even reached those areas with the aid of humans.

2.4.1. Murids – family *Muridae*

The content and taxonomy of the family *Muridae* has been repeatedly revised. According to the classification adopted here (Wilson et al., 2017), the family includes 5 subfamilies (*Deomyinae*, *Gerbillinae*, *Leimacomyinae*, *Lophiomyinae*, *Murinae*), 155 genera, and 816 species, making it the largest family of mammals. Mouse-like body structure occurs in the majority of species, namely 665 species (81%) in 131 genera and three subfamilies (*Deomyinae*, *Gerbillinae* and *Murinae*). Representatives of the non-muridoid subfamilies, each of which includes only one species, are either short-tailed (*Leimacomys buettneri*), or have shortened hind limbs and a bushy tail (*Lophiomys imhausi*).

Among the deomyines (*Deomyinae*) a mouse-like body structure occurs in all 57 species, which belong to 4 genera.

The subfamily *Gerbillinae* (gerbils) includes 14 genera and 101 species. Among them are 18 mudiroid species belonging to 8 genera: *Brachiones*, *Desmodilliscus*, *Desmodillus*, part of *Gerbilliscus*, part of *Gerbillus*, *Microdillus*, *Pachyuromys* and *Tatera*.

Non-muridoid gerbils differ externally from muridoid species only by the presence of a tufted tail.

The subfamily *Murinae* (murines) includes 135 genera and 656 species. Most species have a muridoid body structure, namely, 591 species (90%) in 119 genera. Non-muridoid members of the subfamily either have a tufted tail (*Anisomys*, *Anonymomys*, *Chiropodomys*, *Conilurus*, part of *Grammomys*, *Hapalomys*, part of *Hylomyscus*, *Lorentzimys nouhuysii*, *Margaretamys*, *Mesembriomys*, *Musseromys*, part of *Niviventer*, part of *Thallomys*, *Thamnomys*), bushy tail (*Crateromys*), webbed hind feet (*Hydromys*, *Crossomys*), or are bipedal with a tufted tail (*Notomys*). Some murines have a spiny pelage (e.g. *Tokudaia*, *Acomys*); however, this is not so developed as to affect their general body structure and locomotion, so spiny murines are considered here as muridoids.

Muridoid murids are widespread throughout the Eastern Hemisphere, including Australia, while synanthropic species (house mouse, black rat, and brown rat) are distributed globally with the aid of humans.

Muridoid murids have head and body lengths of 4–48 cm and weights of 3 g to 2.7 kg. Nevertheless, most species are smaller than the brown rat. The largest species are members of the Philippine genus *Phloeomys* (slender-tailed cloud rats); the smallest species are some mice from the African subgenus *Nannomys* belonging to the genus *Mus*. Species larger than the brown rat are found mainly on the islands of the Malay Archipelago and in the Australian zoogeographic region. There are a particularly large number of "giant rats" in New Guinea. Muridoid murids have coats of variable density, softness and length, and some species have spines or spiny bristles on their backs (e.g. spiny mice, *Acomys*). The fur is usually coloured yellowish, brownish, or greyish. Some species have light or dark spots or longitudinal stripes on the back.

Muridoid murids have a medium-length or long muzzle. In many species the vibrissae and ears are long. The eyes in most

species are normally developed or large. Tail length varies from the minimum value for muridoids to very long. Some scansorial species have prehensile tails, and some desert species (*Pachyuromys*, *Zyzomys*) accumulate fat reserves in the tail, affecting its shape. In most species, the tail is scaly with sparse hairs, though in some it is covered with fur.

Murids have 4/5 functional digits. In most species all digits are equipped with claws, except the rudimentary 1st forefoot digit, which has a nail. Some species also have a nail on the 5th and/or 1st digits of the hind feet. One of the extreme digits of the hind feet (1st or, usually, 5th) may be partially opposable.

Most murids have 16 teeth: (I1/1, C0/0, P0/0, M3/3) × 2 though in some species the number is lower due to the absence of some molars: the gerbil *Desmodilliscus braueri* has 14 teeth, and some Australian and Malayan animalivorous species have 12, 8 or 4 teeth. The minimal number of teeth, only 4, is found in the recently described (2012) edented Sulawesi rat (*Paucidentomys vermidax*). Murid molars have roots, range in height from low-crowned to high-crowned, and have a masticatory surface that varies from cuspidate to ridged. However, in most species, the molars are low-crowned and cuspidate.

Muridoid murids inhabit various biotopes – from deserts to forests. Many species live in anthropogenic landscapes, some even in buildings. Although a significant part of muridoid murids does not have a narrow locomotor specialization, the family includes semi-aquatic (e.g. the Ethiopian water rat, *Nilopegamys plumbeus*), subterranean (short-tailed bandicoot rat, *Nesokia indica*) and arboreal (many species) muridoids. Muridoid murids find shelter in burrows (e.g. field mouse, *Apodemus agrarius*), tree hollows (yellow-necked mouse, *Apodemus flavicollis*) and rock crevices (spiny mice), or in nests built on the ground (stick-nest rats, *Leporillus*) or on plants (harvest mouse, *Micromys minutus*). Most species feed mainly on seeds, fruit, and insects, but there are also specialized animalivorous

(e.g. *Rhynchomys*) and herbivorous species (e.g. *Phloeomys*). They are active all year round and mostly at night, though some species are diurnal (e.g. striped grass mice, *Lemniscomys*).

Muridoid murids live alone or in groups. The number of young per litter varies from 1 to 20. In most species, newborns are naked and blind, but in spiny mice and in some other species, they are covered with fur and open their eyes shortly after birth. Young animals reach sexual maturity in the year of their birth. In captivity, they live 1.5–8 years, depending on the species.

2.4.2. Cricetids – family *Cricetidae*

Similar to the family *Muridae*, the content of the family *Cricetidae* has been repeatedly revised. According to the classification adopted here (Wilson et al., 2017), it includes 5 subfamilies (*Cricetinae*, *Arvicolinae*, *Neotominae*, *Sigmodontinae*, *Tylomyinae*), 142 genera, and 765 species. Mouse-like body structure occurs in 505 species (66%) belonging to 93 genera and all five subfamilies.

The subfamily *Cricetinae* (hamsters) includes 7 genera and 18 species. Only 2 species (11%) in 2 genera have a mouse-like body structure: the Gansu hamster (*Cansumys canus*) and the greater long-tailed hamster (*Tscherskia triton*). Other species of hamsters have shorter tails, and almost all hamsters are also relatively short-legged (Miljutin, 2011).

The subfamily *Arvicolinae* (voles) includes 29 genera and 162 species. Muridoid species occur in 9 genera: *Arborimus*, part of *Arvicola*, *Chionomys*, *Dinaromys*, part of *Eothenomys*, part of *Microtus* (*M. longicaudus*, *M. richardsoni*), *Neofiber*, part of *Proedromys* and *Volemys*. Totally 21 species (13%). Non-muridoid voles are shorter-tailed, or have morphological adaptations for digging (mole voles, *Ellobius*) or swimming (muskrat, *Ondatra zibethicus*).

The subfamily *Neotominae* (neotomyines) includes 16 genera and 140 species. All species have a muridoid body structure, except for the bushy-tailed woodrat (*Neotoma cinerea*), which has a bushy

tail, as well as 8 species of *Peromyscus* and 2 species of *Habromys* that have tufted tails. In total, there are 129 muridoid neotomyines (92%) belonging to 16 genera.

The subfamily *Sigmodontinae* (sigmodontines) includes 86 genera and 434 species. The majority of species – 344 species (79%) in 64 genera – have a mouse-like body structure. The exceptions are species with clearly expressed webbing between the digits (*Rheomys*, *Lundomys*, *Holochilus*, *Amphinectomys*, and *Nectomys*), with a distinct tuft at the end of the tail (*Abrawayaomys*, *Aepeomys*, part of *Andalgalomys*, *Calassomys*, part of *Eligmodontia*, *Graomys*, *Juliomys*, *Mindomys*, part of *Neacomys*, part of *Oecomys*, part of *Oligoryzomys*, *Phaenomys*, part of *Phyllotis*, *Rhagomys*, *Rhipidomys* and *Tanyromys*) or with short tails (*Blarinomys*, *Galenomys*, part of *Geoxus*, *Notiomys*, *Paynomys* and *Punomys*).

The subfamily *Tylomyinae* (tylomyines) includes 4 genera and 11 species. Of these, 9 species (82%) in two genera have a muridoid body structure, while representatives of the tribe *Nyctomyini*, which includes two species (*Nyctomys sumichrasti* and *Otonyctomys hatti*), have a distinct tuft at the end of the tail.

Thus, most cricetids have a mouse-like body structure. Non-muridoid members of the family are either short-tailed and short-legged (e.g. hamsters, most voles,), have a tufted tail (many New World scansorial species), or have webbed hind feet (some semi-aquatic sigmodontines) or a flattened tail (muskrat).

Muridoid cricetids are widely distributed in North, Central and South America (*Arvicolinae*, *Neotominae*, *Sigmodontinae*, *Tylomyinae*) as well as in Palearctic Eurasia (*Cricetinae*, *Arvicolinae*).

The head and body length of muridoid cricetids is 5–29 cm, and the weight is 7–630 g. Most species have a weight of less than 100 g, but there are also many species around the size of a rat. The largest extant muridoid cricetid is the woolly giant rat (*Kunsia tomentosus*). However, the extinct Martinique giant rat (*Megalomys desmarestii*), which died out at the beginning of the 20th century, was

significantly larger – its head and body length reached 36 cm. The pelage of most species is soft, though in some it is hard, bristly, or spiny (*Neacomys*, *Scolomys*). The fur is usually coloured brownish, yellowish, greyish, or blackish, with lighter underparts.

The muzzle, vibrissae, eyes, and ears of muridoid cricetids vary in size, but in most the eyes and ears are normally developed or large. True hamsters (*Cricetinae*) have cheek pouches. The tail is scaly or covered with short fur. The number of functional digits is 4/5 (1st forefoot digit reduced). Semi-aquatic muridoid cricetids have a fringe of coarse hair or rudimentary webbing on their hind feet (e.g. *Neofiber* and *Ichthyomys*).

The number of teeth is 16: (I1/1, C0/0, P0/0, M3/3) × 2, except for the oyapock fish-eating rat, *Neusticomys oyapocki*, which has 12 teeth (M2/2). The molars may be with or without roots (in most voles). The height of the molar crown varies from low to high, and the chewing surface varies from cuspidate to ridged.

Muridoid cricetids are found in a variety of habitats, from deserts to rainforests and from lowlands to alpine meadows. Many muridoid cricetids do not have a narrow specialization; however, they include semi-aquatic and subterranean species (e.g. the European water vole *Arvicola amphibius*, which can be considered both a semi-aquatic and subterranean rodent), as well as arboreal species (e.g. *Tylomys*). They shelter in burrows, tree hollows and cracks between stones, as well as in nests made on the ground or on plants. Wood rats build especially large surface nests. Some species are adapted to living among rocks and stones (*Dinaromys*, *Chionomys*). Most species feed primarily on seeds, fruit and insects, but there are also specialized animalivorous (e.g. *Ichthyomys*) and herbivorous species (e.g. wood rats and Eurasian water voles). Most species are mainly active at night. The greater long-tailed hamster remains in its shelter during winter, but does not hibernate. It survives on food reserves collected in the autumn.

Cricetids live alone, in family groups or in colonies (voles). They usually produce 3–7 (up to 13) young in a litter. The degree of newborn development varies between species, but most young are born naked and blind. Most species probably live 2–3 years, but some up to 7 years (*Neotoma*).

2.4.3. Nesomyids – family *Nesomyidae*

The family *Nesomyidae* (nesomyids) includs 6 subfamilies (*Cricetomyinae*, *Delanymyinae*, *Dendromurinae*, *Mystromyinae*, *Nesomyinae*, *Petromyscinae*), 21 genera and 68 species. In total, 47 of the species (69%) are muridoids, occuring in 16 genera and all subfamilies except *Mystromyinae*. Non-muridoid members of the family are either short-tailed (*Mystromys*, *Saccostomus*, *Malacothrix*) or have a tufted (*Eliurus*, *Mactotarsomys*) or bushy tail (*Nesomys lambertoni*).

Muridoid nesomyids are found on the island of Madagascar (subfamily *Nesomyinae*) and in sub-Saharan mainland Africa (other subfamilies).

The head and body length of muridoid nesomyids is 5–45 cm, and the weight is 5 g to 2 kg. The smallest species are Delany's mouse (*Delanymys brooksi*) and some climbing mice (*Dendromus*); the largest species is the southern giant poached rat (*Cricetomys ansorgei*). The characteristics of the fur vary between species. The upperparts are yellowish, reddish, or greyish; the underparts are yellowish, greyish, or white. Some *Dendromus* have one or three dark stripes along their backs, and *Megadendromus nikolausi* has one dark stripe. *Dendroprionomys* and *Prionomys* have dark patches around the eyes, extending to the nose.

The muzzle is of medium length or long. The eyes and ears are normally developed and mostly medium in size. Poached rats (*Cricetomyinae*) have cheek pouches. The tail of muridoid species is long or very long, up to 180% of the head and body length in Delany's mouse. The tail is scaly (in most species) or covered with short hairs. In some species, the tail is prehensile to a certain extent. The

number of functional digits in most species is 4/5 – the first digit of the *manus* is rudimentary, but some climbing mice have only 3 functional forefoot digits (with rudimentary 1st and 5th digits). In most species, the outer digits of the hind feet are opposable, but in *Prionomys* the inner digits are opposable.

The number of teeth is 16: (I1/1, C0/0, P0/0, M3/3) × 2. In many species of *Dendromurinae* the upper incisors have a longitudinal groove on their anterior surface. The molars are rooted, their height is from low to high, and their masticatory surface is from cuspidate to ridged. In some species the cusps of the upper molars are arranged in two longitudinal rows (as in cricetids); in others they are arranged in three rows (as in murids).

Muridoid nesomyids inhabit deserts, semi-deserts, savannahs, bushes, swamps, and forests. Rock mice (*Petromyscus*) live in rocky

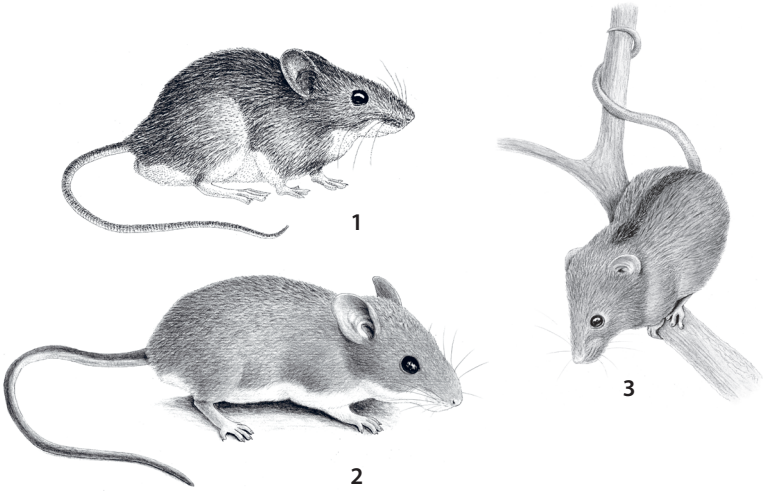


Fig. 8. Muridoids among rodents. 1. Muroidea: 1 – yellow-necked mouse (*Apodemus flavicollis*; Muridae: 665 muridoid species), 2 – eastern deer mouse (*Peromyscus maniculatus*; Cricetidae: 505 muridoid species), 3 – Brants's climbing mouse (*Dendromus mesomelas*; Nesomyidae: 47 muridoid species).

or stony terrain. Nesomyids shelter in burrows, dense vegetation, tree hollows, abandoned bird nests or rock crevices. Some species are terrestrial, others climb herbaceous vegetation, shrubs, and trees. They feed mainly on seeds, fruit, and insects. Dollman's tree mouse (*Prionomys batesi*) mainly eats ants, while the fat mouse *Steatomys opimus* specializes on termites. *Dendroprionomys rousseloti* is probably also insectivorous. Short-tailed rats (*Brachyuromys*) are herbivores. Muridoid nesomyids are active all year round, mostly at night. Poached rats collect food supplies in a burrow. Fat mice (*Steatomys*) accumulate a body fat reserve that helps them survive dry and cold periods of the year in a passive state.

Muridoid nesomyids live solitarily or in small groups. They produce 1–10 young in a litter, which are born naked and blind. In captivity, giant poached rats lived more than 7 years; smaller species live 2–3 years.

2.4.4. Birch mice – family *Sminthidae*

The family *Sminthidae* (birch mice) includes one genus (*Sicista*) and 14 species. All species have a mouse-like body structure. Birch mice are found throughout Palearctic Eurasia from Central Europe to Sakhalin in the Russian Far East and from 68°N to the Himalayas and the Yangtze.

All species of birch mice are approximately the same size. Their body weight fluctuates significantly due to the accumulation of fat reserves for winter. The head and body length is 5–8 cm, and the weight is 4–19 g. The fur is dense, relatively short, and slightly coarse, with yellowish or greyish-brown colouration. Some species have one or three dark stripes along the back. Birch mice have a thin muzzle of medium length. The vibrissae are of medium length or long. The eyes and ears are of medium size. The tail is long or very long, its relative length varying from 101% in the southern birch mouse (*S. subtilis*) to 162% in the long-tailed birch mouse (*S. caudata*). The tail serves as a support when climbing and a balance when jumping.

The number of functional digits is 4/5 (1st forefoot digit reduced). The length of the hind feet in relation to the length of the head and body is 22–31%. All feet are long with long digits and moderately long, weakly curved claws. The size of the plantar pads varies within the genus; however, with the exception of the carpal pads, they are small. The outer digit of the hind foot is partially opposable. The number of teeth is 18: (I1/1, C0/0, P1/0, M3/3) × 2. The molars have a low crown and a cuspidate chewing surface. A more detailed description of birch mice morphology is given in Miljutin, 1999.

Birch mice inhabit various biotopes: from semi-deserts and steppes to forests and alpine meadows. They prefer areas with dense herbaceous vegetation and shrubs. Birch mice are good climbers. When threatened on the ground, they make sudden long jumps. Birch mice shelter in burrows, rotten stumps, heaps of fallen tree branches and hollows between roots, and sometimes build ground nests. They feed mainly on seeds, fruit, and insects. Some species, for example the northern birch mouse (*Sicista betulina*; fig. 9:1), are largely insectivorous. Birch mice are mainly active at night. They spend cold summer days in a state of torpor, and hibernate during the winter.

Birch mice are solitary. They usually produce 2–8 (up to 11) young in a litter, which are born naked and blind. In natural conditions they can live for at least 3 years.

2.4.5. Jumping mice – family *Zapodidae*

The family *Zapodidae* (jumping mice) includes 3 genera (*Zapus*, *Napaeozapus*, *Eozapus*) and 5 species. All species have a mouse-like body structure. Jumping mice are found in North America (*Zapus*, *Napaeozapus*) and Central China (Chinese jumping mouse, *Eozapus setchuanus*).

The body structure of jumping mice is somewhat intermediate between those of birch mice and jerboas (fig. 9:2). They are quite mouse-like in appearance, but their tail and hind limbs are even longer than those of birch mice. All species of jumping mice have approximately the same head and body length, but the body weight

fluctuates significantly due to accumulation of fat reserves for the winter. The head and body length is 7–10 cm, and the weight is 12–40 g. The fur is short, thick and coarse. The upperparts are reddish-brown or yellowish-brown, while the belly is usually white. In all species, a wide dark stripe runs down the middle of the back from head to tail.

The muzzle and vibrissae are of medium length. The eyes and ears are also medium in size. The tail is very long – 140–160% of the head and body length – and serves as a balancer when jumping. In *Napaeozapus*, the tail has a rudimentary tuft at the tip. The number of functional digits is 4/5 (1st forefoot digit reduced). The relative length of the hind foot is approximately 32–35%. All claws are weakly curved and of medium length. The plantar pads are small. The hind foot digits, especially the extreme ones, are relatively shorter than those of birch mice, and the tarsal parts of the hind foot are longer.

The number of teeth is 16 (in *Napaeozapus*) or 18 (in other species): (I1/1, C0/0, P0–1/0, M3/3) × 2. The upper incisors have a longitudinal groove on the front surface. The molars have roots, a relatively high crown and a flat chewing surface with cusps and ridges.

Jumping mice inhabit fields and meadows with dense herbaceous vegetation, forests, shrublands and coastal thickets. The Chinese jumping mouse lives in mountainous areas at an altitude of 1700–4000 m. All jumping mice are predominantly terrestrial, but they may climb herbaceous plants and shrubs in search of seeds and berries. When threatened on the ground, jumping mice make sudden jumps, of up to two metres in the woodland jumping mouse (*Napaeozapus insignis*). Jumping mice shelter in burrows, under stones and logs, or inside tussocks of herbaceous vegetation. Their diet predominantly includes seeds, fruit, fungi, and insects. Jumping mice hibernate during the winter and are mainly active at night during warmer periods of the year.

Jumping mice are solitary. They produce 2–9 young in a litter, which are born naked and blind. In the wild they usually live 1–2 years, but some individuals up to 5 years (*Napaeozapus insignis*).

2.4.6. Dormice – family *Gliridae*

The family *Gliridae* (dormice) includes 9 genera and 29 species. Of these, 4 species (14%) have a mouse-like body structure: all mouse-tailed dormice (*Myomimus*) and the desert dormouse (*Selevinia betpakdalensis*). Non-muridoid members of the family have either tufted tail (*Eliomys*, *Chaetocauda*) or bushy tails (all other species). Muridoid dormice are sporadically distributed from Bulgaria to Iran (mouse-tailed dormice), and in Central and Eastern Kazakhstan (desert dormouse).

The head and body length of muridoid dormice is 7–14 cm, and the weight is 1–70 g. The large variation in weight is partly caused by seasonal fluctuations. Roach's mouse-tailed dormouse (*Myomimus roachi*; fig. 9:3) is slightly larger than the other species. The hair is soft, with grey or reddish-brown coloration on the back and sides and cream or white on the underparts. Mouse-tailed dormice have a diffuse dark stripe running down the back, while the masked mouse-tailed dormouse (*M. prsonatus*) and Setzer's mouse-tailed dormouse (*M. setzeri*) also have indistinct dark rings around the eyes and a dark spot on the upper lip. Both the stripe and the mask may be missing.

The muzzle is of medium length, the vibrissae long. The eyes and ears are normally developed. The tail is long, but shorter than the head and body length. The tail is covered with short hairs through which the scales can be seen. The number of functional digits is 4/5 (1st forefoot digit reduced). The relative length of the hind feet is 17–21%, i.e. the hind feet are either not elongated or slightly elongated. The plantar pads are of medium size. The claws of the desert dormouse are straightened.

The desert dormouse has 16 teeth; other species have 20: (I1/1, C0/0, P0–1/0–1, M3/3) × 2. The upper incisors of the desert dormouse have a longitudinal groove along the front surface. The molars are rooted and low-crowned, and their chewing surface has ridges and basins.

Roach's mouse-tailed dormouse inhabits floodplain thickets, vineyards, vegetable gardens and hedges. Asian mouse-tailed

dormice are found in rocky semi-deserts, steppes, and dry forests. Mouse-tailed dormice shelter in tree-hollows and burrows (especially in winter), and under stones. The desert dormouse lives in desert and semi-desert habitats. It shelters under the roots of shrubs, and possibly also in burrows and cracks in the ground. All muridoid dormice are good climbers. They lead a terrestrial or scansorial way of life. Their diet includes invertebrates, small vertebrates (lizards), fruit and seeds. The desert dormouse is predominantly insectivorous. Muridoid dormice hibernate and are mainly nocturnal during warmer periods of the year. They produce 4–14 young in a litter.

Fig. 9. Muridoids among rodents. 2. Dipodoidea and Gliridae: 1 – northern birch mice (*Sicista betulina*; Sminthidae: all 14 species are muridoids); 2 – woodland jumping mouse (*Napaeozapus insignis*; Zapodidae: all 5 species are muridoids); 3 – Roach's mouse-tailed dormouse (*Myomimus roachi*; Gliridae: 4 muridoid species).

2.4.7. Heteromyids – family *Heteromyidae*

The family *Heteromyidae* (heteromyids) includes 5 genera and 66 species. Mouse-like body structure occurs in 26 species (39%) of heteromyids, belonging to 3 genera: *Heteromys* (spiny pocket mice, all 16 species), *Perognathus* (silky pocket mice, 9 of the 10 species) and *Chaetodipus hispidus* (the hispid pocket mouse). Non-muridoid members of the family have a tufted tail (*Perognathus alticola*, almost all *Chaetodipus*, and all *Dipodomys*) or are bipedal (*Dipodomys* and *Microdipodops*).

Muridoid heteromyids are found in western and central parts of North America, in Central America and in northern South America.

The head and body length of muridoid heteromyids is 5–16 cm, the weight is 5–110 g. The smallest species are some members of *Perognathus*; the largest species is Nelson's spiny pocket mouse (*Heteromys nelsoni*). The pelage varies from soft in *Perognathus* to spiny in *Heteromys*. The colour of the upperparts varies between species, from yellowish to almost black. The underparts are greyish, yellowish, or white.

The muzzle, eyes and ears are of medium size. All species have external cheek pouches, that is, invaginations of the skin on the sides of the head and neck, which are used to transport food items. The pouches are fur-lined inside and are filled and emptied with the help of the paws. To clean them, the animal turns its cheek pouches outward, then pulls them back in. The tail of *Heteromys* is scaly; in other species it is covered with short fur. The relative length of the tail varies from 88 to 130% of the head and body length, though in most species it is approximately equal to the length of the head and body. The number of functional digits is 4/5 (1st forefoot digit reduced). In *Perognathus* the soles of the hind feet are covered with hair, which facilitates movement on sand. The number of teeth is 20: (I1/1, C0/0, P1/1, M3/3) × 2. *Perognathus* and *Chaetodipus* have a longitudinal groove on the outer surface of the incisors. The molars are rooted and have cuspidate chewing surfaces.

Most species of muridoid heteromyids are found in arid areas with sparse vegetation, but some *Heteromys* inhabit tropical forests.

All heteromyids are terrestrial, but *Heteromys* can climb shrubs. Some *Perognathus* can jump on their hind legs. Heteromyids shelter in burrows. During the daytime the entrance of the burrow is usually closed, which preserves the cool and humid microclimate. Species of *Perognathus* dig particularly extensive burrows with nesting chambers, larders and latrines. Like other desert rodents, heteromyids bathe in the sand and produce an alarm signal by drumming on the ground with their hind foot.

Muridoid heteromyids feed mainly on seeds, fruit, leaves, shoots, and insects. They store food for winter consumption in subterranean larders or by burying it near the burrow. Heteromyids are mainly active at night. Species of *Perognathus* and *Chaetodipus* are capable of torpor in case of adverse weather conditions, and some northern populations exhibit seasonal dormancy. Muridoid hetromyids are mostly solitary. There produce 2–9 young in a litter, which are born naked and blind.

2.4.8. Spiny rats – family *Echimyidae*

The family *Echimyidae* (spiny rats or echimyids) includes (in the broad sense, with the hutias and coypu) 27 genera and 99 species. Mouse-like body structure occurs in 66 species (67%), belonging to 17 genera (*Capromys*, part of *Mesocapromys*, *Carterodon*, part of *Trinomys*, *Thrichomys*, *Callistomys*, *Hoplomys*, *Proechimys*, part of *Dactylomys*, *Olallamys*, *Diplomys caniceps*, *Santamartamys*, *Pattonomys*, *Toromys*, *Echimys*, *Makalata*, part of *Phyllomys*). Non-muridoid members of the family are either short-tailed (*Plagiodontia*, *Geocapromys*, *Clyomys*, *Euryzygomatomys*), or have a tufted (part of *Trinomys*, *Isothrix sinnamariensis*, *Lonchothrix*, *Mesomys*, *Dactylomys peruanus*, *Kannabateomys*, *Diplomys labilis*, part of *Phyllomys*) or bushy tail (*Mesocapromys melanurus*, *Mysateles*, part of *Isothrix*), or webbed hind feet (*Myocastor*).

Muridoid echimyids are found in the subtropical and tropical regions of Central and South America.

The head and body length of muridoid echimyids is 14–62 cm, and the weight varies from 92 g to 7 kg. Almost all species are large, the size of a brown rat and larger. The largest species is Desmarest's hutia (*Capromys pilorides*), which is much larger than other muridoid echimyids, especially in weight. Most have spines or spine-like bristles on their backs and sides, between which normal hair grows, but hutias and many scansorial species, such as *Dactylomys*, do not have spines. The coloration of the upperparts is reddish, greyish, or blackish, the underparts are lighter – greyish, yellowish, orange, or white. The painted tree rat (*Callistomys pictus*) is black and white, while the white-faced spiny tree rat (*Echimys chrysurus*) has a white stripe down the middle of the head and a white tip to the tail. In the Amazonian bamboo rat (*Dactylomys dactylinus*), a similar stripe on the head is yellowish and extends to the back of the head. In the punare (*Thrichomys*), the eyes are framed by a light border.

The muzzle of medium length and is blunt in herbivorous species. The eyes and ears are normally developed, but in hutias eyes are relatively small. The tail is usually scaly or it is covered with short hair. It has some degree of grasping ability. The length of the tail in relation to the head and body varies from 50% to 160% in *Olallamys*. The number of functional digits is 4/5 (1st forefoot digit reduced). The structure of the feet may be different. *Carterodon*'s limbs are adapted for digging and have long claws. In hutias the soles of the feet are granulated and with flat pads. Species of *Dactylomys*, which live in bamboo thickets have elongated middle digits (3rd and 4th). While climbing, they grasp the stem between the 3rd and 4th digits of the forefoot and between the 2nd and 3rd digits of the hind foot. The number of teeth is 20: (I1/1, C0/0, P1/1, M3/3) × 2. The molars are with roots in most species, but in hutias (*Capromyinae*) are without roots. The crown of the molars is of variable height, and its chewing surface is flat and ridged.

Muridoid echimyids inhabit forests (most), bamboo thickets (*Dactylomys*, *Olallamys*), and savannahs of various types, but avoid

highlands and deserts. Most species climb well, some of them are arboreal, others are active mainly on the ground. Muridoid echimyids shelter in dense vegetation, in tree hollows, in rock crevices, and in burrows. There are both frugivorous and herbivorous species among them. The former feed mainly on fruit, seeds, and insects, while the latter feed on leaves and other vegetative parts of plants. They are active all year round, mostly at night.

Muridoid echimyids live solitarily or in groups. There are 1–6 young in a litter, which are born covered with fur, sighted and able to move. Tome's spiny rat (*Proechimys semispinosus*) has lived in captivity for 4 years. The hutias live longer.

2.4.9. Chinchilla rats – family *Abrocomidae*

The family *Abrocomidae* (chinchilla rats) includes 2 genera (*Abrocoma* and *Cuscomys*) and 10 species. Nine of the species (90%) have mouse-like body structure: 7 species of *Abrocoma* and both species of *Cuscomys*. The only non-muridoid species, *Abrocoma bolivensis*, has a tufted tail. Muridoid chinchilla rats are found in the western, Andean part of South America, mainly in the mountains: in southern Peru, Bolivia, Chile, and Argentina.

The head and body length of muridoid chinchilla rats is 16–35 cm, and the weight is 90–900 g. *Cuscomys* are much larger than *Abrocoma*. The latter are about the size of a brown rat or slightly smaller. The pelage is silky with a thick undercoat. The upperparts are greyish or greyish-brown; the underparts are lighter. The only known specimen of *Cuscomys ashaninka* had a white tip to the muzzle, a white stripe down the middle of the head, and a white tip to the tail. The only supposed specimen of *Cuscomys oblativa*, caught alive and photographed, had similar coloration.

The muzzle is of medium length and has a blunt appearance. The eyes are normally developed. The ears of *Abrocoma* are large and rounded, while those of *Cuscomys* are of medium length. All species have long vibrissae. The tail is densely covered with short hairs.

In all species, the tail is shorter than the head and body length (50–76%). The number of functional digits is 4/5 (1st forefoot digit reduced). The outer digit of the hind foot is relatively longer in *Cuscomys ashaninka* compared with *Abrocoma*. The middle digits of the hind foot have long coarse hairs. The claws of *Abrocoma* are small, while those of *Cuscomys ashaninka* hook-shaped. The number of teeth is 20: (I1/1, C0/0, P1/1, M3/3) × 2. The incisors are narrow. The molars grow constantly and have a high crown, with a flat and ridged chewing surface. Some species of *Abrocoma* have two tooth-like projections on the palate.

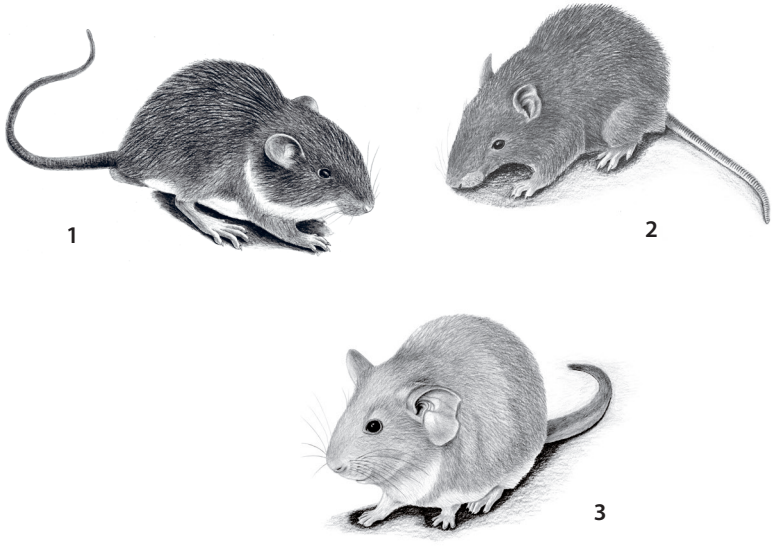


Fig. 10. Muridoids among rodents. 3. New World families: 1 – southern spiny pocket mouse (*Heteromys australis*; Heteromyidae: 26 muridoid species); 2 – short-tailed spiny rat (*Proechimys brevicauda*; Echimyidae: 66 muridoid species); 3 – Bennett's chinchilla rat (*Abrocoma bennettii*; Abrocomidae: 9 muridoid species).

The ecology of chinchilla rats is not well understood. All species except Bennett's chinchilla rat (*Abrocoma bennettii*) inhabit mountains at altitudes 1800–5000 m above sea level. Bennett's chinchilla rat inhabits both mountains and plains. Chinchilla rats are found in forests (*Cuscomys*), shrubs and herbaceous vegetation, and among rocks. They also occur in desert regions. Species of *Cuscomys* are probably arboreal; other species are also able to climb trees and shrubs but are mainly active on the ground. Chinchilla rats shelter among stones, in rock crevices and in burrows dug by themselves or other animals. They feed mainly on the vegetative parts of plants. They are active year-round but their circadian activity is unclear. Species of *Abrocoma* live in colonies, sometimes together with degus. They produce 1–6 young in a litter, which are born well developed.

3. TAXONOMIC COMPOSITION, DISTRIBUTION, MORPHOLOGY, AND ECOLOGY OF MURIDOIDS

This section summarizes the information contained in the previous chapter.

3.1. Taxonomic composition of muridoids

The above review of mammalian families showed that a mouse-like body structure occurs in 1927 species, belonging to 334 genera, 23 families and 9 orders (Table 1). In other words, about a third of all mammalian species are muridoids. Consequently, this is the most common life form of recent mammals in terms of the number of species, and obviously also in terms of the number of individuals. The second most numerous mammalian life form, bats, is represented by about half as many species as there are muridoids.

3.2. Geographic distribution of muridoids

It is enough to consider the ranges of murids (*Muridae*) and New World cricetids (*Sigmodontinae* in the broad sense) to understand that muridoid mammals are found throughout the world. They occur on all continents except Antarctica, and from the Arctic tundra in the north to Tierra del Fuego in the south. However, muridoids are rare in the polar regions. These small animals with a long bare tail and bare legs are clearly not well adapted to the harsh

Table 1. Number of mouse-like species in mammalian orders

Order	Number of muridoid species	Number of genera containing muridoids	Number of families containing muridoids
Didelphimorphia	98	15	1 (*Didelphidae*)
Paucituberculata	7	3	1 (*Caenolestidae*)
Microbiotheria	1	1	1 (*Microbiotheriidae*)
Dasyuromorphia	56	11	1 (*Dasyuridae*)
Peramelemorphia	4	1	1 (*Peramelidae*)
Diprotodontia	7	4	3 (*Burramyidae*, *Tarsipedidae*, *Hypsiprymnodontidae*)
Eulipotyphla	389	27	4 (*Erinaceidae*, *Soricidae*, *Talpidae*, *Solenodontidae*)
Afrosoricida	24	4	2 (*Tenrecidae*, *Potamogalidae*)
Rodentia	1341	268	9 (*Muridae*, *Cricetidae*, *Nesomyidae*, *Sminthidae*, *Zapodidae*, *Gliridae*, *Heteromyidae*, *Echimyidae*, *Abrocomidae*)
TOTAL	**1927**	**334**	**23**

conditions of the Arctic. In addition, most Holarctic muridoids are seed-eaters, which also limits their northward distribution, where such food is scarce. Among muridoids, only some species of shrews (*Sorex*) are found beyond the Arctic Circle. Muridoids are represented by different taxa in different regions (Table 2).

Table 2. Taxonomic composition of the muridoid fauna of zoogeographic regions of the world

Zoogeographic region	**Geographical location**	**The most common muridoid families**	**Other muridoid families**
Nearctic	North America	*Soricidae*, *Cricetidae*, *Zapodidae*, *Heteromyidae*	*Didelphidae*
Palearctic	Non-tropical Eurasia and Northern Africa	*Soricidae*, *Muridae*, *Sminthidae*	*Cricetidae*, *Gliridae*
Oriental	South and Southeast Asia	*Soricidae*, *Muridae*	*Erinaceidae*, *Talpidae*,
Afrotropical	Sub-Saharan Africa and southern Arabian Peninsula	*Soricidae*, *Muridae*, *Nesomyidae*	*Tenrecidae*, *Potamogalidae*
Neotropical	Central and South America	*Didelphidae*, *Cricetidae*, *Heteromyidae*, *Echimyidae*	*Caenolestidae*, *Microbiotheriidae*, *Solenodontidae*, *Soricidae*, *Abrocomidae*
Australian	Australia, New Guinea and nearby islands	*Dasyuridae*, *Muridae*	*Burramyidae*, *Tarsipedidae*, *Peramelidae*, *Hypsiprymnodontidae*

In North America, muridoids are represented predominantly by shrews and cricetids from the subfamily *Neotomiinae*. Jumping mice (*Zapodidae*) and pocket mice (*Heteromyidae*) are also common in some parts of this region. In Eurasia and Africa, shrews and murids predominate. However, birch mice and nesomyids are also widespread in Palearctic Eurasia and Africa, respectively. On the island of Madagascar, shrews are replaced by tenrecs, and native rodents are represented only by nesomyids.

The taxonomic composition of muridoids is especially diverse in Central and South America. Shrews are poorly represented and are present only in the north of the region. In the Neotropics, they are replaced by opossums, and to a lesser degree also by rodents. Muridoid rodents are represented here mainly by the cricetid subfamily *Sigmodontinae* and by echimyids. Pocket mice are also common in the northern part of the region.

In Australia and New Guinea, muridoids are represented mainly by dasyurids and murids.

It is noteworthy that in various parts of the world, muridoids are represented both by animal-eating and plant-eating species.

3.3. Morphological diversity of muridoids

According to the definition, all muridoids have similar general body structure, but the size of animals and details of their body structure can vary considerably. Below is a brief review of morphological variability among muridoids, in order to identify additional morphological features that are characteristic of the life form.

3.3.1. Size

The head and body length is chosen here as a criterion for size, since, among adult animals, this measurement is less variable than weight. Data on body size variability in muridoids are shown in Table 3.

Table 3. Range of variability in head and body length (HB) among mouse-like mammals (measurements are mainly from Wilson et al., 2016, 2017 and Wilson, Mittermeier, 2015, 2018)

Family	**Number of muridoid species**	**Head and body length limits (cm)**		**HB ratio** HB_{max}/HB_{min}
		HB_{min}	HB_{max}	
Didelphidae	98	7	50	7.1
Caenolestidae	7	9	14	1.6
Microbiotheriidae	1	8	13	1.6
Dasyuridae	56	5	27	5.4
Peramelidae	4	14	29	2.1
Burramyidae	5	7	13	1.9
Tarsipedidae	1	7	9	1.3
Hypsiprymnodontidae	1	21	34	1.6
Erinaceidae	3	10	46	4.6
Soricidae	377	4	18	4.5
Talpidae	7	7	8	1.1
Solenodontidae	2	28	32	1.1
Tenrecidae	23	4	14	3.5
Potamogalidae	1	12	15	1.2
Muridae	665	4	48	12.0
Cricetidae	505	5	29	5.8
Nesomyidae	47	5	45	9.0
Sminthidae	14	5	8	1.6
Zapodidae	5	7	10	1.4
Gliridae	4	7	13	1.9
Heteromyidae	26	5	16	3.2
Echimyidae	66	13	62	4.8
Abrocomidae	9	16	35	2.2
All families	**1927**	**4**	**62**	**15.5**

In general, muridoids are characterized by an abundance of small and very small species. The largest muridoids reach the size of a rabbit. However, in all families, species with a body length of more than 30 cm are rare or absent. The head and body length and weight of muridoids vary from 4 cm and 2 g in the Etruscan shrew (*Suncus etruscus*) to 62 cm and 7 kg in Desmarest's hutia (*Capromys pilorides*). Thus, the smallest muridoid is 15 times shorter and 3500 times lighter than the largest muridoid. Within families, differences in size are less marked, but even in the families with only one species (*Microbiotheriidae*, *Hypsiprymnodontidae*), intraspecific variability can lead to HB ratio (maximum/minimum) values of up to 1.6. Within family, the largest difference in head and body length (12 times) is found in the largest family, *Muridae*.

The distribution of head and body length values differs between families. Many families consist mainly of small muridoid species, e.g. shrews. By contrast, the musky kangaroos and solenodons are represented by relatively large species. Yet, other families include species of varying size. Among the latter, there are families with an uneven distribution of sizes (e.g. moles) and families with a relatively even distribution of size variants. Even distribution is characteristic of species-rich families.

The family *Muridae* occupies an exceptional position, both in terms of the number of muridoid species (665) and in the variability of their body sizes. It is to this family that the true "mice and rats" belong. How are body sizes distributed in this family? The answer to this question is of both zoological and linguistic interest: is the division of mouse-like rodents in European languages into mice and rats justified? Does it have any biological sense? In other words, are "mice and rats" divided into two body size categories or there is a gradual transition between them? To clarify this issue, I conducted an analysis of species head and body length in the family *Muridae*. The analysis included all representatives of the

family (both muridoids and non-muridoids), but in its traditional content, without gerbils and the maned rat (*Lophiomys imhausi*).

For the purpose of the analysis, murids were divided into five size categories according to the mean head and body length of adult animals: mice, small rats, medium rats, large rats, and giant rats. The length of 12 cm was taken as a maximum size of "mice". It corresponds to the normal size of the yellow-necked mouse (*Apodemus flavicollis*), the largest European muridoid whose vernacular name in different languages still includes *mouse*. The category "medium rats" had the range 18–24 cm, which corresponds to the normal length of the widespread synanthropic rats: black rat (*Rattus rattus*) and brown rat (*R. norvegicus*). These are precisely the species to which the word *rat* was first applied and with which millions of people associate the idea of a rat. The difference between "mice" and "medium rats" provides a step of 6 cm (18 – 12 = 6), which, in my opinion, aptly reflects people's perception of muridoid body size categories.

The results of the analysis have showed that **mice and rats do not exist as discrete body size categories**. On the contrary, the sizes of murid species of the world are distributed evenly, and most species are intermediate in size between definitely "mice" and definitely "rats" (Table 4).

Considering muridoids in general, it should be noted that small species predominate (Table 3). "Mice" and "small rats" (HB ≤ 18 cm) are present in almost all muridoid families: in 21 out of 23. They are absent among musky rat-kangaroos and solenodons, families which include only 1 and 2 species, respectively. It is noteworthy that there are no "mice" among caviomorph rodents (*Caviomorpha*), which are ancient South America endemics (*Echimyidae*, *Abrocomidae*). "Medium and large rats" (HB=18–30 cm) are present in 9 families, and "giant rats" (HB>30 cm) are present in 6 families (taking into account mean rather than maximum values). Thus, the ratio of the

Table 4. Distribution of murid species (*Muridae* without *Gerbillinae* and *Lophiomyinae*), according to their head and body length (based on data from Wilson et al., 2017)

Conventional name of category	Head and body length (cm)	Number of species	%
"Mice"	≤12	230	32.3
"Small rats"	>12–18	327	45.6
"Medium rats"	>18–24	98	13.8
"Large rats"	>24–30	37	5.2
"Giant rats"	>30	20	2.8
Total	–	**712**	**100**

muridoid body size categories among all mammals approximately coincides with their ratio in the family *Muridae*.

It may be concluded that generally **small body size is a characteristic of mouse-like mammals,** which may be due to the biomechanical constraints of this body form. Larger "rats" perhaps cannot move quickly enough. Large mammals use other gaits and, consequently, have other body forms.

3.3.2. The structure of the pelage

Muridoids are characterized by a particular distribution of hair. The fur usually covers only the body, while the ears, feet and tail are naked or almost naked. Data on the structure and coloration of the body pelage are summarized below. The structure of the tail and limbs will be considered separately.

The pelage of muridoids varies in density and length. In most species, it is of medium density, but in many it is rather dense (e.g. the Eurasian water voles, *Arvicola*). The fur may be short (e.g. in shrews), of medium length or long. In some species, long and relatively sparse guide hairs protrude from the pelage (e.g. in *Didelphis*).

In terms of softness, the hair of muridoids may be soft (e.g. in chinchilla rats, *Abrocoma*), medium soft (in most), hard, bristly or spiny. Spine-like bristles or spines are found in muridoid rodents from the families *Muridae* (*Acomys*, *Halmaheramys*, *Komodomys*, *Tokudaia*, some species of *Leopoldamys*, *Maxomys*, *Mus. Rattus*, *Tarsomys*), *Cricetidae* (*Neacomys*, *Rhagomys longilingua*, *Scolomys*), *Heteromyidae* (*Heteromys*) and in many spiny rats (*Echimyidae*).

Different variants of fur density, length and softness may appear in different combinations. Thus, short, thick, and soft fur feels velvety; longer and sparser soft fur – silky; long thick and soft fur – woolly. Thicker and firmer hair of varying density and length produces a hard, bristly, or spiny pelage.

The colour of the fur on the upperparts of muridoids varies from white to black, but in the vast majority of species it is a shade of grey or brown. The ventral part of the body is usually lighter than the dorsal part, in some cases white.

Most muridoid species are uniformly coloured, but many have spots or stripes that differ from the main colour. The most common patterns are dark rings around the eyes, a dark "mask" on the head, and a dark spot or stripe on the forehead. These patterns occur in many opossums, the monito del monte (*Dromiciops gliroides*), dunnarts (*Sminthopsis*), mouse bandicoots (*Microperoryctes*), pygmy possums (*Burramyidae*), the moonrat (*Echinosorex gymnurus*), in some murids (*Chiruromys*, *Thallomys*, *Echiothrix*) and mouse-tailed dormice (*Myomimus*).

Less common are light areas on the head: light "eyebrows" or light rings around the eyes. Such patterns occur in some opossums (*Metachirus*, *Philander*), antechinuses (*Antechinus*), New World cricetids (*Sigmodon*), gerbils (*Tatera*, *Gerbillus*), murids (*Arvicanthis*) and echimyids (*Thrichomys*). A few species of muridoid rodents have a light stripe in the middle of the head (ancient South American endemics: *Cuscomys*, *Dactylomys dactylinus*, *Echimys chrysurus*).

Many muridoids have dark or light longitudinal stripes on their backs. Most often there is one dark stripe, but there may also be alternating dark and light stripes. Sometimes the stripes are composed of a row of spots. Stripes on the back are seen in opossums (*Monodelphis*, *Philander*, *Thylamys*), dasyurids (*Murexia*, *Myoictis*, *Phascolosorex*), the honey possum (*Tarsipes rostratus*), Drouhard's shrew tenrec (*Microgale drouhardi*), mouse bandicoots (*Microperoryctes*), some or all representatives of the murid genera *Apodemus*, *Chrotomys*, *Hybomys*, *Lemniscomys*, *Mallomys*. *Pelomys*, *Rhabdomys*, cricetids (some *Peromyscus* and *Reithrodontomys*), nesomyids (*Dendromus*, *Megadendromus*), some birch mice (*Sicista*), all jumping mice (*Zapodidae*), mouse-tailed dormice (*Myomimus*) and in some spiny rats (*Dactylomys bolivensis*).

Variegated colouration is much less common among muridoids but is found in the monito del monte (*Dromiciops gliridoides*), the piebald shrew (*Diplomesodon pulchellus*), the Cuban solenodon (*Atopogale cubana*) and in the painted tree rat (*Callistomys pictus*).

Each of these variants of fur pattern is apparently associated with the ecology of the species. For example, dark rings around the eyes or a mask on the head are common in climbing species, while light rings around the eyes are common in terrestrial species. The stripes may serve as camouflage among herbaceous vegetation. At the same time, none of the variants is characteristic exclusively of muridoids.

Thus, **for muridoids, it is typical that hair on the ears, feet, and tail is sparse or completely absent**, while the structure, coloration and patterning of the pelage is variable and not unique to this life form.

3.3.3. The structure of the head

When selecting criteria to define muridoid body structure, head characters were deliberately excluded. Consequently, none of the features considered in this section were directly subjected to preliminary selection.

Of all body parts, the head has the most complex structure. It combines, on one hand, a receptacle for the brain and sensory organs and, on the other hand, the beginning of the digestive tract. If the brain does not have direct contact with the external environment, then the sensory organs, jaws, teeth, and oral cavity interact with it directly, and their evolutionary development is strongly influenced by environmental factors. In this regard, the braincase is less variable than other parts of the head, and is excluded from further analysis. Below is discussed the length of the head, the size and shape of the muzzle (the front part of the head comprising the jaws and nasal cavity), the length of the vibrissae, and the size of the eyes and ears of muridoid mammals.

The length of the head depends both on the size of the braincase and on the length of the facial part, that is, the muzzle; the latter being more variable than the braincase. To estimate the relative length of the head, it is most convenient and accurate to use the length of the skull without taking into account the soft tissues. For example, among muridoid rodents of the Baltic region, the ratio of the length of the skull to the length of the body ranges from 20% in the brown rat (*Rattus norvegicus*) to 28% in the northern birch mouse (*Sicista betulina*). The relative length of the head is greater in smaller species, among species of approximately the same size, the head is larger in arboreal than other species (Miljutin, 1997).

The length of the muzzle can be measured both on the skull or together with soft tissues on a living or dead animal. In the latter case, this is the distance from the tip of the nose to the eye. To obtain a relative value, the length of the muzzle can be compared with the total length of the head. In this case, for convenience of measurement, the distance from the tip of the nose to the ear opening is taken as the length of the head. A rough estimate of the length of the muzzle can also be given in comparison with the distance between the posterior margin of the eye and the ear opening. A muzzle of "medium" length is approximately equal to this

distance, a "long" muzzle is longer than this distance by a third or more, and a "short" muzzle is shorter by a third or more.

In most muridoid mammals, the muzzle is medium in length (30–50% of head length) or long (>50% of head length). Especially long muzzles are found in the honey possum, all muridoid insectivores (especially solenodons), the naked-nosed shrew tenrec (*Microgale gymnorhyncha*) and, among rodents, in shrew-like rats (*Rhynchomys*) and hocicudos (*Oxymycterus*).

Elongation of the muzzle is achieved either by lengthening the bones of the facial skull (e.g. in bandicoots), or through the formation of a mobile proboscis protruding forward (e.g. in shrews). The longest noses are possessed by animals that feed on insects, nectar, and those that rummage in litter on the forest floor. A short muzzle (less than 30% of the head length) is rare among muridoids but it is found among some fossorial and herbivorous species, such as Eurasian water voles (*Arvicola*) and Madagascar short-tailed rats (*Brachyuromys*).

The shape of the muzzle, when viewed from the side or from above, is usually conical and pointed, but in some species it may be blunt. Predominantly insectivorous species have thin and long muzzles, while in herbivorous species the muzzle is blunt, which can be explained by their large incisors, high molars, and large masticatory muscles. In rodents, the width of the tip of the muzzle depends on the width of the incisors. The muzzle, which is blunt when viewed from the side, may when viewed from above, be either narrow or wide, depending on the width of the incisors. Some semi-aquatic muridoids (*Micropotamogale*, *Hydromyini*, *Ichthyomyini*) have a wide muzzle when viewed from above, which is due to both the flat shape of the skull and the thick upper lip, which is the base for hard vibrissae. It can be said that muridoids are characterized by an elongated conical muzzle; however, a similar muzzle is also common among non-muridoid mammals, for example, in artiodactyls.

Tactile hairs, or vibrissae, are well developed on the head of all muridoid mammals. The vibrissae of the upper lip reach the greatest length. Their mean length in different muridoids probably varies between 15% and 50% of the head and body length. For example, in muridoid rodents of the Baltic region, the ratio of vibrissae ranges from 18% in the European water vole (*Arvicola amphibius*) to 34% in the black rat (*Rattus rattus*), while in the pygmy rock mouse (*Petromyscus collinus*) this ratio is 47%. The relative length of vibrissae is greatest in scansorial and arboreal species, regardless of their taxonomic affiliation, as well as in species with nocturnal activity (Miljutin, 1997, 1999). In semi-aquatic species, the vibrissae are hard and dense. The presence of long vibrissae in muridoids, however, is not related to the structure of their body – many non-muridoid mammals of small and medium size, for example cats, have long vibrissae.

An estimate of the size of the eye can be obtained by comparing its anterior-posterior diameter with the distance between the posterior margin of the eye and the ear opening. In other words, how many such eyes would fit between the eye and the ear. The following scale is used here: a ratio of less than one indicates very large eyes; a ratio of approximately one indicates large eyes, a ratio of 2–3 indicates medium-sized eyes, a ratio of greater than 3 indicates small eyes, with a ratio of greater than five indicating very small eyes.

Small or very small eyes occur in some opossums (*Monodelphis*); in all caenolestids (*Caenolestidae*); in some dasyurids (*Antechinus*, *Planigale*); in mouse bandicoots (*Microperoryctes*); in the honey possum (*Tarsipes rostratus*); in all muridoid insectivores and tenrecs; in some murids (animalivorous *Chrotommys*, *Rhynchomys*, *Soricomys*, *Leptomys*, *Pseudohydromys*, *Melasmothrix*, *Paucidentomys*, *Sommeromys*, *Paulamys*, *Tateomys*; semi-aquatic *Waiomys mamasae*; as well as *Hyomys*, *Microhydromys*); in some muridoid voles (*Arvicola*, *Eothenomys*, *Neofiber*; in some sigmodontines (semi-aquatic *Ichthyomyinae*, wetland *Scapteromys*, fossorial

Gyldenstolpia, *Kunsia*, *Brucepattersonius*, *Oxymycterus*; as well as *Thalpomys*, *Podoxymys* and *Deltamys*); and in one species of spiny rat (painted tree rat, *Callistomys pictus*).

Medium-sized eyes occur in most muridoid marsupials and rodents. Namely: in most opossums and dasyurids, in mountain pygmy possums (*Burramys parvus*), in musky kangaroos (*Hypsiprymnodon moschatus*), in most murids and cricetids, in all nesomyids, in birch mice and jumping mice, in the desert dormouse (*Selevinia betpakdalensis*), in most muridoid heteromyids, in spiny rats and in chinchilla rats.

Large eyes occur in the monito del monte (*Dromiciops gliridoides*), in some pygmy possums (*Cercartetus*), in some muridoid gerbils (*Gerbillus*, *Microdillus*, *Desmodilliscus*), in mouse-tailed dormice (*Myomimus*), and in some heteromyids (*Perognathus*) and spiny rats (*Thrichomys*). There are no muridoids with very large eyes, as are seen, for example, in flying squirrels.

Thus, the eye size of muridoids varies widely, but there are no species with completely reduced or very large eyes. Eye size is partly dependent on the size of the animal: in large species the eyes are relatively smaller than in related small species due to allometry. At the same time, this feature is also associated with the ecology of animal.

Thus, among muridoids, small eyes tend to be seen among small animalivorous animals leading a terrestrial or subterranean way of life, living among dense herbaceous vegetation or inside plant litter and soil: for example, short-tailed opossums (*Monodelphis*), shrew opossums (*Cenolestidae*), shrews (*Soricidae*), shrew tenrecs (*Microgale*) and animalivorous terrestrial rodents. The second group of small-eyed muridoids are semi-aquatic animals, such as water shrews, the Nimba otter shrew, and semi-aquatic rodents. Muridoids with large eyes tend to be small climbing species, such as pygmy possums, and inhabitants of open arid regions, such as gerbils and pocket mice.

A rough idea of the relative length of the auricle (the visible external ear) can be obtained by comparing the length of the ear with the distance between the posterior margin of the eye and the ear opening. The following scale is adopted here: a very short ear is equal to or less than a quarter of the distance between the eye and ear; a short ear is approximately equal to half this distance; a medium-sized ear is approximately equal to this distance; a long ear is approximately one and a half times this distance; and a very long ear exceeds this distance about two or more times.

Very short ears are rare among muridoids, and are only seen among some shrews (*Cryptotis*, *Blarinella*). Short ears occur in mouse bandicoots (*Microperoryctes*), in many shrews (*Sorex* and others), in shrew moles (*Uropsilus*), in solenodons, in some shrew tenrecs (*Microgale*), in the Nimba otter shrew (*Micropotamogale lamottei*), in some murids (in white-eared giant rats, *Hyomys*, and semi-aquatic *Baiyankamys*), in semi-aquatic cricetids (all *Ichthyomyinae*, the round-tailed muskrat, Eurasian water voles and their North American counterpart, Richardson's vole, *Microtus richardsoni*), as well as in some echimyids (*Dactylomys*).

Medium-sized ears are found in most muridoid marsupials, in some gymnures, in many shrews, in some shrew tenrecs (*Nesogale*, *Microgale*), in most murids, cricetids and nesomyids, in birch mice and jumping mice, in desert dormouse, in all muridoid heteromyids, and in most echimyids and chinchilla rats.

Long ears are found in some marsupials of the genus *Sminthopsis*, in all pygmy possums, in the long-eared gymnure (*Hylomys megalotis*), in many shrews of the subfamily *Crocidurinae*, in the large-eared tenrec (*Geogale aurita*), in some shrew tenrecs (*Microgale*), in many murids and sigmodontines, in mouse-tailed dormice (*Myomimus*), and in Bennett's chinchilla rat (*Abrocoma bennettii*). The Malagasy giant rat (*Hypogeomys antimena*) has very long ears.

Thus, the length of the auricle varies in muridoids from almost complete absence to a size exceeding half the length of the head.

Most muridoids have ears of medium length. Short ears are characteristic of many shrews and semi-aquatic muridoids, regardless of their taxonomic affiliation. Long-ears are more difficult to associate with the habits of animals. There may be more long-eared species among the climbing muridoids.

The oral cavity and teeth are structures that are not usually visible from the outside, yet they are very important from an ecomorphological point of view. First, the oral cavity and teeth come into direct contact with objects in the external environment. Secondly, the size of the teeth affects the shape of the muzzle.

When considering the soft parts of the oral cavity of muridoids, it is worth noting the unusual structure of the tongue of the nectar-eating honey possum, which is long and has a brush-like tip, similar to those of some nectar-eating bats. Another noteworthy feature is the presence of cheek pouches in some muridoid rodents: in true hamsters (*Cricetinae*), in the poached rats of the nesomyid subfamily *Cricetomyinae* (*Beamys*, *Cricetomys*) and in heteromyids (*Heteromyidae*). Unlike hamsters and poached rats, heteromyids have external cheek pouches.

Teeth are a favourite morphological structure of mammalian taxonomists. This is because the structure of an animal's dentition reflects its phylogenetic position. Moreover, the teeth serve as a very reliable diagnostic feature when trying to identify different species of animals. However, the structure of the teeth reflects the feeding strategies of animals no less clearly.

The number of teeth in muridoid mammals ranges from 4 in the toothless rat (*Paucidentomys vermidax*) to 50 in opossums and the monito del monte (*Dromiciops gliridoides*). That is, the number of teeth varies from the minimum number for a land mammal with teeth to the maximum number for animals with a heterodont (variable tooth morphology) dentition. There are no species with a homodont dental system among muridoids; however, in some taxa, such as shrews, the teeth are poorly differentiated. In addition, some

species have a degenerated dental system: with small, sparse teeth, simplified tooth structure, and a complete disappearance of some teeth (in the nectar-eating honey possum, in some shrew tenrecs, in some animalivorous murids, and in the Oyapok fish-eating mouse, *Neusticomys oyapocki*).

Depending on the number and size of incisors, muridoid mammals can be divided into two groups (similar to the system used once for marsupials): 1) *polyprotodont* – with numerous, relatively small incisors, and 2) *diprotodont* – with enlarged middle incisors and a reduced number of incisors. Among muridoids, all New World marsupials, dasyurids, bandicoots, insectivores and afrosoricids are polyprotodont. Diprotodonts include all representatives of diprotodont marsupials and rodents.

The list of polyprotodont and diprotodont forms shows that this feature is associated with both the phylogenetic position of the species and its ecological characteristics. Polyprotodont species are predominantly animalivorous, while diprotodont species are predominantly plant-eaters. Both types of dentition are also common in non-muridoid mammals.

The middle incisors, however, may also be enlarged in some polyprotodont species: in caenolestids, shrews, solenodons and some afrosoricids. Moreover, the large-eared tenrec (*Geogale aurita*) formally corresponds to the definition of diprotodont given here. Depending on the feeding strategy, the incisors may be pointed or chisel-shaped. In shrews, the upper incisors are bicuspid. Solenodons have second lower incisors (I/2) with a deep slit into which the duct of the poisonous gland opens. In some species of rodents, the outer surface of the incisors may have longitudinal grooves (e.g. in gerbils). In rodents, the incisors grow constantly.

Canine teeth are found in all polyprotodont muridoids and in muridoid diprotodont marsupials. The latter have only upper canines. Canines may be the size of incisors or enlarged. No rodents possess canines.

The number of cheek teeth in one half of the jaw varies from 0 (in the toothless rat) to 7 (for example in opossums), that is, from the minimum to the maximum value for heterodont mammals. Depending on the feeding strategy, the crown of the cheek teeth, may be low or high, and with or without constant growth. The chewing surface of the cheek teeth may be pointed (e.g. in shrews), cuspidate (e.g. in many murids) or ridged (e.g. in voles). Thus, among muridoids, one can find all the main variants of cheek teeth exhibited by mammals in general, without a single type being characteristic of this particular life form.

From this brief overview, it can be seen that the **structure of the head of muridoids is highly diverse and largely unrelated to mouse-like body design.**

3.3.4. The structure of neck and trunk

The neck provides mobility to the head and lengthens the body of an animal. In mammals, the length of the neck is determined by the length of the cervical vertebrae. The relative length of the neck may be estimated relative to the length of the head. All muridoids have a short neck that does not exceed half the length of the head. Many have a neck so short that it is not externally visible. This can be explained by the short forelimbs of muridoids and the low position of the body above the ground: they do not need a long neck in order to reach the ground with their nose.

The trunk serves as a container for the internal organs and the structure onto which the limbs are attached. The shape of the body depends on the shape of the chest, the volume of the abdominal cavity and the development of the muscles of the proximal part of the limbs. In an evolutionary sense, overall body shape is the least variable feature of the external structure of mammals. However, it is subject to significant individual and temporal variability, as it can vary depending on the condition of the animal, the fullness of the digestive tract, or due to pregnancy in females.

Muridoids are characterized by a conical body when viewed from above, expanding towards the tail. This is due to the peculiarities of muridoid locomotion – in particular, the well-developed musculature of the hind limbs, since only these are used for are take off when running and jumping. Some herbivorous subterranean muridoids, such as the European water vole, have a cylindrical body. When viewed from the side, muridoids are characterized by a hunched back in its normal position, which is associated with a difference in the length of the fore and hind limbs.

3.3.5. The structure of the tail

According to the definition, the tail of muridoids is long, oval in cross section and covered with dermal scales or short fur. The minimum length of the muridoid tail assumed here is 50% of the head and body length. This limit is, of course, artificial. While it allows for a formal separation of true muridoids from similar short-tailed forms, in nature, the transition from long-tailed to short-tailed forms and *vice versa* occurs gradually, without a gap.

The length of the tail is associated with locomotion. Shorter tails (50–80%) occur in predominantly terrestrial species, while arboreal species usually have long tails (80–110%). Very long tails (> 110%) are found in both climbing (e.g. in murids *Haeromys*, *Vernaya*) and terrestrial jumping species (birch mice, jumping mice) (Miljutin, 1997, 1999). The longest tails among muridoids, with a relative length of over 200%, occur in some shrew tenrecs (*Microgale longicaudata*, *M. principula*).

In most muridoids, the tail is covered with sparse bristles, through which the scaly surface of the skin is visible. A densely hairy tail is found mainly in certain, more specialized forms (climbing, semi-aquatic, desert inhabitants). In many opossums, only the proximal part of the tail is densely hairy, while its distal part is naked (*Caluromys*, *Marmosa*, *Lutreolina*, *Didelphis*, *Philander*). The same distribution of fur is found in pygmy possums (*Cercartetus*)

and, among rodents, in the trefoil-toothed giant rat (*Lenomys*, *Muridae*). The presence of a bare tip to the tail may be related to its grasping function. The hairless distal part of the tail surface is also found in non-muridoid species with prehensile tails, for example cuscuses (*Phalanger* and others), anteaters (*Tamandua*, *Cycliopes*), and spider monkeys (*Ateles* and related taxa).

Many shrews in the subfamily *Crocidurinae* have vibrissae on their tails (e.g. *Crocidura*, *Suncus*). In semi-aquatic shrews, a "keel" of stiff hair is formed on the lower surface of the tail (*Chimarrogale*, *Neomys*).

The colour of the tail depends both on the colour of the hair and of the skin. Tail skin may be fully pigmented, partially pigmented, or not pigmented at all. In the latter case, a bare or almost bare tail looks pink. Dark pigmentation of the hair of the tail makes the overall colour of the tail darker. In the absence of pigment in the hair, the tail looks pink (in case of sparse hairs and uncoloured skin) or white if the fur is thick enough. White or pink colour usually occurs on the underside of the tail or at its tip.

In some species, e.g. in the yellow-necked mouse (*Apodemus flavicollis*), the transition from dark coloration on the upper side of the tail to light coloration on the underside is abrupt, with a clear border, but in most species the transition is gradual.

A white or pink tail tip is found in many muridoids. It is especially characteristic of some opossums, mouse bandicoots (*Microperoryctes*), the moonrat (*Echinosorex gymnura*), the Cuban solenodon (*Atopogale cubana*) and of many species of rodents: murids, cricetids, nesomyids, heteromyids (*Heteromys*), echimyids and chinchilla rats (*Cuscomys*).

The tail of many muridoids is prehensile to some extent. The grasping ability of the tail is especially developed in many opossums, all pygmy possums (*Burramys*, *Cercartetus*), the honey possum (*Tarsipes rostratus*), the musky kangaroo (*Hypsiprymnodon moschatus*), long-tailed shrew tenrecs (*Microgale longicaudata*,

M. majori, *M. principula*), and some climbing murids (e.g. *Haeromys*, *Chiruromys*, *Coccymys*, *Melomys*, *Pogonomys*, *Pithecheir*, *Sommeromys*). Some species of opossum can hang by their tail and even mate in this position, holding a partner with their feet (*Marmosops noctivagus*; Astúa, 2015).

In species with a prehensile tail, there may be a bare area in its distal part (grasping pad), designed to grasp branches. Depending on the grasp direction (top or bottom) this area may be on the lower (e.g. in many opossums and the monito del monte, *Dromiciops gliridoides*) or upper surface of the tail (in long-tailed shrew tenrecs and in murids: *Chiruromys*, *Coccymys*, *Melomys*, *Pogonomys*, *Sommeromys*).

In some muridoids, the tail serves as a reservoir of fat: namely in opossums (*Lestodelphys*, *Thylamys*), in the Chilean shrew opossum (*Rhyncholestes raphanurus*), in the monito del monte (*Dromiciops gliridoides*), in some dasyurids (*Pseudantechinus*, *Sminthopsis*), in the eastern pygmy possum (*Cercartetus nanus*), in Dobson's shrew tenrec (*Nesogale dobsoni*), in some gerbils (*Microdillus*, *Pachyuromys*) and in the rock rats (*Zyzomys*, *Muridae*).

It may be concluded that there are no tail features specific to or characteristic exclusively of muridoids. At the same time, muridoids have a distinctive combination of tail characters. These are the traits that have been included in the definition of a muridoid, namely, **the tail of muridoids is long, oval in cross section and covered with dermal scales or short fur.**

3.3.6. The structure of limbs

The structure of the limbs is directly connected with locomotion. For this reason, it reflects the locomotor strategy of species better than any other feature. According to the definition adopted here, muridoids are four-legged, morphologically plantigrade animals whose hind legs are longer than the front legs, and where the digits of all limbs are mostly unfused and unshortened, and usually

end with claws. Thus, the mammals discussed here have already been selected according to certain limb characteristics. However, let us consider whether there are other limb features associated with mouse-like body structure.

By definition, the hind limbs of muridoids are longer than the forelimbs. But by how much? The length of a limb may be measured as the sum of the lengths of its free segments. Among muridoid rodents of the Baltic region, **the ratio of the lengths of the hind and forelimbs** ranges from 1.38 in the northern birch mice (*Sicista betulina*) to 1.51 in the wood mice of the subgenus *Sylvaemus* (Miljutin, 1997). In general, these rodents, which belong to three different families and 9 species, exhibit a fairly constant ratio of hind and fore limbs, averaging 1.45; that is, their hind limbs are about one and a half times as long as their front limbs. The consistency of this ratio is explained by the fact that in both short-legged (subterranean or terrestrial) and long-legged species (climbing and jumping), both pairs of legs shorten or lengthen approximately equally. It therefore seems possible that this ratio is typical of most muridoids. For comparison, in a dog (fox terrier) the ratio is 1.2; that is, the hind legs of the dog are also longer, but the difference between the length of the hind and front legs is smaller.

The length of the forelimb in relation to the length of the head and body varies among the muridoid rodents of the Baltic region from 39.9% in the European water vole to 54.3 in the northern birch mice. The relative length of the humerus (16–20%) and the forearm (15–20%) is approximately equal, while the forefoot in all species is the shortest limb segment (9–14%) (Miljutin, 1997). In a dog (fox terrier), the forelimbs are longer due to the lengthening of the forearm and metacarpal part of the forefoot. In addition, when sitting, standing, or moving, the dog's metacarpals are raised above the ground.

However, due to differences between muridoids and dogs in the length of the neck, it is more correct to compare the length of the limb not in relation to the length of the head and body, but to the

length of the trunk. Here, the oblique length of the trunk – the distance from the shoulder joint to the ischial tuberosity – is used for this purpose. Using such a comparison, the difference in the length of the forelimb between, for example, a brown rat and a dog is clear. The relative lengths of the forelimb in this example are 61.4% and 74.9%, respectively for rat and dog. While the shoulder section of rat and dog forelimbs are similar, the dog's forearm is 8.4% longer, and its forefoot is 5.6% longer (despite the fact that the dog's digits are shortened).

The length of the hind limb in relation to the length of the head and body varies among muridoid rodents in the Baltic region from 56.8% in the European water vole to 75.1% in the northern birch mouse. The relative length of the femur (16–20%) is shorter than the length of the tibia (23–29%), while the hind foot is intermediate (17–25%) (Miljutin, 1997). In a dog (fox terrier), the relative length of the hind limb and its segments fall within these ranges.

The number of digits in muridoid mammals varies in the forefoot from 3 to 5, while the hind foot of all species comprises 5 digits (if fused digits are counted separately). This can be written as a formula, as follows: 3–5/5 (forefoot/hind foot). In all non-rodent muridoids, the number of digits is 5/5; that is, in muridoid marsupials, insectivores and tenrecs, all limbs are morphologically pentadactyl. All muridoid rodents have 4/5 digits (the first forefoot digit is rudimentary), with the exception of some climbing mice (*Dendromus*), which have 3/5 digits (the first and fifth digits are rudimentary).

In most muridoids, all digits are separate from each other, but in bandicoots, diprotodont marsupials, and otter shrews, the 2nd and 3rd hind foot digits are fused. Thus, morphologically, they have 5 digits on the hind foot, but functionally only 4. The extreme digits of the hind foot in many terrestrial species are shorter than the middle digits, and they are especially short in bandicoots. Climbing muridoids generally have longer digits compared with terrestrial muridoids.

In some species, one of the extreme digits (1st or 5th) of the hind foot is opposable. The inner digit is opposable in opossums, monitos, pygmy possums, musky kangaroos, and partially opposable in some rodents. Partial opposition of the outer digit of the hind foot occurs in many muridoid rodents. Wolly opossums (*Caluromys*), in which the hind foot inner digit is opposable, are also able to grasp branches between the 2nd and 3rd digits of the forefoot. An unusual manifestation of opposition is seen in Neotropical bamboo rats (*Dactylomys*): while climbing, they gasp stems between the 3rd and 4th digits of the forefoot and between the 2nd and 3rd digits of the hind foot.

In muridoids, all functional digits of the forefoot and middle digits of the hind foot have claws (an exception is *Dactylomys*, which have nails on all digits). Among rodents the rudimentary first digit of the forefoot is protected by a flat nail. The opposing digits of some marsupials and rodents also have a nail. The length and shape of the claws, especially those of the forefoot, depend on the habits of the animal. In fossorial species, they are relatively long and straightened, in terrestrial species they are of medium length and weakly curved, and in climbing species the claws are curved and sharp. In species that rummage in litter, the claws of the middle digits of the forefoot may be very long, for example, in bandicoots and solenodons.

The number and size of the plantar pads vary. In fossorial and terrestrial muridoids, the pads are relatively small and flat, while in climbing species, they are large and convex.

In some semi-aquatic muridoids, for example in water shrews (*Neomys*), the hind feet are bordered by stiff hairs. Others have rudimentary swimming membranes (e.g. *Neofiber* and *Ichthyomys*). In silky pocket mice (*Perognathus*) the soles of the hind feet are covered with hair, which facilitates their movement on sand. Chinchilla rats have long coarse hair growing on their middle digits.

This brief review of the structure of the limbs does not reveal features unique to or characteristic of muridoids, with the exception of those features that are already indicated in the definition of the life form. It may be noted that all muridoid mammals have morphologically pentadactyl hind feet. Yet the pentadactyl foot is a primitive feature that is found in other mammals, even those that are very different from muridoids in body structure, such as monkeys and bats.

3.3.7. Conclusions: morphological features of muridods

According to the definition used here, muridoids are four-legged, morphologically plantigrade animals, without a protective armour or flying membrane, whose hind legs are longer than their front legs; the digits of all limbs are mostly unfused and unshortened and usually end with claws; the tail is oval in cross section in length is equal to or exceeds half the head and body length, and is covered either with bare skin (with or without scales) or short fur without a tuft at the end. The above analysis of the morphology of the 1927 mammal species that correspond to this definition revealed some additional characteristic morphological features of muridods:

- **small body size,** which may be due to biomechanical constrains of the structure;
- **sparse or no hair on the ears, feet and tail;**
- **elongated conical muzzle;**
- **short neck;**
- **hunched back** when stationary;
- **morphologically pentadactyl hind foot.**

None of these features are unique to muridoids, but their combination is unique.

3.4.1. Habitats and use of space

Muridoids are found almost everywhere where terrestrial flightless mammals occur: from the arctic tundra to tropical deserts and rainforests, and from lowlands to highlands. They are found in all ecozones and occupy a variety of habitats: various types of forests, shrublands, tundra, meadows (including alpine meadows), steppes, deserts, and savannahs. In addition, muridoids successfully inhabit anthropogenic landscapes, and some have become synanthropes. In many habitats, muridoids are represented by a large number of species and individuals. Only in the extreme conditions of the tundra and deserts are they less numerous.

Muridoids use various media and substrates for movement and shelter: water, soil, the surface of the ground, trees, shrubs and herbaceous vegetation. Most species do not have a narrow substrate (locomotor) specialization; that is, they use several media and substrates. Strictly speaking, there are no specialized terrestrial forms among muridoids. Most muridoid species forage on the ground. Others forage mainly in the water (some true shrews, otter shrews, some murids and cricetids), underground (*Nesokia indica*, *Arvicola amphibius*) or in trees, shrubs and herbaceous vegetation (many species). Some muridoid voles (*Dinaromys*, *Chionomys*), spiny mice (*Acomys*) and rock mice (*Petromyscus*) are adapted to living among rocks.

Since all muridoids are vulnerable to predators, due to their small size, they cannot do without shelter. As shelter and nesting sites they use burrows (most often); cracks in the ground; cavities under stones, roots and fallen trees; hollows between stones and crevices in rocks; hummocks; dense herbaceous vegetation; the base of shrubs; plant litter; rotten stumps; hollows and cracks in logs; hollows and cracks in the trunks of standing trees; the branches of trees and shrubs; and bird nests. From this list it is clear that muridoids use all suitable and accessible shelters, up to a piece of bark that has fallen to the ground.

3.4.2. Feeding

Various muridoid species feed on insects and other invertebrates (including aquatic invertebrates), small vertebrates, carrion, fungi, fruit, seeds, flowers, nectar and other plant exudates, as well as leaves, stems and belowground plant parts. Thus, muridoids as a whole feed on absolutely all food objects conceivably available to a small mammal. Of course, "absolute omnivores", capable of eating both meat and hay, do not exist. Among muridoids there are animalivorous, omnivorous, frugivorous and herbivorous species, and some may have a rather narrow specialization, for example, the nectar-eating honey possum. Foraging strategies also differ: swimming and diving, walking in shallow water, digging burrows to obtain roots, rummaging in plant litter, collecting food on the ground, climbing trees, shrubs, and herbaceous vegetation.

3.4.3. Activity, sociality, reproduction and development

Most muridoids are predominantly nocturnal, but some are diurnal or active day and night. Muridoids are mostly active year-round, but some species fall into seasonal hibernation or a shorter torpor during unfavourable periods. True winter hibernation occurs in the monito del monte, birch mice, jumping mice and dormice. Some marsupial mice, pygmy possums, honey possums, some tenrecs and pocket mice (*Perognathus*) may exhibit temporary torpor. During hibernation, torpor, and prolonged confinement in a shelter, muridoids use fat accumulated in the body during periods of food abundance. In areas with seasonal fluctuations in climate, many species store food in their shelter or other caches.

Different muridoids live alone, in small groups, or in colonies. Opossums, marsupial mice, musky kangaroos, gymnures, shrews, tenrecs, otter shrews, birch mice, jumping mice, dormice, and heteromyids are predominantly solitary. Many murids, cricetids, nesomyids, and echimyids are mainly group-living. Some voles and chinchilla rats live in colonies. In general, a solitary way of life is

more characteristic of animalivorous muridoids, while plant-eating species tend to be social.

Most muridoid species have a short pregnancy (from 12 days in marsupials, and from 15 days in rodents), as a result of which the young are born naked and with closed eye and ear openings. However, in some murids, e.g. *Acomys*, new-borns are covered with fur and open their eyes shortly after birth. In echimyids and chinchilla rats, the young are born covered with fur, sighted and capable of movement. Muridoid species produce from 1 to 21 young in a litter, which develop rapidly, and in many species become sexually mature in the year of their birth. The longevity of muridoids is from one year (e.g. shrews) to 11 years (solenodons). However, most species, especially the smaller ones, have short life spans.

3.4.4. Conclusions: ecological features of muridods

From the above brief overview, it can be seen that the ecology of muridoids is diverse and does not have features unique to the life form. Nevertheless, some characteristic features of muridoids can be distinguished:

- most muridoids do not have a narrow locomotor specialization; that is, they regularly use several media and surfaces for movement (water, soil, ground surface, plants);
- muridoids are characterized by a short pregnancy, large litters, rapid maturation of offspring, and a short lifespan.

Both ecological features of muridoids are partly explained by their small size, and not by body structure. Without locomotor versatility, movement is challenging for a small animal. A surface that appears smooth to a large mammal, can represent rugged terrain for a small animal, which requires an ability to climb and jump. A puddle that a human might step over or wade through, may to a small animal seem like a lake that can only be crossed by swimming. No matter

how fast a small animal runs, even a slow large animal can overtake it, so, for its own safety a small animal should be able to dig burrows or climb branches. Insecurity due to small size may also explain the rapid life cycle of muridoids.

4. ECOMORPHOLOGICAL DIVERSITY OF MURIDOIDS

As shown in previous chapters, muridoids are heterogeneous in their morphology and especially in their ecology. But are there systematic patterns within this heterogeneity? Can certain muridoid morphotypes be explained by the peculiarities of their ecology? The ecomorphological analysis below provides positive answers to these questions.

Identification of ecomorphological structure requires reliable data on the morphology and ecology of all muridoid species. These data were mainly taken from Nowak, 1991; Wilson et al., 2016, 2017 and Wilson, Mittermeier, 2015, 2018. In unclear cases, I also made use of of faunistic surveys and descriptions of taxa (among them Kingdon, 1974; Dieterlen and Statzner, 1980; Strahan, 1983; Ludwig, 1984; Voss, 1988; Panteleyev et al., 1990; Skinner & Smithers, 1990; Voss & Carleton, 1993; Miljutin, 1997; Stalling, 1997; Whitaker & Hamilton, 1998; Garbutt, 1999; Menkhorst, 2004; Helgen, 2005; Vogel, 2013; Happold, 2013; Patton et al., 2015; Heany and al., 2016; Ribble & Rathbun, 2018; Voss & Jansa, 2021).

Literary data on morphology were compared with photographs and realistic drawings of animals, and, where possible, with collection specimens. In some cases, my own data were used (measurements, photographs, drawings, and the results of observations of live animals). When reliable average measurements were not

available, the maximum limits were used to calculate the relative length of the tail, feet, and ear in relation to head and body length. Determination of ecological strategies was often complicated by the inadequacy of ecological data or a complete absence for some species. When determining the ecological strategy of a species, morphological characters were deliberately not used.

The ecomorphological diversity of muridoids is reflected here by means of life forms and ecological strategies. The first two sections of this chapter introduce concepts and methodology. Then, the ecomorphological features of the four main ecological groups of muridoids are discussed: semi-aquatic, subterranean, terrestrial, and arboreal.

4.1. Life forms of muridoids

According to the definition adopted here **the life form (ecomorph) is a system of morphological adaptations that determines the general structure of an organism's body.**

The muridoid is an ecomorph, but ecomorphs, like taxa, have different hierarchical levels. Among almost two thousand species of muridoid, there are various types of body structure, which are determined by the ecological strategy of species. The presence of certain combinations of ecologically significant morphological traits allows ecomorphs of a lower rank to be distinguished within muridoids.

In the definition of a muridoid, I deliberately did not consider the shape of the head. This made it possible to identify a group of species exhibiting similar combinations of morphological characters associated mainly with locomotion (**locomorph**). Now that the boundaries of this group (muridoids) are known, it is possible to identify within it locomorphs of a lower rank as well as their combinations with various types of head structure. The external features of the head, especially the jaws, are mainly associated with feeding, so head structure types may be called **trophomorphs.** Locomorphs and trophomorphs form various combinations with

each other (**tropho-locomorphs**). Among non-muridoid mammals, there are also **protectomorphs** – groups of species that have a similar appearance due to the same means of protection: an armour of spines, plates or scales.

The facial part of the head, the muzzle, is especially variable. According to the shape of the muzzle, muridoids can be divided into three main groups: 1) **sharp-muzzled** – muridoids with a sharply conical muzzle; 2) **normal-muzzled** – muridoids with a blunt conical muzzle; and 3) **blunt-muzzled –** muridoids with a blunt muzzle. All three types are ecologically significant and are associated with a common dietary strategy: animalivory, frugivory and herbivory, respectively.

In addition to the muzzle, other features of the external structure of the head, trunk, tail, and limbs of muridoids also vary. Despite the abundance of combinations of ecologically significant morphological characters, many or even all of the combinations are not random: the characters correlate with one other to collectively contribute to certain functions that define the ecological strategies of the species. Thus, some combinations of characters are more common, others are less common, and some theoretically possible combinations have not emerged in the evolution of the group, or do not exist because they are meaningless.

A detailed study of the ecomorphological diversity of muridoids is a task for future research. Based on the analysis below, 13 ecomorphs (that is, 13 combinations of ecologicaly significant morphological characters) can be tentatively distinguished. The ecomorphs are named after typical representatives. However, one should not forget that ecomorphs are not discrete; during evolution, they gradually transform into each other. Therefore, along with the species exhibiting clearly expressed typical combinations of characters, there are species with features that are transitional from one combination to another.

The ecomorphs of muridoids distinguished here are listed below in the order of most to least common.

Ecomorphs of muridoids:

Rattoids (from *Rattus*, "rat-like" in body shape, not size) are muridoids that do not have a clearly expressed narrow morphological specialization. They have a moderately long tail (usually 70–90% of the head and body length) and their feet are not specialized for swimming, digging, running, or climbing. This is a locomorph: rattoids may be sharp-muzzled, normal-muzzled or blunt-muzzled. The brown rat (*Rattus norvegicus*; fig. 2) is an example of rattoid.

Gliridoid muridoids (from *Gliridae*, "dormouse-like"; should not be be called simply "gliridoids" to avoid confusion with non-muridoid species) are muridoids that are morphologically adapted to an arboreal way of life. This adaptability is manifested primarily in the structure of the feet (hook-shaped sharp claws, long digits, convex plantar pads, wide hind foot). In addition, gliridoid muridoids are characterized by large eyes, long vibrissae, and a long tail (>90%). This is a locomorph: gliridoid muridoids may be sharp-muzzled, normal-muzzled, or blunt-muzzled. The monito del monte (*Dromiciops gliridoides*; fig. 4:3) is an example of gliridoid muridoid.

Sorexoids (from *Sorex*, "shrew-like") are muridoids that are initially morphologically adapted to foraging in plant litter. Such animals are characterized by the combination of a long muzzle, small eyes, and long claws on the forefeet; however, small forms that penetrate the litter through natural hollows may not have long claws. In addition, small sorexoids are characterized by a velvety pelage and backward or reduced ears. Both features facilitate movement through the litter and soil. This is a tropho-locomorph. Sorexoids are always sharp-muzzled. The common shrew (*Sorex araneus*; fig. 6:2) is an example of sorexoid.

Gerbilloid muridoids (from *Gerbillus*, "gerbil-like"; should not be called simply "gerbilloids" to avoid confusion with non-muridoid species) are muridoids that are morphologically adapted to rapid terrestrial locomotion. They have relatively long and narrow hind feet,

with shortened extreme or all digits, but with an elongated tarsometotarsal part. Gerbilloid muridoids are characterized by a long or thickened tail, long vibrissae, large eyes, and sometimes large ears. As a locomorph, gerbilloid muridoids may be sharp-muzzled, normal-muzzled, or blunt-muzzled. Muridoid gerbils (*Gerbillinae*) are an example of gerbilloid muridoids.

Arvicoloid muridoids (from *Arvicola*, "vole-like"; should not be called simply "arvicoloids" to avoid confusion with non-muridoid species) are short-tailed (50–70%), blunt-muzzled muridoids that are morphologically adapted to digging and herbivory. They have straightened claws, wide incisors, and a heavily-built body. This is a tropho-locomorph: arvicoloid muridoids are always blunt-muzzled. Muridoid water voles (*Arvicola*) are an example of arvicoloid muridoids.

Hydromyoid muridoids (from *Hydromys*, "similar to Australian water rats"; should not be called simply "hydromyoids", to avoid confusion with non-muridoid species) are muridoids that are morphologically adapted to a semi-aquatic way of life and to animalivory. They are characterized by long and wide (oar-like) hind feet, sometimes bordered by hair or with incomplete webbing, by thick pelage, a swollen upper lip, and hard vibrissae. This is a locomorph: hydromyoid muridoids may be sharp-muzzled, normal-muzzled, or blunt-muzzled. Sigmodontines of the genus *Ichthyomys* are an example of hydromyoid muridoids.

Sicistoids (from *Sicista*, "similar to birch mouse") are muridoids that are morphologically adapted to climbing herbaceous vegetation: with long digits, long hind feet, small or flat plantar pads, short straightened or reduced claws and a very long tail. This is a locomorph: sicistoids may be sharp-muzzled, normal-muzzled, or blunt-muzzled. The birch mice (*Sicista*) are an example of sicistoids.

Deomyoids (from *Deomys*) are long-legged muridoids with a thin muzzle. This is a tropho-locomorph. All deomyoids are sharp-muzzled. *Deomys ferrugineus* (*Muridae*) is an example of a deomyoid.

Capromyoids (from *Capromys*, "similar to hutias") are muridoids that are morphologically adapted to herbivory with "bear-like" feet: flat plantar pads, relatively short digits, and strong claws. This is a tropho-locomorph: all capromyoids are blunt-muzzled. Desmarest's hutia (*Capromys pilorides*) is an example of a capromyoid.

Colomyoids (from *Colomys*) are muridoids that are morphologically adapted to foraging in shallow water. Long feet, thick fur, and a thickened upper lip are combined with medium-sized (not reduced) eyes and ears. This is a locomorph; the colomyoids known to me are normal-muzzled. *Colomys goslingi* (*Muridae*) is an example of a colomyoid.

Lutreolinoids (from *Lutreolina*) are normal-muzzled, animalivorous muridoids that are morphologically adapted to foraging in hollows and burrows. They are distinguished by a weasel-like appearance: a long body and short legs. Lutrine opossums (*Lutreolina*; fig. 11:3) are the only example of lutreolinoids.

Hypogeomyoids (from *Hypogeomys*) are muridoids that are morphologically similar to rattoids, but exhibiting the initial stage of transition to bipedal locomotion. They have large hind feet and a thickened tail. This is a locomorph. The only example is the Malagasy giant rat (*Hypogeomys antimena*).

Tarsipedoids (from *Tarsipes*, "similar to honey possum") are sharp-muzzled muridoids with a long muzzle and small eyes. They are morphologically adapted to climbing with the aid of digits and to feeding on nectar. The only example is the honey possum (*Tarsipes rostratus*; fig. 5:4).

4.2. Ecological strategies: concepts and principles of identification

The life form is a morphological characteristic of species, whereas for the short description of ecological features it is convenient to use ecological strategies. Moreover, the ecological strategies of species may serve as the basis for ecological classification.

Ecological strategy refers to the way a species adapts to environmental factors. An animal interacts with a wide variety of physical, chemical, and biological environmental factors. However, here we will confine ourselves to those that lead to the formation of life forms, that is, affect the overall body structure of animals.

In terms of impact on the overall body structure of an animal, the following three environmental factors are most significant: substrate, food, and predators. These factors respectively shape the locomotor, feeding, and defence strategies of species during the course of evolution.

Principles upon which the ecological strategies of mammals may be described and classified are detailed in a separate article (Miljutin, 2009). Those principles are taken here as a basis.

The locomotor strategy is determined by the medium or surface *usually* used by the animal for locomotion when foraging or sheltering. The word "usually" indicates that this refers to the behaviour typical of the species. Non-flying mammals use four media or surfaces: water, soil, ground surface and plants. According to these, non-flying mammals may be divided into four main categories: 1) **aquatic** (**Aq**), 2) **subterranean** (**S**), 3) **terrestrial** (**T**), and 4) **arboreal** (**Ar**). The term "arboreal" encompasses all species using plants for locomotion, including those that climb herbaceous plants, for example, the harvest mouse (*Micromys minutus*).

If highly specialized **monobionts** that forage and sleep in the same media or on the same substrate (foraging-sleeping: AqAq, SS, TT, ArAr) are easily assigned to the categories of aquatic, subterranean, terrestrial, and arboreal species, the classification of **generalist species** (di-, tri- and tetrabionts) is more complicated. Aquatic-subterranean species (AqS) are classified here as aquatic. The remaining semi-aquatic species (AqT, AqST), as well as semi-subterranean species (ST) and semi-arboreal species (TAr, STAr) are at the same time "semi-terrestrial"; therefore, their ecologically least specialized representatives are classified here as terrestrial animals. The

criteria used to divide more specialized "multibiont" species into aquatic, subterranean, terrestrial, and arboreal are given below in the relevant sections.

The feeding strategy of an animal is determined here by the category of food that is *predominantly* exploited. There are three main food categories: 1) other animals, 2) the generative parts of plants (fruit, seeds, flowers) or their exudates (nectar, sap, gum), and 3) the vegetative parts of plants (leaves, stems, roots). In accordance with these categories, muridoids are divided here into three main groups: 1) **animalivores** (**An;** animal food makes up more than 50% of their annual diet), 2) **frugivores** (**F;** animal food and vegetative parts of plants make up less 50% of their annual diet) and 3) **herbivores (H;** vegetative parts of plants make up more than 50% of their annual diet).

Species that use different categories of food in approximately equal proportion are called here **mixivores.** They correspond to two subcategories: animalivores-frugivores (omnivores; **AnF**) and frugivores-herbivores (**FH**).

The defensive strategy is not considered in the further text, since it does not differ greatly among muridoids and does not significantly affect muridoid appearance. Usually, muridoids attempt to escape to a shelter or hide; less often they attack a predator. However, some muridoids protect themselves in different ways. Birch mice and jumping mice make sudden long jumps to escape an enemy, some muridoid rodents have spines, many insectivores (gymnures, shrews) scare away enemies with an unpleasant smell, and solenodons and some shrews (*Blarina*, *Neomys*) inject poison when they bite. However, poison is primarily used to immobilize prey.

The locomotor and trophic strategies of a species can be represented as **an ecological strategy formula.** The formula may be in a complete or shortened form. From left to right, the complete formula conveys information about: surface or media for

foraging – surface or media for sheltering and / feeding strategy. For example, the formula for the yellow-necked mouse (*Apodemus flavicollis*) would look like this: TAr-SAr/F. This means that the animal usually gathers food on the ground and in trees, usually has a subterranean (in burrows) or arboreal shelter, and mainly feeds on the generative parts of plants (fruits and seeds). The corresponding short formula for this species is STAr/F, indicating semi-arboreal frugivorous species.

To avoid confusion, the characters in each half of the formula should be written in a defined order. For locomotor strategies, the order is the sequence Aq-S-T-Ar (from bottom-up, that is, "from under the water to up the tree"); for feeding strategies it is in the order An-F-H (from animalivorous to herbivorous). In the complete formula, the foraging place is separated from the place of shelter by a dash (-), and locomotor from trophic strategies by a slash (/).

Locomotor and feeding strategies are almost completely independent of each other, so they can form various combinations. Only Aq/F and S/F combinations are not found, since there are no or almost no fruits in the water or belowground. Combinations of major ecological strategies found among non-flying mammals are shown in Table 5.

Table 5. Possible combinations of the main ecological strategies in non-flying mammals

	Animalivores (An)	Frugivores (F)	Herbivorous (H)
Aquatic (Aq)	Aq/An	–	Aq/H
Subterranean (S)	S/An	-	S/H
Terrestrial (T)	T/An	T/F	T/H
Arboreal (Ar)	Ar/An	Ar/F	Ar/H

Such a table serves as a possible option for **ecological classification.** Species falling into the same cell of the table belong to single ecological type. Here, **ecological type** is understood as a certain combination of locomotor and trophic strategies, for example, aquatic herbivore (Aq/H) or terrestrial animalivore (T/An).

However, it should be remembered that this classification is artificial. In nature, strategies exist along a continuum, without boundaries and gaps. The breakdown of this continuum into characteristic parts is just a methodological technique that makes it possible to classify strategies and understand their essence. There are also inevitably **generalist species** that use two or more strategies almost equally: "semi-aquatic" (AqS, AqT, AqST), "semi-subterranean" (ST), "semi-arboreal" (TAr, STAr) and " mixivores " (AnF, FH). Theoretically, there may be more possible combinations of ecological strategies, but not all possible combinations are realized in nature, mainly because of their biological incoherence.

The ecological diversity of muridoids at the order level is shown in Table 6. Where the same order is repeated in two or more cells of the table, this indicates that different species in the same order belong to different ecological types; however, single species can occupy only one table cell.

It is apparent from Table 6 that muridoids have mastered almost all the main ecological strategies conceivable for non-flying mammals. However, as will be shown below, the level of ecological specialization in most species is low.

Table 6. Main ecological strategies of muridoid mammals at the order level

	Animalivores	**Frugivores**	**Herbivores**
Aquatic	*Eulipotyphla* *Afrosoricida* *Rodentia*	–	*Rodentia*
Subterranean	–	–	*Rodentia*
Terrestrial	*Didelphimorphia* *Paucituberculata* *Dasyuromorphia* *Peramelemorphia* *Eulipotyphla* *Afrosoricida* *Rodentia*	*Diprotodontia* *Rodentia*	*Rodentia*
Arboreal	*Didelphimorphia* *Microbiotheria* *Dasyuromorphia* *Afrosoricida* *Rodentia*	*Didelphimorphia* *Diprotodontia* *Rodentia*	*Rodentia*

4.3. Semi-aquatic muridoids

Water is the most difficult media to inhabit for mammals, which are originally terrestrial animals, besides they are warm-blooded ones. The problem is that water is much more thermally conductive and denser than air, and mammals are not adapted to breathing in water. Adopting an aquatic way of life therefore means that mammals must be able to minimize heat loss, adapt to movement in a dense environment, and hold their breath for a long period of time while diving. There is another significant problem: under water mammals cannot use their sense of smell. Therefore, the search for food in the water has to be carried out 1) by touch using the vibrissae, forefeet or proboscis (in many semi-aquatic species), 2) by

vision (seals), 3) electroreception (platypus), echolocation (toothed whales) or filtering water (baleen whales).

It is therefore unsurprising that the transition to living in water requires significant morphological, behavioural, and physiological adaptations, which inevitably affect the appearance of animals. This is why the appearance of a dolphin is so unlike that of a rat (even more so than that of a mole or a bat). However, the difficulty of living in the aquatic environment is compensated by positive aspects. Moving into water provides a release from terrestrial predators. It also allows animals to exploit alternative food sources that are not available to terrestrial competitors.

In the category of aquatic mammals, muridoids are represented only by semi-aquatic forms. By **semi-aquatic mammals** here is meant species that regularly forage by swimming and diving, or rest and sleep in the water, or in shelters on the water, but spend part of their lives on land. This ecological group does not include **wetland mammals** that forage by wading in shallow water, or those that forage by swimming only occasionally.

Semi-aquatic muridoids are found in three orders: insectivores, afrosoricids, and rodents. Despite its rat-like appearance, the only semi-aquatic marsupial, the water opossum (*Chironectes minimus*; fig. 11:1), does not formally meet the definition of a muridoid due to its webbed hind feet.

4.3.1. Semi-aquatic muridoids among insectivores

Among the muridoid insectivores, a semi-aquatic way of life is led by 16 species of shrews (*Soricidae*), belonging to four genera. In the subfamily *Soricinae*, these are representatives of the Palearctic genus *Neomys* (all 3 species), predominantly Indo-Malay *Chimarrogale* (all 7 species) and some North American *Sorex* (5 related species: *alaskanus*, *albibarbus*, *bendirii*, *navigator*, and *palustris*). Among the *Crocidurinae*, the sole semi-aquatic species is the Zairian shrew (*Ruwenzorisorex suncoides*), which lives in East Africa. Together,

semi-aquatic muridoids make up approximately 4% both of all species of muridoid shrews and of muridoid insectivores in general. In addition to the species noted above, some other shrews are also associated with water bodies, but to a lesser extent, for example, the white-toothed shrews *Crocidura lasiura* and *C. stenocephala*. They are considered here as wetland terrestrial species.

Semi-aquatic muridoid shrews forage in water and on the ground. They swim and dive well. Semi-aquatic *Sorex* can even run for a few seconds on the surface of the water. When swimming, shrews are propelled by their hind legs. On land, they make surface runways in the grass. Nests are located in burrows (often dug by other animals), in hollows under the roots of trees, under stones, under and inside logs, and in cavities in the banks of waterbodies. Shrew burrows often have access into water. All are animalivores. They feed mostly on aquatic and terrestrial invertebrates, less often on small vertebrates. When searching for food, they check cracks on land and at the bottom of water bodies with their snouts.

Semi-aquatic muridoid shrews are small animals, but they are usually larger than related terrestrial species. The head and body length and weight of semi-aquatic muridoid shrews vary from 56 mm and 6 g in *Sorex navigator* to 135 mm and 50 g in *Chimarrogale platycephalus*. The relative length of the tail varies from 66% of the head and body length in *Neomys anomalus* to 93% in *S. navigator*. The relative length of the hind feet varies from 18% in *Ch. hantu* up to 24% in *Ch. phaeura* and *S. navigator*. Semi-aquatic muridoid shrews generally have a typical shrew appearance: a long muzzle, in the form of a mobile proboscis, pointed teeth, enlarged middle incisors, small eyes, and ears pressed to the head. Nevertheless, they differ from other shrews in the presence of morphological adaptations to a semi-aquatic way of life.

Among the external morphological adaptations to a semi-aquatic way of life are thick, water-repellent fur, hard vibrissae, a thickened upper lip, relatively small ears (this is especially noticeable

in *Ruwenzorisorex suncoides* in comparison with related species from the genus *Sylvisorex*), lockable ear openings (*Chimarrogale*), a somewhat laterally compressed tail (in semi-aquatic *Sorex*), a keel of coarse hair along the lower surface of the tail (except for *Ruwenzorisorex*), and long and wide feet, especially the hind feet. Many species have a fringe of stiff hair along the edges and around the digits (there is no fringe in *Ruwenzorisorex*), as well as incomplete webbing on the hind feet (in *Chimarrogale* and semi-aquatic *Sorex*). The most specialized seem to be the *Chimarrogale*.

Ecological strategies of semi-aquatic muridoid shrews: semi-aquatic (subterranean-terrestrial-aquatic) animalivores (**AqST/An**).

Ecomorph of semi-aquatic muridoid shrews: *sharp-muzzled hydromyoid muridoids* – all 16 species.

4.3.2. Semi-aquatic muridoids among afrosoricids

Among the muridoid afrosoricids, only one species (4%) – the Nimba otter shrew (*Micropotamogale lamottei*; fig. 7:2) from equatorial West Africa – leads a semi-aquatic way of life. It is the only muridoid species in the otter shrew family (*Potamogalidae*). Other species in the family are also semi-aquatic, but have a more specialized body structure.

The Nimba otter shrew is similar to its closest relative, the Ruwenzori otter shrew, *Micropotamogale ruwenzorii*, but lacks webbing on its feet. Both species are somewhat reminiscent of true shrews, especially the semi-aquatic species, but have differently shaped heads. Although the muzzle is long, it is not pointed and lacks a proboscis. The muzzle of otter shrews is blunt conical, and wide when viewed from above. In addition, the Nimba otter shrew exceeds semi-aquatic true shrews in size, being the size of a small rat. A more detailed description of this species is given above in the systematic review (2.3.2).

Among the external morphological adaptations to a semi-aquatic way of life exhibited by the Nimba otter shrew are a thick

fur, hard vibrissae, thickened upper lip, flat skull, small eyes and relatively small ears. There is neither stiff hair nor webbing on the feet, or a keel on the tail.

Ecological strategies of the Nimba otter shrew: semi-aquatic (subterranean-terrestrial-aquatic) animalivore (**AqST/An**).

Ecomorph of the Nimba otter shrew: ***normal-muzzled hydromyoid muridoid*.**

4.3.3. Semi-aquatic muridoids among rodents

There are 23 semi-aquatic species among muridoid rodents (1.7%). They belong to the families *Muridae* and *Cricetidae*.

4.3.3.1. Semi-aquatic muridoids among murids

There are 4 semi-aquatic species among muridoid murids (*Muridae*): the New Guinean *Baiyankamys* (both species), the Sulawesian species *Waiomys mamasae*, and possibly also the little studied Ethiopian species *Nilopegamys plumbeus* (the closest relative of which, *Colomys goslingi*, is rather a wader). These three genera belong to three different tribes in the subfamily *Murinae*. Semi-aquatic species make up only 0.6% of all muridoid murid species. However, some other muridoid murids are also closely associated with water, but are here considered as terrestrial, because they predominantly forage either in shallow water or on the coast (e.g. *Colomys*, *Dasymys*, *Malacomys*, *Xeromys*), or they can also successfully live without water bodies (e.g. the brown rat).

Semi-aquatic muridoid murids forage in water and on the ground. They shelter, apparently, in burrows and natural cavities (burrows are reliably known only for *Baiyankamys shawmayeri*). All species are animalivorous. They feed mainly on aquatic invertebrates and small vertebrates.

Among semi-aquatic muridoids, the head and body length varies from 129 mm (*Waiomys mamasae*) to 160 mm (*Baiyankamys habbema*), and the weight varies from 64 g (*W. mamasae*) to 88 g

(*B. shawmayeri*). The relative length of the tail is from 117% of the head and body length (*B. habbema*) to 123% (*W. mamasae*), while the relative length of the hind foot is from 24% (*B. habbema*) to 28% (*W. mamasae*), and the relative length of the ear is from 6% (*B. habbema*) up to 11% (*B. shawmayeri*). Thus, semi-aquatic muridoid murids belong to the most common size class in the family – to "small rats" (Table 4), are long-tailed, like many murids, but differ from most related species in possessing relatively long hind feet and short ears.

External morphological adaptations to semi-aquatic life include thick pelage, thickened upper lip, flattened skull, small eyes and ears, hard vibrissae, a keel of coarse hair along the underside of the tail (in *Waiomys mamasae*), as well as long and wide hind feet. In *Baiyankamys*, the hind feet have rudimentary webbing.

The body structure of semi-aquatic muridoid murids resembles the more specialized semi-aquatic murids of the genera *Crossomys* and especially *Hydromys*. Moreover, they are very similar to the semi-aquatic neotropical cricetids of the tribe *Ichthyomyini* (*Sigmodontinae*).

Ecological strategies of semi-aquatic muridoid murids: semi-aquatic (subterranean-terrestrial-aquatic) animalivores (**AqST/An**).

Ecomorph of semi-aquatic muridoid murids: *normal-muzzled hydromyoid muridoids* – all 4 species.

4.3.3.2. Semi-aquatic muridoids among cricetids

There are 19 semi-aquatic species among muridoid cricetids (*Cricetidae*), belonging to 7 genera and two subfamilies: voles (*Arvicolinae*) and sigmodontines (*Sigmodontinae*). It is noteworthy that these species have different feeding specializations: semi-aquatic voles are herbivorous, while semi-aquatic sigmodontines are animalivorous. However, among the non-muridoid semi-aquatic sigmodonines, there are also herbivorous species (*Holochilus*).

Semi-aquatic species make up 3.6% of all muridoid cricetids. As in the case of murids, semi-aquatic muridoid cricetids differ externally only slightly from both more-specialized, related semi-aquatic species (by the absence of developed webbing or a flattened tail), and ecologically less-specialized wetland cricetids. The latter include "swamp rats" from the genera *Oryzomys* (*O. palustris* and related species) and *Scapteromys*. Here they are formally regarded as terrestrial, because they apparently do not regularly forage by swimming.

Among the muridoid **voles,** there are 5 semi-aquatic species (24%) belonging to 3 genera: the North American round-tailed muskrat (*Neofiber alleni*), Richardson's vole (*Microtus richardsoni*) and Eurasian water voles (*Arvicola*, 3 out of 4 species: *amphibius*, *italicus*, *sapidus*). These species belong to two tribes: *Ondatrini* (*Neofiber*) and *Arvicolini* (*Arvicola*, *Microtus*).

Semi-aquatic voles forage mainly in water and belowground; to a lesser extent on the ground. They dig an extensive system of burrows with exits under water. The round-tailed muskrat also builds lodges from aquatic vegetation with an underwater exit, just as the common muskrat does. Eurasian water voles sometimes build spherical surface nests, especially during periods of flood: on the ground, in tussocks, among floating aquatic vegetation, and above the water or ground surface on strong plant stems (Panteleyev, 1968). Unlike most terrestrial voles, semi-aquatic voles feed mainly on the vegetative parts of plants with a low cellulose content, for example, the succulent stems and rhizomes of aquatic plants, roots, bulbs, and tubers.

The body structure of semi-aquatic muridoid voles resembles both those of terrestrial voles and their more specialized semi-aquatic relative, the muskrat. At the same time, externally, they differ significantly from animalivorous semi-aquatic muridoids in their rounded head, thick body, and relatively long claws. The round head shape of semi-aquatic voles is determined by the relatively

short and wide muzzle, wide incisors, wide zygomatic arches, and powerful chewing muscles. The thickness of the body is due to the fact that the abdominal cavity accommodates a long intestine. Rather long claws, as well as some features of the skull, are associated with digging. Thus, the appearance of semi-aquatic voles is explained by the peculiarities of their ecological specialization: herbivory and a fossorial way of life.

Semi-aquatic muridoid voles are the size of small to medium-sized rats. They are large representatives of their subfamily. Only the common muskrat (*Ondatra zibethicus*) exceeds their size. Their head and body length varies from 120 mm to 230 mm (both limits belonging to the European water vole *Arvicola amphibius*), while their weight varies from 72 g (*Microtus richardsoni*) to 350 g (*Neofiber alleni*). The relative length of the tail varies from 53% of the head and body length (*Arvicola italicus*) to 82% (*A. amphibius*); the relative hind foot length from 17% (*A. amphibius*) to 23% (*N. alleni*); and relative ear length from 9% (*A amphibius*, *A. sapidus*) to 11% (*Microtus richardsoni*). Compared with related terrestrial species, semi-aquatic muridoid voles have longer tails and feet.

External morphological adaptations to a semi-aquatic way of life include thick pelage, small eyes and ears (though they are already small in most voles) and a fringe of coarse hair framing the hind feet of the round-tailed muskrat. Richardson's vole is the least specialized for living in water; the round-tailed muskrat the most specialized. In general, the morphological adaptations of voles to a semi-aquatic way of life are less obvious than those of animalivorous semi-aquatic rodents.

Semi-aquatic voles differ from all other semi-aquatic muridoids in their strong adaptation to a subterranean way of life and to herbivory. Eurasian water voles (*Arvicola*) are especially good diggers. One species in the genus, the mountain water vole (*A. monticola*) is completely subterranean. Moreover, some populations of the European water vole (*A. amphibius*) are also subterranean and live far

from water bodies. Other populations of this species either live permanently near water or alternate between subterranean and aquatic habitats seasonally, being subterranean in winter and semi-aquatic in summer.

Ecological strategies of semi-aquatic muridoid voles: semi-aquatic (subterranean-terrestrial-aquatic and possibly also subterranean-aquatic) herbivores (**AqST /H** and **AqS/H**).

Ecomorph of semi-aquatic muridoid voles: *arvicoloid muridoids* – all 5 species.

Among the muridoid **sigmodontines,** there are 14 semi-aquatic species (4%): *Anotomys leander*, *Chibchanomys* – both species, *Ichthyomys* – all 4 species, and *Neusticomys* – all 7 species. That is, this group includes almost all species in the tribe *Ichthyomyini*, with the exception of the morphologically more-specialized genus *Rheomys*. They are found in the north and northeast of South America, as well as on the Isthmus of Panama. Some sigmodontines from the tribe *Oryzomyini* also lead a semi-aquatic way of life (*Amphinectomys*, *Holochilus*, *Lundomys*, *Nectomys*); however, they have well-developed webbing on the hind feet, so formally they are not muridoids.

Semi-aquatic muridoid sigmodontines apparently prefer flowing water bodies. They forage in the water and on the ground, and probably shelter in burrows and natural cavities. All species are animalivorous. They feed mainly on aquatic invertebrates and small vertebrates.

Semi-aquatic muridoid sigmodontines are relatively small rodents, covered with thick brownish-grey fur. They have a rather blunt muzzle, small eyes and ears, large hind feet, and a hairy tail (Voss, 1988). Their head and body length varies from 94 mm (*Neusticomys mussoi*) up to 197 mm (*Ichthyomys tweedii*), while their weight varies from 21 g (*N. oyapocki*) to 155 g (*I. tweedii*). The relative length of tail varies from 69% of the head and body length (*N. mussoi*) to 125% (*Anotomys leander*), the relative length of the hind foot from 17% (*Ichthyomys pittieri*) to 30% (*A. leander*),

and the relative length of the auricle varies from almost complete absence in *Anotomys leander* to 13% in *Chibchanomys orcesi*. In terms of average size, *Ichthyomys* species fall into the category of "small rats", while other species are mouse-sized (HB ≤ 12 cm). Thus, the semi-aquatic muridoid sigmodontines do not differ in size or in the relative length of the tail from the vast majority of non-aquatic sigmodontines, but they are characterized by short ears and long hind feet.

External morphological adaptations to a semi-aquatic way of life among muridoid sigmodontines include thick pelage; thickened upper lip, into which dense, hard vibrissae are sunk; flattened skull, and small eyes and ears; a keel of stiff hair along the lower surface of the tail (in *Anotomys leander*); and long hind feet, which are narrow in *Neusticomys* and wide in other species. The edges of the hind feet and digits have a fringe of coarse hair. In *Neusticomys*, this fringe is less developed. All species have rudimentary webbing between the middle digits, which does not reach the end of the first phalanx of the digits (Voss, 1988). The most morphologically specialized to the aquatic way of life is *Anotomys leander*; the least specialized are *Neusticomys*, especially *N. venezuelae*. According to R.S. Voss, this species may serve as a living model for the ancestral phenotype of *Ichthyomyini*. (Voss, 1988: 469).

The semi-aquatic muridoid sigmodontines externally resemble both the more-specialized members of their tribe (*Rheomys*) as well as the semi-aquatic murids, in particular the Australian *Hydromyini*.

Ecological strategies of semi-aquatic muridoid sigmodontines: semi-aquatic (subterranean (?) -terrestrial-aquatic) animalivores (**AqS**(?)**T/An**).

Ecomorph of semi-aquatic muridoid sigmodontines: *normal-muzzled hydromyoid muridoids* – all 14 species.

4.3.4. Semi-aquatic muridoids: summary

Among muridoid mammals, there are 40 semi-aquatic species, belonging to three orders (insectivores, afrosoricids and rodents) and four families: shrews (*Soricidae*), otter shrews (*Potamogalidae*), murids (*Muridae*) and cricetids (*Cricetidae*). Collectively, these species make up only a small fraction of muridoids – approximately 2%. This figure presumably reflects both the difficulty of mastering the aquatic environment for a terrestrial mammal and, possibly, the constraints on an aquatic lifestyle imposed by muridoid body structure and small size. Indeed, the more-specialised, semi-aquatic representatives of the same orders (desmans, giant otter shrew, muskrat, coypu, and beavers) have not only additional morphological adaptations (webbed hind feet, flattened tail), but are also much larger. Among muridoids, a tendency towards larger body size during the transition to a semi-aquatic way of life can be seen in shrews and voles.

Semi-aquatic muridoids are found in all zoogeographic regions of the planet; however, many species occur sporadically and have small distribution areas. The most widespread are Holarctic semi-aquatic shrews and voles. It is noteworthy that animalivorous semi-aquatic rodents are found in regions where semi-aquatic shrews are not present.

All semi-aquatic muridoids live near fresh water bodies. Many animalivorous species apparently prefer flowing water bodies, while herbivorous species prefer standing water or slow-flowing rivers with abundant aquatic and semi-aquatic vegetation. Different semi-aquatic muridoids may be found in forests (e.g. *Ichthyomyini*), floodplain meadows (e.g. water voles) and swamps. Some live in the lowlands or the foothills of mountain ranges; others occur in mountainous regions up to an altitude of at least 4000 m (Voss, 1988).

Semi-aquatic muridoid mammals forage in water, on the ground and underground (water voles). They are skillful swimmers and

divers. For shelter, they use burrows, natural cavities under roots and stones, under and inside logs, cavities in the banks of waterbodies, tussocks, floating vegetation, lodges (round-tailed muskrat), and sometimes nests suspended on plant stems (water voles). Burrows dug by semi-aquatic mudidoids often have an exit under water. Semi-aquatic voles are herbivorous; other species are animalivorous. The latter feed mainly on aquatic invertebrates (insects, molluscs, worms, crustaceans) and small vertebrates (fish, amphibians). There are no frugivorous species among semi-aquatic and aquatic mammals, since little fruit is found in water (e.g. falling from trees into water) and it is much more efficient for a frugvorous mammal to collect fruit and seeds on the ground, or directly from plants.

Semi-aquatic muridoid mammals are relatively small. Their head and body length varies from 56 mm (*Sorex navigator*) to 230 mm (*Arvicola amphibius*), and their weight from 6 g (*S. navigator*) to 350 g (Neofiber *alleni*). Thus, they belong to the size classes of "mice" (26 species), "small rats" (10 species) and "medium rats" (4 species of voles), with mouse-sized species (HB ≤ 12 cm) predominating (65%).

The relative length of the tail varies from 53% (*Arvicola italicus*) to 125% (*Anotomys leander*) of the head and body length, the relative length of the hind foot from 14% (*Micropotamogale lamottei*) to 30% (*A. leander*), and the relative length of the auricle from almost complete absence in *Anotomys leander* and some shrews (*Neomys*, *Chimarrogale*) to 13% in *Chibchanomys orcesi*. The relative length of the tail in semi-aquatic muridoids does not differ from that of terrestrial species, while most semi-aquatic species have shorter ears and longer hind feet than most terrestrial species. Voss (1988) noted that the longest-tailed and longest-footed *Ichthyomyini* species occur in mountainous habitats, which may be due to the difficult swimming conditions in fast mountain streams compared with slow-flowing lowland rivers. Curiously, the hind feet of the Nimba otter shrew are short (14%) and narrow (Vogel, 2013). In

non-muridoid otter shrews, the hind feet are also relatively short, but wide.

Morphological adaptations to a semi-aquatic way of life in small animalivorous animals are considered in detail in the study of Voss (Voss, 1988). The list of 9 features given in that work is supplemented with additional features by Peterhans and Patterson (1995). Below are listed only those adaptive traits that affect the body shape of the animal and are found in semi-aquatic muridoids. These traits can be combined into 7 functional complexes:

1) thick pelage, which prevents heat loss in the water and increases buoyancy;
2) hard vibrissae, which provide a sense of touch in the dense aquatic environment, and a thickened upper lip (lip cushions) in which the vibrissae bases, receptors and nerves are located;
3) a flattened skull, perhaps to align the nostrils, eyes and ear openings on the same horizontal plane, which allows a swimming animal to breathe and use all its senses simultaneously without lifting its head completely out of the water;
4) small eyes, apparently due to their limited functioning in the aquatic environment;
5) small ears, which increases the streamlining of the body, besides, the auricles are ineffectual under water; Voss (1988) also notes an increased hairiness of the ears in comparison with related terrestrial species, which increases thermal insulation, but may simply be a consequence of a reduction in the size of the ears;
6) a somewhat laterally compressed tail (in semi-aquatic *Sorex*) and a keel of coarse hair along the lower surface of the tail (in *Chimarrogale*, *Neomys*, *Waiomys mamasae* and *Anotomys leander*), which increases the efficiency of the tail as a rudder and propulsor;

7) long and wide hind feet: the main body parts used for propulsion when swimming and diving. In some species, the area of the hind foot is increased by a fringe of coarse hair (*Chimarrogale*, *Neomys*, *Neofiber alleni*, *Ichthyomyini*) or incomplete webbing between digits (*Chimarrogale*, *Sorex*, *Baiyankamys*, *Ichthyomyini*).

Any given species of semi-aquatic muridoid may exhibit the complete set of these features, or only some of them.

It should be noted that all of the listed adaptive traits are associated with adaptation to living in water, that is, with locomotion, but not with feeding. On the basis of their feeding strategies, semi-aquatic muridoids can be divided into two groups: animalivorous and herbivorous; however, there are three morphological types (trophomorphs) corresponding to these strategies. Thus, animalivorous species are either sharp-muzzled (shrews) or normal-muzzled (Nimba otter shrew and animalivorous semi-aquatic rodents), while herbivorous species are blunt-muzzled (voles). This discrepancy cannot always be explained by the difference in food objects, since some of both sharp-muzzled and normal-muzzled semi-aquatic species are predominantly insectivorous; that is, they practically do not differ in their choice of food objects. Clearly, one reason for such a morphological discrepancy is a different origin; that is, a difference in the structure of the head of ancestral terrestrial forms. But it is also possible that preservation of the ancestral morphology is associated with differences in foraging behaviours: using the proboscis or vibrissae, respectively. In favour of this interpretation is the hypertrophy of the proboscis in the closest, more specialized semi-aquatic relatives of shrews – the desmans.

Finally, some conclusions of a general nature: 1) semi-aquatic muridoids have a body structure intermediate between that of related terrestrial species and morphologically more-specialized semi-aquatic species; 2) morphological adaptations to a semi-aquatic

life are repeated in different taxa, regardless of the phylogenetic position of the species; 3) types of the general body structure (locomorphs) and head structure (trophomorphs) can occur in various combinations; that is, they are as independent of each other as locomotor strategies are from feeding strategies.

Ecological strategies of aquatic muridoids. semi-aquatic (subterranean-terrestrial-aquatic, possibly also subterranean-aquatic, **AqST**, **AqS**) animalivores (**An:** shrews, Nimba otter shrews, part of rodents) and herbivores (**H:** voles).

Ecomorphs of aquatic muridoids: 1) ***normal-muzzled hydromyoid muridoids*** – 19 species: Nimba otter shrew and animalivorous semi-aquatic rodents; 2) ***sharp-muzzled hydromyoid muridoids*** – 16 species: semi-aquatic shrews; 3) ***arvicoloid muridoids*** – 5 species: semi-aquatic muridoid voles.

4.4. Subterranean muridoids

Soil and other belowground substrates are, due to their density, the most difficult media through which to move. In subterranean tunnels with little ventilation, the concentration of carbon dioxide may increase to high levels. Subterranean food is different and often scarcer than that found aboveground. Furthermore, finding a sexual partner is challenging in the subterranean environment. It is therefore unsurprising that only a small fraction of mammals adopts a completely subterranean way of life, that is, they not only shelter but also forage belowground.

On the other hand, the difficulty of moving underground is also the main virtue of the soil: subterranean shelters are the safest. Therefore, in addition to completely subterranean species, there are many "semi-subterranean" mammals that shelter in burrows, but feed mainly aboveground (e.g. marmots). For physical reasons, burrows are used mainly by small mammals, of which many have a muridoid body structure. Most of these muridoids, however, do not correspond to the definition of a subterranean species accepted

here, since they do not use burrows for feeding. In contrast to a refuge burrow, a feeding burrow is usually much longer and runs close to the surface of the ground, where the subterranean parts of plants and most subterranean invertebrates are found.

Among mammals, several levels of specialization for subterranean locomotion can be distinguished. Firstly, there are **subterranean-terrestrial** species that use shelter belowground but forage mainly on the ground, or forage belowground, but do not dig burrows themselves (e.g. weasel). Secondly, there are **terrestrial-subterranean** species that shelter and forage belowground, digging feeding burrows, but part of their food is regularly obtained aboveground. Thirdly, there are **completely subterranean** species such as moles and mole rats that shelter and forage belowground, making use of feeding burrows. Here, by "**subterranean**" only completely subterranean and terrestrial-subterranean species are considered, while subterranean-terrestrial species are included in the category "terrestrial", and subterranean-aquatic species are regarded as "aquatic".

Unlike "completely aquatic" species, "completely subterranean" species still sometimes come to the ground surface, for example, during the dispersal of young. Thus, in terms of the level of specialization to the habitat, they are more comparable to pinnipeds than to cetaceans.

Completely subterranean mammals, such as moles and mole rats, did not appear suddenly in the course of evolution. Even among extant species, it is possible to trace the transition from subterranean-terrestrial to subterranean forms through the terrestrial-subterranean stage. However, in the course of evolution, all completely subterranean and most terrestrial-subterranean species have lost the muridoid body structure, and hence there are no completely subterranean species among muridoids. Even terrestrial-subterranean muridoids are rare.

Identification of subterranean species is hampered by the fact that it is not always clear whether an animal is fossorial or rather an inhabitant of the plant litter that does not dig burrows at all, as is the case for many shrews. Litter dwellers are common among forest species, especially in tropical forests where the litter layer is especially deep and digging feeding burrows is pointless. In such places, invertebrates are mostly found in the litter, and edible subterranean plant parts are scarce, since the cover of herbaceous vegetation is sparse or absent. Unsurprisingly, herbivorous fossorial animals prefer open habitats.

Despite the fact that specialized subterranean forms are found in many orders of mammals (marsupial moles, true moles, golden moles, mole rats and others), I could not find a single muridoid species among the marsupials, afrosoricids and even insectivores, that digs feeding burrows. It is possible, that some muridoid shrews, for example, *Sorex mirabilis* and *S. unguiculatus*, make feeding burrows, but there are no definitive data on this. Among muridoid rodents, some murids and cricetids are terrestrial-subterranean.

4.4.1. Subterranean muridoids among rodents

There are many subterranean species among rodents (mole voles, blind mole rats, zokors, bamboo rats, African mole-rats, gophers, tuco-tucos and others), but very few have a mouse-like body structure. Probably, only 4 species of subterranean (terrestrial-subterranean) mammal have muridoid body structure, corresponding to 0.3% of all species of muridoid rodents. They belong to two families: murids (*Muridae*) and cricetids (*Cricetidae*).

4.4.1.1. Subterranean muridoids among murids

Among muridoid *Muridae*, only one species (i.e. < 0.2% of all muridoid murids) leads a subterranean (terrestrial-subterranean) way of life: the short-tailed bandicoot rat (*Nesokia indica*). The ecology of the second representative of this genus, *N. bunnii*, is unknown.

Judging by its habitat and morphology, it is likely a wetland species. Of course, among muridoid murids there are many burrowing species, but other species, even the closest relatives of the *Nesokia*, the bandicoot rats (*Bandicota*), which dig long tunnels with numerous chambers, are not specialized in feeding on the subterranean parts of plants, nor do they make feeding burrows (Nowak, 1991; Wilson et al., 2017). Moreover, there are no subterranean species among the non-muridoid murids. Thus, the short-tailed bandicoot rat is the most specialized to a subterranean way of life of all murids.

The short-tailed bandicoot rat is found mainly in the dry subtropics of Asia and North Africa: from the Nile Delta in the west to Bangladesh and Xinjiang (China) in the east.

Short-tailed bandicoot rats inhabit river valleys, lake shores, irrigated lands, and oases. These are the places where plant food and water can be obtained all year round in an otherwise arid environment. Short tailed bandicoot rats dig an extensive system of feeding, protective and nesting tunnels. They leave burrows only for a short time to feed on aboveground vegetation during the growing season. When digging burrow, the animal throws out the excavated soil, which forms well-marked mounds along the course of tunnel. In human constructions, the rats make tunnels in earth floors and even inside adobe walls. Short-tailed bandicoot rats feed mainly on the subterranean parts of plants: roots (including tree roots), rhizomes, tubers, bulbs. In the spring and summer, they also eat above-ground plant parts. Animal food, mainly insects, is eaten in small quantities (Sludsky, 1977; Poche et al., 1982; Davydov, 1988).

It is important to note that the alternation between aboveground and subterranean food is seasonal. During the growing season, the above-ground parts of plants predominate in the diet, and in the dry and cold period, when the above-ground parts of plants die, the animals switch to feeding on the subterranean parts. Thus, the transition to a subterranean way of life serves as an adaptation to the scarcity of above-ground food in an arid climate.

The head and body length of short-tailed bandicoot rats is 165–218 mm, and the weight is 182–388 g. The tail is shorter than the head and body: 63–75%. The relative length of the hind foot is 18–20%, and the relative length of the ear is 7–12% (Panteleyev et al., 1990). Thus, the short-tailed bandicoot rat resembles the brown rat both in size and body proportions, but has, on average, a shorter tail and heavier build. In addition, the short-tailed bandicoot rat has relatively small eyes and rather long, wide, and weakly-curved claws.

The proportions of the head also differ. In comparison with the skull of the brown rat, that of the short-tailed bandicoot rat is more strongly built, with a relatively smaller braincase, more developed frontal-parietal ridges, wider-spaced zygomatic arches, and shorter and wider nasal bones. The incisors are wide, the molars have a fairly high crown, and the molar cusps merge at an early age into transverse ridges.

External morphological adaptations to the subterranean way of life include a dense, muscular body, relatively small eyes, a shortened tail, elongated, weakly-curved claws, well-developed head muscles and wide incisors. Unlike most rodents, short tailed bandicoot rats are able to gnaw on smooth surfaces. Indeed, one of my captive short-tailed bandicoot rats easily escaped from its cage, gnawing through doors made of acrylic glass and even aluminum, while other rodents lived in such cages for years.

Ecological strategies of the short-tailed bandicoot rat: subterranean (terrestrial-subterranean, **ST**) frugivore-herbivore (**FH**) or herbivore (**H**).

Ecomorph of the short-tailed bandicoot rat: *normal-muzzled rattoid*. Despite certain morphological adaptations to digging, the body structure of the short-tailed bandicoot rat is still more like that of the brown rat than, for example, a gopher (*Geomyidae*) or a bamboo rat (*Rhyzomys*, *Spalacidae*).

4.4.1.2. Subterranean muridoids among cricetids

Among muridoid *Cricetidae*, only some species in the subfamily *Sigmodontinae* lead a subterranean (terrestrial-subterranean) way of life: the woolly giant rat (*Kunsia tomentosus*) and both species of fossorial giant rats (*Gyldenstolpia fronto* and *G. planaltensis*). All three taxa were previously placed in the same genus *Kunsia*. The remaining fossorial muridoid sigmodontines (*Juscelinomys*, *Oxymycterus*) seem to be adapted to living in the forest floor, and their habits resemble those of shrews (*Soricidae*), the more so that most of them feed predominantly on invertebrates. These species, like shrews, are included here in the category "terrestrial", since, as far as we know, they do not construct feeding burrows.

Thus, there are probably no more than three muridoid species of cricetids that lead a subterranean (terrestrial-subterranean) way of life, as defined here. These three species make up approximately 0.6% of all muridoid cricetids.

Among non-muridoid cricetids, subterranean species are found in two subfamilies: *Arvicolinae* and *Sigmodotinae*. Among voles, the montane water vole (*Arvicola monticola*), the long-clawed mole vole (*Prometheomys schaposchnikowi*) and mole voles (*Ellobius*) are subterranean. All of them are herbivorous. Among the non-muridoid sigmodontines, species of *Blarinomys*, *Geoxus*, and *Notiomys* are presumed to be subterranean. All of them are predominantly insectivorous.

Muridoid subterranean cricetids are found in Central Brazil (*K. tomentosus*, G. *planaltensis*), northeastern Bolivia (*K. tomentosus*) and northern Argentina in the Chaco (*G. fronto*).

Available data on the ecology of the woolly and fossorial giant rats is scarce and contradictory. These animals prefer grasslands and savannahs, and fossorial giant rats, apparently, tend to live near water bodies. Judging by their morphological features, all species are good diggers. It has been suggested that the woolly giant rat spends the entire dry season belowground. Nevertheless, this

species has also been trapped aboveground during the dry season. Judging by the structure of the teeth and skull, all species are herbivorous; however, observations in captivity suggest that woolly giant rats can catch and eat insects (Bezerra et al., 2007; Bezerra and Pardiñas, 2016).

Subterranean muridoid cricetids are fairly large rodents. The head and body length and weight vary from 16 cm and 98 g in *Gyldenstolpia planaltensis* up to 29 cm and 630 g in woolly giant rat (*Kunsia tomentosus*). The woolly giant rat is the largest living species of *Sigmodontine*. The relative length of the auricle in subterranean muridoid sigmodontines is 9–12%. The tail is scaly. Its relative length in fossorial giant rats is approximately 50% of the head and body length or less; in the woolly giant rat it is on average 65%. The relative length of the hind foot in all three species is 18–19%.

Thus, subterranean muridoid cricetids are rodents the size of a brown rat or somewhat larger, with a clearly shortened tail and small eyes, while the hind feet and ears are of average relative size, approximately like those of the brown rat. They have coarse fur and short digits with long and strong claws. The forefoot claws of *Kunsia tomentosus* are longer than those of *Nesokia indica*.

External morphological adaptations to the subterranean way of life include a dense (muscular) body, small eyes, a shortened tail, elongated, weakly curved claws on the fore and hind feet, and wide incisors. That is, the same characters as exhibited by the short-tailed bandicoot rat.

Ecological strategies of subterranean muridoid cricetids: subterranean (terrestrial-subterranean) herbivores (**ST/H**).

Ecomorph of subterranean muridoid cricetids: *normal-muzzled rattoids* – all 3 species: *Kunsia tomentosus* and *Gyldenstolpia* (2 species). (Comments on the short-tailed bandicoot rat ecomorph are also valid here.)

4.4.2. Subterranean muridoids: summary

Among muridoid mammals, only four species are subterranean, which is only 0.2% of all muridoid mammal species. They are rodents from the families *Muridae* and *Cricetidae* (murids and cricetids): among murids, the short-tailed bandicoot rat (*Nesokia indica*); and among cricetids, the woolly giant rat (*Kunsia tomentosus*) and fossorial giant rats (*Gyldenstolpia fronto*, and *G. planaltensis*). All are terrestrial-subterranean; that is, they forage both below- and above-ground.

Thus, there are 10 times fewer subterranean than aquatic muridoids. This difference is unrelated to the frequency of subterranean mammals in general. According to my calculations, about 220 species (3.6%) of recent mammals (together with cetaceans and sirenians) lead an aquatic or semi-aquatic way of life, while about 250 species (4.0%) of mammals are subterranean. Clearly, mouse-like body structure is better suited to a semi-aquatic than subterranean way of life.

It can be assumed that muridoids lose their mouse-like body structure during the early stages of evolution towards a subterranean way of life. At the same time, the morphological and phylogenetic proximity of specialized subterranean species to muridoids, as well as the presence of transitional forms between them, indicate that the immediate ancestors of all recent, completely subterranean mammals had a mouse-like body structure.

While subterranean mammals are found on all continents, the geographical distribution of subterranean muridoids is very limited, due to their scarcity. However, there is similarity in the biotopic distribution of species as distant from each other as the Afro-Eurasian short-tailed bandicoot rat and the South American subterranean muridoid sigmodontines. All four species live in warm and seasonally arid climates. Moreover, both the short-tailed bandicoot rat and the fossorial giant rats live near water bodies.

A more detailed comparison of the lifestyle of the short-tailed bandicoot rat and subterranean muridoid sigmodontines is

impossible due to a lack of data on the ecology of the latter. However, a clear difference between the two groups is that short-tailed bandicoot rats have successfully adapted to life in anthropogenic landscapes. The construction of irrigation canals by humans and irrigated agriculture are favourable for this species, while occurrence in anthropogenic landscapes has not been recorded for the woolly and fossorial giant rats.

The morphological similarity of the terrestrial-subterranean muridoids also merits attention. They are all about the size of a brown rat, or slightly larger in the case of woolly giant rat (head and body length 16–29 cm). All species have small eyes, a shortened tail (50–75% of the head and body length) and medium-sized hind feet and ears (18–20% and 7–12%, respectively), as well as elongated claws. Nevertheless, subterranean muridoids are externally more similar to their terrestrial relatives than to specialized subterranean species.

Ecological strategies of subterranean muridoids. Subterranean (terrestrial-subterranean) herbivores or frugivores-herbivores: **ST/H**(**FH?**).

Ecomorph of subterranean muridoids: *normal-muzzled rattoids* – 4 species: rodents *Nesokia indica*, *Kunsia tomentosus* and *Gyldenstolpia* (2 species). Strictly speaking, the general body structure of subterranean muridoids is intermediate between the generalized structure characteristic of the brown rat and a body structure, for example, that of bamboo rats (*Rhyzomys*, *Spalacidae*), that already exhibits clear morphological adaptations to a subterranean way of life.

4.5. Terrestrial muridoids

For a four-legged animal, terrestrial locomotion is the evolutionarily ancestral and simplest strategy. It does not expend as much energy as swimming, digging, climbing or flying, and does not require very special morphological, physiological or behavioral adaptations. The ground surface abounds with easily accessible

food. It is tempting to imagine that herds of similar, lumbering animals should graze aboveground. There are indeed many terrestrial mammals, but they are not of the same type and, in general, are not lumbering. The abundance of coexisting competitors and predators force animals to find new ecological niches and constantly enhance methods of defence.

Among terrestrial mammals, small species are especially vulnerable to predators; and most of these species are muridoids. When attacked by a large predator, in most cases small animals are not only unable to scare it away, but cannot even run away, since a large animal moves on the ground faster than a small one. This is why the survival of terrestrial small mammals depends strongly on the availability of shelters. Most often, they shelter in burrows and other subterranean cavities, among dense vegetation or in tree hollows. Therefore, most terrestrial muridoids are capable not only of running, but also of swimming, digging and climbing.

On the basis of their preferred habitat, terrestrial muridoids can be divided to 1) **hydrophiles** – wetland species; 2) **geophiles** – fossorial and rummaging species; 3) **herbiphiles** –inhabitants of dense herbaceous vegetation; 4) **petrophiles** – inhabitants of rocks and stones; 5) **xerophiles** – inhabitants of arid regions with sparse vegetation; 6) **dendrophiles** – inhabitants of tree and shrub thickets; and 7) ecological **generalists,** which use various habitats.

The transition from a terrestrial to an aquatic, subterranean or arboreal way of life is gradual, so in many cases it can be difficult to distinguish a terrestrial animal from, for example, a subterranean one and especially from an arboreal one. By **terrestrial species** here is meant: 1) species whose representatives **forage *mainly* on the surface of the ground and *usually* do not shelter or raise offspring in water or on plants,** 2) species whose foraging and sheltering habits are unknown, but they are closest relatives (of the same or the closest genus) of the definitely terrestrial species and are morphologically similar to them; and 3) species whose sheltering habits

are unknown, but they definitely forage mostly on the ground. The latter two categories are necessary due to the fact that there are many terrestrial muridoid species whose ecology is insufficiently studied or inadequately described.

According to the definition used here, terrestrial muridoids are found in 8 orders of mammals: among opossums, caenolestids, carnivorous marsupials (dasyuromorphs), bandicoots, diprotodont marsupials, insectivores, afrosoricids and rodents. That is, in all orders where muridoids are found, with the exception of microbiotheres.

4.5.1. Terrestrial muridoids among marsupials

Among the marsupials, terrestrial muridoids are found in 5 orders: opossums, caenolestids, dasyuromorphs, bandicoots, and diprotodont marsupials.

4.5.1.1. Terrestrial muridoids among opossums

The order *Didelphimorphia* includes one family *Didelphidae* (opossums). Mouse-like body structure occurs in 98 species belonging to 15 genera. Of these, representatives of 6 genera can be regarded as terrestrial: *Chacodelphys*, *Lestodelphys*, *Lutreolina*, *Metachirus*, part of *Monodelphis* (up to 19 species) and *Thylamys*; in total, 35 species or 36% of muridoid opossums, i.e., slightly more than one third. Other muridoid opossums are arboreal. There are no terrestrial species among non-muridoid opossums.

Terrestrial muridoid opossums are found in Central and South America from southern Mexico (*Metachirus nudicaudatus*) to Patagonia (*Lestodelphys*, *Thylamys pallidior*), but predominantly in tropical and subtropical South America.

Terrestrial muridoid opossums inhabit forests and shrublands (*Lutreolina*, *Metachirus*, *Monodelphis*, *Thylamys*), savannahs (*Chacodelphys*, *Lutreolina*, *Monodelphis*, *Thylamys*), grasslands (*Lestodelphys*, *Lutreolina*, *Monodelphis* and *Thylamys*), semi-deserts

(*Lestodelphys*), and wetlands (*Lutreolina*). Thus, terrestrial muridoid opossums are found in various habitats, but seem to prefer open ones.

There are no completely terrestrial species among opossums. All of them hide underground or in trees. Many terrestrial opossums, possibly all species, occasionally forage in trees, shrubs or grasses. All terrestrial opossums are predominantly animalivorous. They feed mainly on invertebrates, small vertebrates and fruit. Feeding on small vertebrates is characteristic of larger opossums. Unlike arboreal opossums, there are no clearly expressed frugivores among terrestrial species.

There are both large (*Lutreolina*, *Metachirus*) and small species among terrestrial muridoid opossums. Head and body length and weight vary between 6 cm and 10 g in small forms (*Chacodelphys*, some *Monodelphis*) and 40 cm and 0.9 kg in *Lutreolina crassicaudata*. The fur is coloured various shades of brown and grey, up to almost black; the underparts are lighter, up to white. Some species have dark rings around the eyes or a dark "mask" extending from the eyes to the nose (*Chacodelphys*, *Lestodelphys*, *Metachirus*, *Thylamys*). *Metachirus* also have light "eyebrows". *Metachirus* and some *Thylamys* have a dark stripe on the forehead. Some *Monodelphis* have three longitudinal stripes on their backs.

Most opossums have a relatively long and pointed muzzle, but in *Lutreolina*, the muzzle is of medium length and somewhat blunt. The eyes are of medium size or small (*Lutreolina*, *Monodelphis*). The ears are short (*Lutreolina*), of medium length or long (*Lestodelphys*, *Thylamys*).

In *Chacodelphys*, *Lestodelphys* and *Monodelphis* the tail is moderately long (50–80% of head and body length), while in *Lutreolina* and some *Thylamys* it is approximately equal to the head and body length, and in other *Thylamys*, as well as in *Metachirus*, it exceeds the length of the head and body, up to 130%. In all species, the tail is to some extent prehensile. Even *Monodelphis*, the shortest-tailed opossums, carry nesting material with their tail (Astúa, 2015). In

most species, the hind feet are of medium length (1.5–2 times longer than the forefeet). In the brown four-eyed opossum (*Metachirus nudicaudatus*) the forearm, shank, and hind foot are elongated. In all species, the inner digit of the hind foot is opposable to some extent. The plantar pads are not enlarged in most or all species.

A morphological adaptation to the terrestrial way of life may be the limb elongation in *Metachirus nudicaudatus*. It is possible that this adaptation to running is the beginning of a transition from a four-legged ricochet to a gallop. At the same time, some morphological characters of terrestrial opossums, like the long prehensile tail and opposing hallux, betray an originally arboreal specialization. Unsurprisingly, they all can climb.

According to their general body structure, most terrestrial opossums can be divided into two groups: generalized muridoids (*Chacodelphys*, *Lestodelphys* and *Thylamys*) and shrew-like muridoids (many or all *Monodelphis*). These two groups do not include the species most adapted to fast movement on the ground – *Metachirus* and *Lutreolina* – whose adaptation to the terrestrial way of life followed different paths. While *Metachirus* has elongated limbs, lutrine opossums (*Lutreolina*) take advantage of their short legs, which make it possible to pursue prey in burrows, crevices and hollows. The similarity in body structure between *Metachirus* and long-legged murids, which are regarded here as a deomyoid ecomorph, is notable.

Lutrine opossums (fig. 11:3) differ from all other opossums in their weasel-like appearance: short legs, elongated body, relatively short ears, and a blunter and shorter muzzle. The shape of the muzzle is associated with the carnivorous habits of these opossums (that is, feeding on vertebrates), while the other characters are connected with locomotion. It is important to note that *Lutreolina's* legs are not only relatively shorter than those of other opossums, but also the difference in length between the fore and hind limbs is reduced, which is characteristic of galloping mammals. Indeed, the use of

a gallop by these opossums is mentioned in a study by Santori et al. (2005). It may be said that, in the morphological sense, lutrine opossums are somewhere between a "rat" and a "mongoose".

Ecological strategies of terrestrial muridoid opossums: terrestrial (subterranean-terrestrial and subterranean-arboreal-terrestrial: **ST**, **STAr**) animalivores (**An**).

Ecomorphs of terrestrial muridoid opossums: 1) ***sorexoids*** **–** up to 19 species: many or all *Monodelphis*. However, strictly speaking, *Monodelphis* occupy rather an intermediate position between rattoids and sorexoids; **2)** ***sharp-muzzled rattoids*** **–** 14 species: *Chacodelphys*, *Lestodelphys*, *Metachirus*, and *Thylamys*. (*Metachirus* possibly deserves to be regarded as a separate ecomorph); **3)** ***lutreolinoids*** **–** 2 species of *Lutreolina*.

4.5.1.2. Terrestrial muridoids among shrew opossums

The order *Paucituberculata* includes one family *Caenolestidae* (shrew opossums or caenolestids), 3 genera, and 7 species. All shrew opossums have a mouse-like body structure and are predominantly terrestrial. A description of the order is given in Section 2.1.2.

Both in appearance and way of life, shrew opossums resemble shrews. They are adapted to searching for and capturing small prey in dense herbaceous vegetation or in plant litter. This is facilitated by a small size, a long, thin muzzle, and forward-directed incisors, working together with the upper incisors like tweezers.

Ecological strategies of shrew opossums: terrestrial (subterranean-terrestrial) animalivores (**ST/An**).

Ecomorph of shrew opossums: ***sorexoids*** **–** all 7 species.

4.5.1.3. Terrestrial muridoids among carnivorous marsupials

In the order *Dasyuromorphia* (carnivorous marsupials or dasyuromorphs), muridoid species are represented in the family *Dasyuridae* (dasyurids). Among dasyurids, there are 43 muridoid terrestrial species from 11 genera: some *Antechinus* (*arktos*, *minimus*, *swainsonii*),

Dasykaluta, *Myoictis wavicus*, part of *Murexia* (*habbema*, *rothschildi*), possibly *Neophascogale*, *Ningaui*, *Parantechinus*, *Phascolosorex*, *Planigale*, *Pseudantechinus* and 18 species of *Sminthopsis*). In terms of the number of species, terrestrial muridoids make up 77% of the muridoid dasyurids and 58% of all dasyurids. Among the non-muridoid dasyurids, all species are terrestrial except for the arboreal *Phascogale* and some *Dasyurus*.

Terrestrial muridoid dasyurids are found throughout mainland Australia (*Antechinus*, *Dasykaluta*, *Ningaui*, *Parantechinus*, *Planigale*, *Pseudantechinus*, *Sminthopsis*), including its driest parts, as well as on the islands of Tasmania (*Antechinus*, *Sminthopsis*) and New Guinea (*Myoictis*, *Murexia*, *Neophascogale*, *Phascolosorex*, *Planigale*, *Sminthopsis*).

Terrestrial muridoid dasyurids inhabit a variety of habitats, from tropical rainforests to deserts. They are active mainly on the ground, but many are good climbers. All species are predominantly animalivorous. They feed mainly on insects and other invertebrates, small vertebrates and, to a lesser extent, fruit.

The head and body length and weight of terrestrial muridoid dasyurids range from 5 cm and 4 g in some *Planigale* to 22 cm and 212 g in *Neophascogale lorentzii*. The fur is coloured various shades of brown and grey; the underparts are lighter, up to white. Some *Sminthopsis* have dark eye rings and a dark forehead stripe. *Murexia rothschildi* and *Phascolosorex* have one dark stripe along the back, while *Myoictis* has two light stripes between three dark stripes on the back.

The muzzle is pointed, of medium length or long (e.g. in *Neophascogale lorentzii*). The eyes are relatively large in *Sminthopsis*, while other species have medium or small eyes. The ears are of medium length or relatively long (in some *Sminthopsis*).

The relative length of tail varies from 64% in *Dasykaluta rosamondae* up to 129% in *Murexia habbema*; however, in most species, the tail is approximately the length of the head and body. The

tail is non-prehensile. In some desert species of *Pseudantechinus* and *Sminthopsis*, as well as in *Dasykaluta rosamondae*, fat reserves are deposited in the tail, due to which it takes on a conical shape. In most species, the hind feet are of medium length, but in *Sminthopsis* are elongated due to the lengthening of the tarsus and metatarsus, while the digits are somewhat shortened. All terrestrial dasyurids have shortened hallux.

A morphological adaptation to the terrestrial way of life may be the elongation of the tarso-metatarsal part of the hind foot in *Sminthopsis*. Other than that, terrestrial muridoid dasyurids have a generalized body structure; that is, their proportions are average for muridoids, with the exception of the muzzle elongation in some species.

It is interesting that despite ecomorphological similarity between muridoid dasiurids and muridoid opossums, the ratio of terrestrial and arboreal species is opposite: dasyurids are mostly terrestrial, and opossums are mostly arboreal. This is partly explained by the drier climate and lower forest cover in Australia, but also by the likely origin of terrestrial opossums from arboreal ancestors.

Ecological strategies of terrestrial muridoid dasyurids: terrestrial (subterranean-terrestrial, subterranean-arboreal-terrestrial and arboreal-terrestrial: **ST**, **STAr** and **TAr**) animalivores (**An**).

Ecomorphs of terrestrial muridoid dasyurids: 1) *sharp-muzzled rattoids* – 20 species: part of *Antechinus* (3 species), *Dasykaluta*, *Myoictis wavicus*, part of *Murexia* (2 species), *Neophascogale*, *Ningaui*, *Parantechinus*, *Phascolosorex* and *Pseudantechinus*; **2) *sharp-muzzled gerbilloid muridoids*** – up to 18 species: many or all muridoid *Sminthopsis*; **3) *sorexoids*** – 5 species: *Planigale*.

4.5.1.4. Terrestrial muridoids among bandicoots

In the order *Peramelemorphia* (bandicoots), all species are predominantly terrestrial. Muridoids are represented by 4 species of the genus *Microperoryctes* (mouse bandicoots) in the family *Peramelidae*. Their description is given in Section 2.1.5.

A morphological adaptation to the terrestrial way of life may be elongated hind feet. In general, mouse bandicoots have a body structure that is intermediate between those of muridoids and more specialized bandicoots. The latter have an even longer muzzle, longer hind feet, and a shorter tail.

Ecological strategies of the mouse bandicoots: terrestrial (subterranean-terrestrial) animalivores-frugivores (**ST/AnF**).

Ecomorph of the mouse bandicoots: ***sorexoids*** – all 4 species.

4.5.1.5. Terrestrial muridoids among diprotodont marsupials

In the vast order *Diprotodontia*, only 7 species in three families have a muridoid body structure. Terrestrial muridoids are represented in two of them: among pygmy possums (*Burramyidae*) and musky kangaroos (*Hypsiprymnodontidae*); in total two species (representing 29% of muridoid diprotodonts). Other muridoid diprotodonts are arboreal. Among non-muridoid diprotodonts there are highly-specialized terrestrial forms, such as kangaroos.

In the family *Burramyidae* (pygmy possums), only one species leads a predominantly terrestrial way of life: the mountain pygmy possum (*Burramys parvus*; fig. 5:3), which is found in Southeast Australia.

The mountain pygmy possum lives in the alpine and subalpine zone of mountains among boulder fields and screes, overgrown with herbaceous vegetation and trees. In summer, its diet consists mainly of arthropods; in the cold period it eats seeds and berries. It also feeds on nectar and pollen.

Externally, the mountain pygmy possum resembles a mouse. Its head and body length is 10–12 cm while its weight is 30–82 g. The weight of the animal fluctuates significantly between seasons due to the accumulation of fat for the winter. The fur is soft and dense, with brownish-grey coloration above and lighter underparts. The animal has a face mask: dark spots around the eyes, which extend towards the nose.

The muzzle is of medium length, conical, and less pointed than in muridoid dasyurids. The vibrissae are long. The eyes are of medium size, and the ears are relatively large. The tail is prehensile and long: about 120% of the head and body length. The number of digits is 5/5, but on the hind feet the 2nd and 3rd digits are fused. The hind feet are of medium length. The inner digit of the hind foot is opposable. The claws are short; the digital pads are quite large. The last premolars have the shape of a vertical plate with a sharp edge.

The mountain pygmy possum has a generalized body structure with no obvious special adaptations to a terrestrial way of life. In terms of body structure, it resembles its closest relatives – the scansorial pygmy possums of the genus *Cercartetus*. However, the forefeet and hind feet of the mountain pygmy possum are less specialized than those of other pygmy possums.

Ecological strategies of the mountain pygmy possum: terrestrial (subterranean-terrestrial), animalivore-frugivore (**ST/AnF**).

Ecomorph of the mountain pygmy possum: *normal-muzzled gliridoid muridoid*.

In the family *Hypsiprymnodontidae* the only member of the family, the musky rat-kangaroo (*Hypsiprymnodon moschatus*; fig. 5:5), has a mouse-like body structure and is predominantly terrestrial. A description of the family is given in Section 2.1.6.3.

A morphological adaptation to the terrestrial way of life may be the structure of the hind foot: its elongation, narrowness, flat plantar pads and weakly curved claws.

Ecological strategies of musky kangaroo: terrestrial (subterranean-arboreal-terrestrial) frugivore (**STAr/F**).

Ecomorph of musky rat-kangaroo: *normal-muzzled rattoid*. It differs from typical rattoids in having a somewhat elongated muzzle and in the structure of the hind foot.

4.5.1.6. Terrestrial muridoids among marsupials: summary

Among marsupials, muridoid body structure occurs in 173 species belonging to 35 genera, 8 families and 6 orders. Approximately half of the muridoid marsupials are terrestrial: 91 species (53%). These species belong to 23 genera, 6 families and 5 orders (*Didelphimorphia*, *Paucituberculata*, *Dasyuromorphia*, *Peramelemorphia*, and *Diprotodontia*). The remaining muridoid marsupials lead an arboreal way of life.

Terrestrial muridoid marsupials are widely distributed throughout the range of *Metatheria*, however, there are relatively fewer terrestrial species among New World compared with Australian marsupials (40% and 73%, respectively). This discrepancy may be explained by the greater aridity and lower forest cover of mainland Australia compared with the Neotropics.

Terrestrial muridoid marsupials inhabit various biotopes. They share many biotopes with arboreal species; however, in open habitats, especially in deserts and semi-deserts, marsupials are represented mainly or exclusively by terrestrial species. Still, there are no completely terrestrial species among muridoid marsupials – they all use subterranean, and sometimes also arboreal, shelters. Many species of terrestrial muridoid marsupials climb well and occasionally forage on trees, shrubs or grasses.

Most terrestrial muridoid marsupials are predominantly animalivorous. They feed mainly on invertebrates, small vertebrates and fruit, but among them there are also omnivores (e.g. mouse bandicoots) and one predominantly frugivorous species: the musky kangaroo.

The head and body length and weight of terrestrial muridoid marsupials range from 5 cm and 4 g in some *Planigale* to 40 cm and 0.9 kg in the lutrine opossum (*Lutreolina crassicaudata*). The fur on the upperparts is various shades of brown and grey, up to almost black; the underparts are lighter, up to white. Some species have dark rings around the eyes or a dark "mask" extending from

the eyes to the nose (in *Chacodelphys*, *Lestodelphys*, *Metachirus*, *Thylamys*, some *Sminthopsis*, *Microperoryctes*, *Burramys*). *Metachirus* also have light "eyebrows". *Metachirus*, some *Thylamys* and *Sminthopsis* have a dark stripe on the forehead. Some species also have dark longitudinal stripes on the back: one in *Murexia rothschildi*, *Phascolosorex* and *Microperoryctes aplini*; and three in some *Monodelphis*, *Myoictis* and *Microperoryctes*. *Myoictis* has two light stripes between three dark stripes.

The muzzle is moderately long or long. In most species it is pointed, while in lutrine opossums (*Lutreolina*), the mountain possum (*Burramys parvus*), and musky kangaroo (*Hypsiprymnodon moschatus*) the muzzle has a blunt conical shape. The vibrissae vary from short to long. In most species the eyes are medium-sized or small, while those of *Sminthopsis* are relatively large. The ears are short, of medium length or long.

The relative length of the tail varies in terrestrial muridoid marsupials from about 60% in many species up to 130% in some *Thylamys*, *Metachirus nudicaudatus* and *Murexia habbema*. However, in most species, the tail is about the length of the head and body or shorter. All opossums and diprotodont terrestrial muridoids have a prehensile tail. The tails of shrew opossums, dasyurids and bandicoots do not have grasping ability. Some opossums (*Lestodelphys*, *Thylamys*), one caenolestid (*Rhyncholestes raphanurus*), and some desert dasyurids (*Dasykaluta rosamondae*, some *Pseudantechinus* and *Sminthopsis*) store fat deposits in the tail, causing the tail to change shape.

The hind feet are of medium length or somewhat elongated (especially in *Sminthopsis*). The brown four-eyed opossum (*Metachirus nudicaudatus*) also has elongated forearms and shanks. In opossums, caenolestids, and dasyurids, all limbs are pentadactyl (5/5). In bandicoots and diprotodonts, the hind feet are also morphologically pentadactyl, but the 2nd and 3rd digits are fused. In all opossums, the mountain pygmy possum and the musky kangaroo,

the inner digit of the hind foot (hallux) is well developed and to some extent opposable, while in terrestrial dasyurids, and especially in bandicoots, this digit is shortened. In bandicoots, the 2nd and 3rd digits of the forefoot are longer than others and are equipped with long, weakly curved claws.

Terrestrial muridoid marsupials have different sizes and different variants of body structure. Most of the variants and body size groups are also found among arboreal species. Moreover, terrestrial and arboreal species may belong to the same genus (e.g. *Antechinus*) and have a similar body form. At the same time, the morphology of the most specialized terrestrial forms may differ significantly from that of arboreal species.

Among muridoid marsupials, the following are most adapted to terrestrial locomotion: *Lutreolina*, *Metachirus*, *Monodelphis*, *Caenolestidae*, *Planigale*, *Sminthopsis* and *Microperoryctes*. What is remarkable about this list is that the species included in it are morphologically very different. Based on these species, it is impossible to derive a single "terrestrial type"; rather their morphological diversity clearly demonstrates the absence of such a type. The reason for this is that adaptation to the terrestrial way of life progresses in different directions.

What are the directions of terrestrial specialization? Among terrestrial muridoid marsupials, four directions may be distinguished: 1) adaptation to searching for large prey in burrows, hollows and other narrow refuges (*Lutreolina* – elongation of the body); 2) adaptation to fast running as a means of protection (*Metachirus* – lengthening of the forelimbs); 3) adaptation to foraging in plant litter and dense vegetation (*Monodelphis*, *Caenolestidae*, *Planigale*, *Microperoryctes* – elongation of the muzzle, reduction of the eyes, and lengthening of the forefeet claws); 4) adaptation to foraging in areas with sparse vegetation (*Sminthopsis* – enlargement of the eyes and ears, lengthening of the hind feet).

Of course, the appearance of a species is also influenced by its phylogenetic position. For example, terrestrial opossums have retained the climbing adaptations inherent in this taxon: a prehensile tail and an opposable hallux, while in muridoid bandicoots and diprotodont marsupials, the 2nd and 3rd digits are fused, like in all representatives of these orders.

Marsupials demonstrate another important point – adaptive evolution proceeds not only from a generalized structure to a specialized one, but also from one specialization to another. If the body structure of *Antechinus*, mouse bandicoots, and musky kangaroo is well suited to the role of the ancestral structure for more specialized related forms, then the terrestrial specialization of opossums and mountain pygmy possum is clearly secondary to arboreal.

Based on analysis of the structural features of terrestrial muridoid marsupials, it can be seen that, during the course of evolution, morphological features change more slowly than ecology and behaviour. Moreover, if an existing body structure is suitable for a new ecological niche, its transition to a new ecomorph may be very slow or may not occur at all.

Ecological strategies of terrestrial muridoid marsupials: terrestrial (subterranean-terrestrial, subterranean-arboreal-terrestrial, and arboreal-terrestrial: **ST, STAr, TAr**) animalivores (**An**), animalivores-frugivores (**AnF**) and frugivores (**F**).

Ecomorphs of terrestrial muridoid marsupials: 1) *sharp-muzzled rattoids* – 34 species: 14 opossums and 20 dasyurids; **2) *normal-muzzled rattoids*** – 1 species: musk kangaroo; **3) *sorexoids*** – 35 species: 19 opossums, 7 caenolestids, 5 dasyurids and 4 bandicoots; **4) *sharp-muzzled gerbilloid muridoids*** – up to 18 species: many or all muridoid *Sminthopsis*; **5) *lutreolinoids*** – 2 species: *Lutreolina*; **6) *normal-muzzled gliridoid muridoids*** – 1 species: mountain pygmy possum.

Terrestrial muridoid marsupials confirm the fact that one ecomorph can be represented in different taxa, regardless of their phylogenetic position.

4.5.2. Terrestrial muridoids among insectivores

Among the muridoid insectivores (*Eulipotyphla*), the overwhelming majority of species in all four families (hedgehogs, shrews, moles, and solenodons) are predominantly terrestrial.

4.5.2.1. Terrestrial muridoids among hedgehogs

In the family *Erinaceidae* (hedgehogs), all 26 species are terrestrial. Mouse-like body structure occurs in 3 species of gymnures (*Galericinae*): the moonrat (*Echinosorex gymnura*), the long-eared gymnure (*Hylomys megalotis*) and the shrew gymnure (*Neotetracus sinensis*). A description of the family is given in Section 2.2.1.

Muridoid gymnures are adapted to foraging in plant litter and soil, using their long snouts and forefeet claws. The moonrat is partly a wetland species, and can feed in shallow water. A morphological adaptation to terrestrial locomotion may be the lengthening of the hind foot in *Neotetracus*, which contributes to the lengthening of the jump.

Ecological strategies of muridoid gymnures: terrestrial (subterranean-terrestrial: **ST**) animalivores (**An**); possibly *Neotetracus* is animalivore-frugivore (**AnF**).

Ecomorph of muridoid gymnures: *sorexoids* – all 3 species.

4.5.2.2. Terrestrial muridoids among shrews

Approximately 377 species of shrews (*Soricidae*) have a mouse-like body structure. Of these, about 361 species (81%), belonging to 18 genera, are probably terrestrial. The remaining muridoid shrews either do not have a mouse-like body structure or lead a semi-aquatic way of life. Among non-muridoid shrews there are semi-aquatic, subterranean and terrestrial forms. Data on the ecology of many shrew

species are very scarce; therefore, some species considered here as terrestrial may actually be subterranean or arboreal.

Terrestrial muridoid shrews are widespread in Eurasia, North America and Africa. They are found in various habitats. Shrews are mainly active on the ground among dense vegetation, as well as in forest litter and belowground. Due to their small size, shrews are able to penetrate all kinds of cracks and holes. All species are capable of climbing. Shrews feed mainly on invertebrates, and rarely on small vertebrates. Plant food, such as seeds, are eaten to a lesser extent.

Shrews are small animals; most of them around the size of a mouse. The head and body length and weight of muridoid shrews, and of shrews in general, range from 4 cm and 2 g in the Etruscan shrew (*Suncus etruscus*) to 18 cm and 105 g in the Asian house shrew (*Suncus murinus*). Shrews have short, dense hair. The upperparts are greyish, brownish or black; the underparts are usually lighter, up to white.

Despite the diversity of species, the general body structure of terrestrial muridoid shrews is fairly uniform. They are characterized by a narrow and flat head, with a long, thin and mobile proboscis. The eyes are small. The ears usually do not protrude above the head. Many species have short ears, and if the ears are large, then they are directed backwards, not upwards. The tail is covered with short hair or scales, and with vibrissae in some species (e.g. white-toothed shrews, *Crocidura*). The relative length of the tail varies in different species from the minimum for muridoids up to 150% in *Suncus megalurus*. The number of digits is 5/5. All digits are equipped with claws. The length of the claws and the size of the plantar pads vary, but in most terrestrial muridoid shrews they are of medium size, as is the length of the hind feet.

The middle incisors of the upper jaw are enlarged and have two apices. Together with the large lower incisors directed forward, they form "tweezers" for catching prey. There are no zygomatic arches,

which makes the shrew's already narrow head even narrower, allowing it to penetrate narrow openings.

Among muridoid mammals, shrews have achieved the most perfect adaptation to living in dense vegetation and plant litter. Their small size, thin body and flat, narrow head allow them to penetrate the narrowest of cracks. Shrews can hide, move and feed inside plant litter without needing to dig. With such a way of life, good eyesight is unnecessary, while long fur and ears sticking out above the head would be a hindrance. Indeed, shrews have small eyes, velvety fur, and reduced or backward-directed ears. Versatile (muridoid) body design allows these small animals to overcome natural obstacles, whether it be a pit, a fallen tree or a puddle.

Some shrews breed above ground in dense vegetation; nevertheless, due to their foraging strategy, they cannot be considered completely terrestrial animals. Among terrestrial muridoid shrews there are fossorial (*Feroculus feroculus*, *Sorex mirabilis*, *S. unguiculatus*), scansorial (*Crocidura douceti*, *C. elongate*, some *Episoriculus*, *Suncus megalurus*) and wetland (e.g. *Crocidura stenocephala*) species.

Ecological strategies of terrestrial muridoid shrews: terrestrial (aquatic-subterranean-terrestrial, subterranean-terrestrial, and subterranean-arboreal-terrestrial: **AqST**, **ST**, **STAr**) animalivores (**An**), less often animalivores-frugivores (**AnF**).

Ecomorph of terrestrial muridoid shrews: *sorexoids* – 361 species.

4.5.2.3. Terrestrial muridoids among moles

The family *Talpidae* (moles or talpids) includes 7 muridoid species. All of them belong to the genus *Uropsilus* or shrew moles, and all are predominantly terrestrial. Among the non-muridoid talpids, species in the tribe *Urotrichini* are terrestrial. Other members of the family are subterranean or aquatic. A description of the family is given in Section 2.2.3.

In size and appearance, shrew moles are similar to shrews. In general, their body has a generalized muridoid structure without special adaptations to the terrestrial way of life.

Ecological strategies of muridoid moles: terrestrial (subterranean-terrestrial) animalivores (**ST/An**).

Ecomorph of muridoid moles: ***sorexoids*** – all 7 species.

4.5.2.4. Terrestrial muridoids among solenodons

There are 2 genera and 2 species in the family *Solenodontidae* (solenodons): the Cuban solenodon (*Atopogale cubana*) and the Hispaniolan solenodon (*Solenodon paradoxus*). Both species are predominantly terrestrial and have a muridoid body structure. A description of the family is given in Section 2.2.4.

Solenodons are the size of a very large rat. With the exception of the head and long claws of the forefeet, the body of solenodons has a generalized muridoid structure without any special adaptation to the terrestrial way of life.

Ecological strategies of solenodons: terrestrial (subterranean-terrestrial) animalivores (**ST/An**).

Ecomorph of solenodons: ***sorexoids*** **–** both species.

4.5.2.5. Terrestrial muridoids among insectivores: summary

Among insectivores (*Eulipotyphla*), 389 species belonging to 27 genera and to all 4 families have a muridoid body structure. The vast majority of species – up to 373 species (i.e., 96%) from 24 genera and all four families – lead a predominantly terrestrial way of life. The remaining muridoid insectivores are semi-aquatic (16 species). It is possible that some shrews lead an arboreal way of life, but there are no definite data on this.

Terrestrial muridoid shrews are widely distributed in Eurasia, North America and Africa, while other muridoid insectivores have more restricted distributions. Solenodons inhabit the Antilles, and muridoid hedgehogs and moles are found only in Southeast Asia.

Terrestrial muridoid insectivores occur in various habitats. Most are mainly active on the ground among dense vegetation, as well as in the forest floor, or belowground. For shelter, they use plant litter, burrows, cracks in rocks, and natural cavities under roots, stones and logs. Some species live near water bodies (e.g. the moonrat). All species are capable of climbing. They feed mainly on invertebrates; less often on small vertebrates. To a lesser extent, they consume plant foods: fruit, seeds and belowground plant parts.

The head and body length and weight of terrestrial muridoid insectivores range from 4 cm and 2 g in the Etruscan shrew to 46 cm and 2 kg in the moonrat, which corresponds to the smallest and largest values for the order as a whole. In most species, the fur is short, soft and dense; in the moonrat and solenodons, it is relatively long and stiff. They do not have spines. The coloration is mostly monochromatic greyish, brownish or black, with lighter underparts in most species, up to white. The solenodons and the moonrat are more variegated. The latter may have a dark "mask" on the head.

The muzzle is sharp, with a proboscis. The eyes are small. The ears do not usually protrude above the head. In many species, the ears are short, and when they are large, then they are directed backwards rather than upwards. The tail is long, but is in most species shorter than the head and body. The number of digits is 5/5. All digits have claws. In some species, the claws of the forefeet are enlarged (e.g. in the solenodons). In most species the hind feet are of medium size.

The general body structure of terrestrial muridoid insectivores is fairly uniform. All are characterized by a long, thin and mobile proboscis. The rest of the body has a generalized muridoid structure without special adaptations to the terrestrial way of life. Terrestrial muridoid insectivores are adapted to foraging in plant litter and the upper soil layer with the help of a mobile proboscis and claws of the forefeet. All species are capable of climbing. Among terrestrial

muridoid insectivores, there are fossorial, scansorial, and wetland species.

Ecological strategies of terrestrial muridoid insectivores: terrestrial (aquatic-subterranean-terrestrial, subterranean-terrestrial, and subterranean-arboreal-terrestrial: **AqST**, **ST**, **STAr**) animalivores (**An**), less often animalivores-frugivores (**AnF**).

Ecomorph of terrestrial muridoid insectivores: *sorexoids* – all 373 species.

4.5.3. Terrestrial muridoids among afrosoricids

Among the afrosoricids (*Afrosoricida*), 24 species belonging to 4 genera and 2 families have a mouse-like body structure. Among them, predominantly terrestrial species are found only in the family *Tenrecidae* (tenrecs); in total, about 20 species (83%) including *Geogale aurita*, both species of *Nesogale*, and about 17 species of *Microgale*. It is difficult to determine the exact number of terrestrial species due to a scarcity of information about their ecology. The remaining muridoid tenrecs are arboreal (part of *Microgale*). Among the non-muridoid tenrecs, most are also terrestrial, but some are semi-aquatic, subterranean or arboreal (respectively *Microgale mergulus*, *Oryzorictes* and *Echinops telfair*).

All terrestrial muridoid tenrecs are found only on the island of Madagascar. They live mainly in forests: both wet and dry forests. They forage mainly in the forest floor. Nests are built in or under fallen trees, under tree roots or stones. Obviously, they also use burrows, but they probably do not dig them themselves. They all appear to be capable of climbing. Terrestrial muridoid tenrecs feed mainly on invertebrates and, to a lesser extent, on small vertebrates (larger species). The large-eared tenrec (*Geogale aurita*) seems to be specialized in feeding on termites.

Terrestrial muridoid tenrecs are externally similar to shrews, but in contrast to the latter, there are no species with reduced ears among them. The head and body length is 4–14 cm, the weight is

2.5–49 g. The smallest species is the pygmy shrew tenrec (*Microgale parvula*); the largest species is Talazac's shrew tenrec (*Nesogale talazaci*; fig. 7:1). The pelage is short, soft and dense.

The muzzle is long, thin and pointed. In some, it has the appearance of a bare proboscis (e.g. in the naked-nosed shrew tenrec, *Microgale gymnorhyncha*). The eyes are very small, the ears are of various sizes, but in all species are normally developed (15–24% of the head and body length). The large-eared tenrec has the longest ears. Unlike shrews, many species have ears protruding above their heads. The tail is long or very long. The relative length of the tail varies from the minimum for muridoids in *Microgale brevicaudata* and *M. grandidieri* up to 135% in *M. pusilla*. The surface of the tail is covered with scales and sparse hairs. In Dobson's shrew tenrec (*Nesogale dobsoni*), the tail thickens from fat stores in the wet season before becoming thinner the dry season. The limbs are pentadactyl (5/5), and all digits have claws. Hind foot length varies from relatively short to relatively long (15–23%).

In the large-eared tenrec and the shrew-toothed shrew tenrec (*Microgale soricoides*) the first (middle) incisors are enlarged, similar to the incisors of shrews. In *M. gracilis* and *M. gymnorhyncha*, the teeth are somewhat reduced and sparse. The zygomatic arch is not closed, due to the absence of the zygomatic bone.

In general, the body of terrestrial muridoid tenrecs has a generalized muridoid structure without any special adaptation to the terrestrial way of life. In terms of their external morphology and habits, terrestrial muridoid tenrecs are similar to shrews, as well as to some small opossums and marsupial mice.

Ecological strategies of terrestrial muridoid tenrecs: terrestrial (subterranean-terrestrial and subterranean-arboreal-terrestrial: **ST**, **STAr**) animalivores (**An**).

Ecomorph of terrestrial muridoid tenrecs: *sorexoids* – all 20 species.

4.5.4. Terrestrial muridoids among rodents

Among rodents (*Rodentia*), terrestrial mouse-like species are represented in all 9 families which include muridoids: among murids (*Muridae*), cricetids (*Cricetidae*), nesomyids (*Nesomyidae*), birch mice (*Sminthidae*), jumping mice (*Zapodidae*), dormice (Gliridae), heteromyids (*Heteromyidae*), spiny rats (*Echimyidae*), and chinchilla rats (*Abrocomidae*).

4.5.4.1. Terrestrial muridoids among murids

Among murids (*Muridae*), 665 species belonging to 131 genera and three subfamilies (*Deomyinae*, *Gerbillinae* and *Murinae*) have a mouse-like body structure. All three subfamilies include terrestrial forms, while the *Deomyinae* and *Gerbillinae* consist exclusively of terrestrial species. Since the necessary data on the ecology of many murids are insufficient or entirely absent, their division into arboreal and terrestrial species based on the criterion adopted here (whether or not they regularly reproduce on plants) is difficult to apply and inevitably somewhat inaccurate. In the absence of certain data, it was necessary to rely on hypothetical assumptions from literary sources or on morphological similarity to closely-related and definitely terrestrial species.

In other words, terrestrial muridoid murids are those muridoid species that do not fall into the categories of semi-aquatic, subterranean or arboreal. There are 505 such species belonging to 92 genera. Taking into account the morphological features of poorly-studied species, the number may be somewhat less – 474 species. Consequently, from 71% to 76% of muridoid murids lead a predominantly terrestrial way of life. Species and genera of muridoid murids leading a different way of life are listed in the relevant sections. There are probably no muridoid murids that are completely terrestrial. All of them are capable of swimming, digging and climbing to some extent, and use these abilities in everyday activities.

Among non-muridoid murids, *Leimacomys buettneri*, *Lophiomys imhausi*, gerbils and bipedal rodents from the Australian genus *Notomys* are terrestrial; other non-muridoid murids are either arboreal (most) or semi-aquatic (*Hydromys*, *Crossomys*).

Terrestrial muridoid murids are widespread throughout the Eastern Hemisphere, including Australia, but synanthropic species (house mouse and brown rat) have been spread by humans around the world.

Terrestrial muridoid murids inhabit various biotopes: from deserts to forests. Many species live in anthropogenic landscapes and some, such as the house mouse and the brown rat, in human buildings. For shelter, they mainly use burrows and natural hollows under stones, tree roots and fallen trees. Many terrestrial muridoid murids forage not only on the ground, but also in water, in plant litter and soil, or in trees. Most species feed mainly on seeds, fruit, and insects, but there are also specialized animalivorous (e.g. *Rhynchomys*) and herbivorous (e.g. *Hyomys*) species.

Terrestrial muridoid murids do not differ in size from arboreal species. Among terrestrial muridoid murids, there are both very small species, for example, the African pygmy mouse (*Mus minutoides*), with a head and body length of about 5 cm and a weight of 5 g, and giants, such as the eastern white-eared giant rat (*Hyomys goliath*), which is 36 cm long and weighs 750 g. The pelage is of varying density, softness and length. Some species have spines or spine-like bristles on their backs (*Acomys*, *Halmaheramys*, *Komodomys*, *Tokudaia*, and some species of *Rattus*, *Maxomys* and *Tarsomys*). The fur is usually yellowish, brownish or greyish. Some species have light or dark spots or longitudinal stripes on the back.

Thus, some muridoid gerbils (*Tatera*, *Gerbillus*) and *Arvicanthis* have light "eyebrows" or light rings around the eyes. *Echiothrix* has a facial mask: a dark muzzle, from which dark stripes extend along the sides of the head, covering the eyes. Many terrestrial murids (especially African ones) have longitudinal stripes on their backs

and sides (*Apodemus agrarius*, *Chrotomys*, *Hybomys*, *Lemniscomys*, *Mallomys*, *Pelomys*, *Rhabdomys*). In most striped species, one dark stripe stretches along the centre of the back, but in *Chrotomys* and *Rhabdomys* the middle stripe is light and has a dark border. Some *Hybomys* have three dark stripes, while *Rhabdomys* have four dark stripes with light stripes between them. In most *Lemniscomys*, in addition to the central dorsal dark stripe, there are up to seven light stripes along the sides, which are partially intermittent, becoming rows of spots. It is noteworthy that most of the striped species are inhabitants of grassy thickets. The exceptions are some forest inhabitants: *Chrotomys*, *Hybomys* and *Mallomys aroaensis*.

In most species, the muzzle is blunt conical and of medium length. However, in some herbivorous species the muzzle is blunt (*Hyomys*, *Mallomys*, *Otomys*, *Parotomys*), and in many insectivorous and worm-eating species the muzzle is pointed (*Echiothrix*, *Hyorhynchomys*, *Melasmothrix*, *Paucidentomys*, *Rhynchomys*, *Soricomys*, *Tateomys*). In many sharp-muzzled murids, the muzzle is elongated. The eyes vary in size from small, such as those of *Rhynchomys*, to large, such as those of gerbils. The ears are short (e.g. *Hyomys*), medium length (in most) or long (e.g. *Deomys*).

The relative length of the tail varies from the minimum for muridoids, for example, in *Lophuromys* and *Otomys*, up to 140% of the head and body length in *Deomys ferrugineus*; however, in most species, the tail is shorter or roughly equal to head and body length. Among the terrestrial muridoid murids, there are probably no species that have a fully grasping tail, as seen in some arboreal forms. Nevertheless, even in the brown rat, the tail serves as a support when climbing. Some desert species (*Pachyuromys*, *Zyzomys*) accumulate fat reserves in the tail, which affects the shape of the tail.

The limbs of most species are of medium length for muridoids, but in some wetland species they are elongated (*Deomys*, *Malacomys*, *Colomys*). The number of functional digits in all murids is 4/5 (pollex reduced). The length of digits, their ratio and the size of

the plantar pads all vary. The outer digit of the hind foot is partially opposable in many species.

Most of terrestrial murids have 16 teeth: (I1/1, C0/0, P0/0, M3/3) × 2. Only a few species have fewer, due to the absence of some molars. Thus, the gerbil *Desmodilliscus braueri* has 14 teeth, and some Australian and Malayan animalivorous species have 12, 8 or 4 teeth. The edented Sulawesi rat, *Paucidentomys vermidax*, has fewest teeth – only 4 incisors.

A morphological adaptation to terrestrial locomotion may be the adaptation of limbs to rapid bounding gait in some species, for example, in gerbils. Good jumpers usually also have a long tail.

Terrestrial muridoids are the most diverse group of murids both in terms of the number of species, as well as in their morphology and ecology. On the basis of their predominant foraging strategy, terrestrial murids can be divided into several groups: 1) wetland species that forage on the coast or in shallow water (*Deomys*, *Colomys*, *Dasymys*, *Malacomys*, *Xeromys*, wild populations of the brown rat); 2) species rummage in plant litter or soil (*Echiothrix*, *Hyorhynchomys*, *Melasmothrix*, *Paucidentomys*, *Pseudohydromys*, *Rhynchomys*, *Soricomys*, *Tateomys*); 3) running species that primarily forage on the ground, such as gerbils, 4) climbing species that obtain part of their food in trees or herbaceous vegetation, and 5) generalists, that use several locomotor strategies.

Many "running", "climbing" and generalist muridoid murids are adapted to living among rocks and stones (petrophiles), including: part of *Acomys*, *Aethomys*, some *Apodemus*, *Micaelamys*, *Saxatilomys*, *Xenuromys*, *Zyzomys*. In addition, there are several inhabitants of herbaceous thickets (herbiphiles) among terrestrial muridoid murids, for example, various "grass mice" of the African savannahs, and inhabitants of arid regions with sparse vegetation (xerophiles), for example, gerbils.

The various ecological groups have typical locomorphs. Thus, among the wetland inhabitants there are high-legged species

(e.g. *Deomys*), vole-like species (*Dasymys*), and species that are somewhat similar to hydromyoid muridoids (e.g. Colomys). They are referred to here as deomyoids, arvicoloid muridoids, and colomyoids, respectively. Rummaging species have a long snout and small eyes, and some have velvety fur (sorexoids). Running species have long and narrow hind feet (gerbilloid muridoids). Climbing species have grasping feet (curved claws, long digits, and large plantar pads), often also large eyes, and a long tail (gliridoid muridoids). Finally, the least ecologically specialized forms have a generalized structure, that is, average values for most morphological characters (rattoids).

Within each locomorph, one to three trophomorphs can be distinguished. Rummaging murids (sorexoids) and some wetland species (deomyoids) are predominantly animalivorous, therefore, many have a long, pointed snout. Arvicoloid murids are blunt-muzzled, and gerbilloid muridoid murids are normal-muzzled, while among gliridoid and rattoid murids there are all three trophomorphs: normal-muzzled (which predominate), sharp-muzzled and blunt-muzzled.

The classification of ecomorphs of terrestrial muridoid murids presented here should be regarded as preliminary and approximate. For example, gliridoid muridoids and rattoids are far from homogeneous from an ecomorphological point of view. In addition, many of the species assigned here to these two ecomorphs are actually intermediate in terms of body structure. Nevertheless, the most typical representatives of various ecomorphs differ significantly from each other, and the presence of transitional forms rather confirms the reality of the existence of these ecomorphs. Indeed, it is impossible to transform from nothing to nothing. Unlike taxa, clearcut ecomorphs exist side by side with transitional forms.

Ecological strategies of terrestrial muridoid murids: terrestrial (aquatic-subterranean-terrestrial, subterranean-terrestrial, and subterranean-arboreal-terrestrial: **AqST**, **ST**, **STAr**) animalivores (**An**), frugivores (**F**, majority) and herbivores (**H**).

Ecomorphs of terrestrial muridoid murids. Most muridoid murids have rattoid or gliridoid body structure. The assignment of species to these ecomorphs is complicated by the abundance of intermediate forms and the scarcity of data on the key feature, the structure of the feet. For this reason, many assignments rely on an indirect and, unfortunately, ambiguous criterion: the length of the tail.

Among terrestrial muridoid murids a total of 7 ecomorphs may be identified. They are listed below in ascending order of rarity.

1) *Rattoids* – approximately 299 species: *Acomys* (21 species), part of *Apodemus* (4), part of terrestrial *Apomys* (8), *Archboldomys* (2), Arvicanthis (7), *Bandicota* (3), *Bullimus* (3), part of *Bunomys* (6), *Chrotomys* (5), *Crunomys* (4), *Desmomys* (2), *Diomys* (1), *Golunda* (1), *Hadromys* (2), *Halmaheramys* (1), *Hybomys* (6), *Hyomys* (2), *Komodomys* (1), *Lamottemys* (1), *Leggadina* (2), *Lemniscomys* (11), *Leporillus* (1), *Lophuromys* (34), part of *Mallomys* (3), *Mammelomys* (2), *Mastomys* (8), part of *Maxomys* (17), *Microhydromys* (2), *Millardia* (4), *Mirzamys* (2 An), *Mus* (41), *Mylomys* (2), *Nesokia bunnii*, *Papagomys* (1), *Paramelomys* (nine); *Pelomys* (5), *Pseudomys* (20), part of *Rattus* (about 37 species), *Rhabdomys* (5), part of terrestrial *Taeromys* (1), *Tarsomys* (2), *Tokudaia* (3), *Tonkinomys* (1), *Tryphomys* (1) *Uranomys* (1), *Xenuromys* (1), *Zelotomys* (2); **2) *gliridoid muridoids*** – approximately 96 species: *Abeomelomys* (1), *Aethomys* (9), part *Apodemus* (13 or fewer species), part of the terrestrial *Apomys* (9), *Berylmys* (4), *Brassomys* (1), part *Bunomys* (2), *Cremnomys* (2), *Eropeplus* (1), *Gracilimus* (1), *Heimyscus* (1), *Lenomys* (1), *Limnomys* (2), *Macruromys* (2), *Madromys* (1), part of *Maxomys* (1), *Micaelamys* (2), *Myomyscus* (4), *Nesoromys* (1), *Palawanomys* (1), *Paruromys* (1), part of *Rattus* (about 13 species), *Saxatilomys* (1), *Srilankamys* (1), *Sundamys* (4), part of terrestrial *Taeromys* (5), part of *Uromys* (7 species or less), *Stenocephalemys* (4), *Stochomys* (1); **3) *arvicoloid muridoids*** – 45 species: *Dasymys* (14), *Mastacomys* (1), *Otomys* (28), *Parotomys* (2); **4) *sorexoids*** – 28 species: *Echiothrix*

(2 species), *Hyorhynchomys* (1), *Melasmothrix* (1), *Paucidentomys* (1), *Paulamys* (1), *Pseudohydromys* (12), *Rhynchomys* (4), *Soricomys* (4), *Tateomys* (2); **5) *gerbilloid muridoids*** – 23 species: all muridoid gerbils (18 species), *Zyzomys* (5); **6) *deomyoids*** – 11 species: *Deomys* (1 species), *Leptomys* (5), *Malacomys* (3), *Paraleptomys* (2); **7) *colomyoids*** – 3 species: *Colomys goslingi*, *Xeromys myoides*, probably also *Parahydromys asper*.

Most terrestrial muridoid murids have a normal muzzle. Sorexoids and deomyoids are sharp-muzzled, while arvicoloid muridoids and some herbivorous rattoids (*Hyomys*, *Mallomys*) are blunt-muzzled.

4.5.4.2. Terrestrial muridoids among cricetids

Among cricetids (*Cricetidae*), 505 species belonging to 93 genera and all 5 subfamilies (*Cricetinae*, *Arvicolinae*, *Neotominae*, *Sigmodontinae*, *Tylomyinae*) have a mouse-like body structure. All five subfamilies include terrestrial forms. As in the case of murids, a scarcity of data on the ecology of many cricetids makes it difficult to divide them into terrestrial and arboreal forms based on the criterion adopted here (whether or not they regularly reproduce on plants). In the absence of certain data, it was necessary to rely on hypothetical assumptions from the literature or on morphological similarity to to closely related and definitely terrestrial species.

Among the muridoid hamsters (*Cricetinae*), both muridoid species – Gansu hamster (*Cansumys canus*) and the greater long-tailed hamster (*Tscherskia triton*) – apparently lead a predominantly terrestrial way of life. They are subterranean-terrestrial (**ST**) frugivorous (**F**) rattoids.

Among the muridoid voles (*Arvicolinae*), 13 species (62%), belonging to 6 genera, lead a predominantly terrestrial way of life: *Chionomys* (4 species), *Dinaromys* (1), muridoid *Eothenomys* (4), *Microtus longicaudus*), muridoid *Proedromys* (1) and *Volemys* (2). They are subterranean-terrestrial (**ST**) and

subterranean-arboreal-terrestrial (**STAr)** herbivorous (**H)** arvicoloid muridoids. Of these, *Chionomys* and *Dinaromys* are petrophiles.

Among the muridoid neotomyines (*Neotominae*), up to 109 species (78%), belonging to 10 genera, lead a predominantly terrestrial way of life: *Baiomys* (2 species), *Nelsonia* (2), part of *Neotoma* (19 out of 22 muridoid species), *Neotomodon* (1), *Onychomys* (3), possibly *Osgoodomys* (1), part of *Peromyscus* (54 or fewer of 58 muridoid species), *Podomys* (1), *Reithrodontomys* (24) and *Scotinomys* (2). They are terrestrial (subterranean-terrestrial, subterranean-arboreal-terrestrial, and arboreal-terrestrial: **ST**, **STAr**, **TAr)** animalivorous (**An)**, frugivorous (**F)** and herbivorous (**H)** gliridoid muridoids (78) and rattoids (31). Many are dendrophiles, while some species of *Neotoma* seem to be petrophiles.

Among the muridoid sigmodontines (*Sigmodontinae*), up to 244 species (71%), belonging to 50 genera, lead a predominantly terrestrial way of life: *Abrothrix* (10 species), *Aegialomys* (4), *Akodon* (38), muridoid *Andalgalomys* (1), *Andinomys* (1), *Auliscomys* (3), *Bibimys* (3), *Brucepattersonius* (3), *Calomys* (17), *Castoria* (1), *Chilomys* (2), *Chinchillula* (1), *Delomys* (3), *Deltamys* (2), muridoid *Eligmodontia* (4), *Eremoryzomys* (2), *Euneomys* (4), *Euryoryzomys* (6), *Handleyomys* (9), *Hylaemys* (7), *Juscelinomys* (2), *Lenoxus* (1), *Loxodontomys* (1), *Melanomys* (6), *Microakodontomys* (1), *Microryzomys* (2), muridoid *Neacomys* (9), *Necromys* (7), *Neomicroxus* (2), *Neotomys* (1), *Nephelomys* (13), *Nesoryzomys* (3), *Oreoryzomys* (1), *Oryzomys* (6), *Oxymycterus* (15), muridoid *Phyllotis* (17), *Podoxymys* (1), *Pseudoryzomys* (1), *Reithrodon* (3), *Salinomys* (1), *Scapteromys* (3), *Scolomys* (2), *Sigmodon* (14), *Sigmodontomys* (1), *Sooretamys* (1), *Tapecomys* (2), *Thalpomys* (2), *Thaptomys* (1), *Transandinomys* (2), *Zygodontomys* (2). They are terrestrial (subterranean-terrestrial, possibly completely terrestrial, subterranean-arboreal-terrestrial, and arboreal-terrestrial: **ST**, **T**, **STAr**, **TAr**), animalivores (**An)**, frugivores (**F)** and herbivores (**H)**.

Terrestrial muridoid sigmodontines include rattoids (183 species), gliridoid muridoids (37), sorexoids (18: *Brucepattersonius*, *Oxymycterus*) and gerbilloid muridoids (6: *Andalgalomys*, *Eligmodontia*, *Salinomys*). Many species of rattoid sigmodontines have a body structure intermediate between a rattoid on one hand and a gliridoid, gerbilloid (*Phyllotis*), sorexoid (*Juscelinomys*, *Podoxymys*) or arvicoloid (*Necromys*, *Sigmodon*) on the other. Most species of terrestrial muridoid sigmodontines are normal-muzzled, but animalivorous *Juscelinomys* and *Oxymycterus* are sharp-muzzled, while *Sigmodon* are rather blunt-muzzled. Terrestrial muridoid sigmodontines include hydrophiles (*Scapteromys*, *Oryzomys*), rummaging species (e.g. *Oxymycterus*), grassland dwellers (e.g. *Akodon*, *Sigmodon*), desert dwellers (e.g. *Salinomys*), petrophiles (e.g. *Euneomys*), and dendrophiles (many species).

Among the muridoid tylomyines (*Tylomyinae*), both species of the genus *Ototylomys* (22%) probably lead a predominantly terrestrial way of life. They are terrestrial (subterranean-arboreal-terrestrial: **STAr**) frugivorous (**F)** gliridoid muridoids, and dendrophiles.

Thus, among all muridoid cricetids, 370 species (73%) from 70 genera lead a predominantly terrestrial way of life. Other muridoid cricetids are semi-aquatic, subterranean, or arboreal.

Among non-muridoid cricetids, all hamsters, most voles, and some sigmodontines are terrestrial. The remaining non-muridoid cricetids are either semi-aquatic (e.g. muskrat), subterranean (e.g. mole voles), or arboreal (all non-muridoid *Neotominae* and *Tylomyinae*, many sigmodontines).

Terrestrial muridoid cricetids are found in North America (*Microtus longicaudus*, *Neotominae*), Central America (*Neotominae*, *Sigmodontinae*, *Tylomyinae*), and South America (*Sigmodontinae*), as well as in Palaearctic Eurasia (*Cricetinae*, *Arvicolinae*).

Terrestrial muridoid cricetids occur in a variety of habitats: from deserts to rainforests and from lowlands to alpine grasslands. They mainly shelter in burrows, cavities between stones or in nests built

on the ground. Especially large ground nests are built by woodrats (*Neotoma*). Some species are adapted to a life among rocks and stones (*Dinaromys*, *Chionomys*). Most species feed primarily on seeds, fruit, and insects, but there are also specialized animalivorous (e.g. *Oxymycterus*) and herbivorous species (e.g. voles).

Most terrestrial muridoid cricetids are about the size of mice or small rats. Nevertheless, among them there are both very small species, for example, *Baiomys taylori*, which has a head and body length of 5 cm and a weight of 6 g, and species the size of large rats, for example, *Neotoma magister*, which has a head and body length of 24 cm and a weight of 400 g. The pelage of most species is soft, but in some species is coarse, bristly or spiny (*Neacomys*, *Scolomys*). The colour of the fur is usually brownish, yellowish, greyish or blackish, with the underparts generally lighter. Some *Peromyscus* and *Reithrodontomys* have a dark stripe running down the centre of the back.

The muzzle, vibrissae, eyes and ears are of medium size in most species. Some animalivorous species have an elongated muzzle and small eyes (*Brucepattersonius*, *Juscelinomys*, *Oxymycterus*). Small eyes and ears (not protruding) are found in in voles (except petrophilous species) and some sigmodontines (*Delomys*, *Castoria*, *Podoxymys*). The ears are especially large in some highland and desert species (*Auliscomys*, *Chinchillula*, *Eligmodontia*).

The relative length of the tail varies from minimal for muridoids (in hamsters, voles, *Baiomys*, *Scotinomys*) to long (about 120% of the head and body length in *Eligmodontia*). However, in most species, the tail is shorter or approximately equal to the length of the head and body. The structure and relative length of the fore and hind feet vary. In some species, the hind feet are short (e.g. in hamsters); in others they are quite long (e.g. in *Eligmodontia*). However, in most species, the hind feet are of medium length, and are either adapted for movement on the ground, or have a versatile structure that allows animals to both run and climb. In fossorial and rummaging species, the forefoot claws are elongated.

As in the case of murids, another species-rich group of muridoids, terrestrial muridoid cricetids are distinguished not so much by their adaptations to the terrestrial way of life proper, but by an apparent manifestation of adaptive radiation in its initial stage. Among them there are 1) wetland species (*Scapteromys*, *Oryzomys*); 2) species that rummage in plant litter or in the soil (*Brucepattersonius*, *Juscelinomys*, *Oxymycterus*); 3) inhabitants of grassy thickets (*Sigmodon* and many others); 4) inhabitants of arid regions (e.g. *Salinomys*); 5) inhabitants of stones and rocks (*Chionomys*, *Dinaromys*, *Euneomys*); 6) climbing species that collect a significant part of their food in trees or other vegetation (many species) and 7) generalists (many species). Among the terrestrial muridoid cricetids there are animalivorous, frugivorous (most) and herbivorous species. Each of these ecological groups is characterized by certain ecomorphs. Ecomorphological diversity is greatest in sigmodontines, the most species-rich subfamily of cricetids.

Ecological strategies of terrestrial muridoid cricetids: terrestrial (aquatic-subterranean-terrestrial, subterranean-terrestrial, possibly completely terrestrial, subterranean-arboreal-terrestrial, and arboreal-terrestrial: **AqST**, **ST**, **T**, **STAr**, **TAr**) animalivores (**An**), frugivores (**F**, majority) and herbivores (**H**).

Ecomorphs of terrestrial muridoid cricetids. Most terrestrial muridoid cricetids have a rattoid or gliridoid body structure. As in the case of murids, the assignment of species to these ecomorphs is complicated by the abundance of intermediate forms and the scarcity of data on the key feature, the structure of feet. For this reason, many assignments rely on an indirect and, unfortunately, ambiguous criterion: the length of the tail.

Within terrestrial muridoid cricetids 5 ecomorphs have been identified: **1) *rattoids*** – approximately 214 species: all muridoid hamsters (2 species), part of neotomyines (31), part of sigmodontines (183); **2) *gliridoid muridoids*** – approximately 117 species: part of neotomyines (78), part of sigmodontines (37), tylomyines

(2: *Ototylomys*); **3) *sorexoids*** – 20 species: *Brucepattersonius* (3), *Juscelinomys* (2), *Oxymycterus* (15); **4) *arvicoloid muridoids*** – 13 species: all terrestrial muridoid voles; **5) *gerbilloid muridoids*** – 6 species: *Andalgalomys* (1), *Eligmodontia*, (4), *Salinomys* (1).

Species of *Reithrodontomys* are included here under gliridoid muridoids, though they are somewhat similar to the birch mice (*Sicista*) and should probably be considered as sicistoids.

Most of terrestrial muridoid cricetids are normal-muzzled, but animalivorous *Juscelinomys*, *Brucepattersonius* and *Oxymycterus* are sharp-muzzled, and all voles, and to some extent *Sigmodon*, are blunt-muzzled. In contrast to arboreal muridoid cricetids, terrestrial cricetids include animalivorous and rummaging species and rattoids predominate.

4.5.4.3. Terrestrial muridoids among nesomyids

Among nesomyids (*Nesomyidae*), 47 species belonging to 16 genera and five out of the six subfamilies have a mouse-like body structure (*Cricetomyinae*, *Delanymyinae*, *Dendromurinae*, *Nesomyinae*, *Petromyscinae*). Of these, representatives of 10 genera lead a predominantly terrestrial way of life: *Beamys* (2 species), *Brachyuromys* (2), *Cricetomys* (4), *Gymnuromys* (1), *Hypogeomys* (1), probably *Megadendromus* (1), *Nesomys* (2), *Petromyscus* (4), *Steatomys* (8), and *Voalavo* (2). In total, terrestrial are approximately 27 species, or 57% of all muridoid nesomyids. The remaining muridoid nesomyids lead an arboreal way of life. Among the non-muridoid nesomyids, all species are terrestrial except for the arboreal *Eliurus*.

Terrestrial muridoid nesomyids are found on the island of Madagascar (*Nesomyinae*) and in mainland Africa south of the Sahara Desert (other subfamilies). They inhabit deserts, semi-deserts, savannahs, bushes, swamps and forests. Rock mice (*Petromyscus*) live among rocks and stones. Terrestrial nesomyids mostly shelter in burrows, dense vegetation, and cavities between stones. They feed mainly on seeds, fruit and insects. Short-tailed rats (*Brachyuromys*)

are herbivorous, while the fat mouse *Steatomys opimus* feeds mainly on termites.

Terrestrial muridoid nesomyids are variable in size. They include both mouse-sized species (*Petromyscus*, *Steatomys*, *Voalavo*) and "giant rats" (*Cricetomys*, *Hypogeomys*). The smallest species, the tiny fat mouse (*Steatomys parvus*), has a head and body length of 5.5–8 cm and a weight of 8–15 g, while the largest species, the southern giant poached rat (*Cricetomys ansorgei*), reaches 41 cm and 2.8 kg. The fur has different structure. The upperparts are greyish, yellowish or reddish; the under part is lighter, up to white. *Megadendromus nikolausi* has a black stripe running along its back.

The muzzle, vibrissae, eyes and ears are in most of medium size. In *Brachyuromys* the vibrissae are shortened, and the muzzle is slightly shortened and blunt. In some species, the eyes are slightly reduced (*Beamys*, *Brachyuromys*, *Cricetomys*, *Gymnuromys*, *Voalavo*). *Hypogeomys* has large eyes and long ears.

The relative length of the tail varies from the minimum for muridoids in *Brachyuromys* and *Steatomys* up to 140% in *Voalavo*. In most species, the tail is shorter than the head and body, but it exceeds the head and body length in *Cricetomys*, *Gymnuromys*, *Petromyscus*, and *Voalavo*. In most species the feet have a generalized structure (in *Beamys*, *Cricetomys*, *Gymnuromys*, *Nesomys*, *Petromyscus*). *Hypogeomys antimena* has long hind feet with small plantar pads. Species of *Steatomys* have long and narrow forefoot claws. The claws are also elongated in *Brachyuromys*, but to a lesser extent and they are not narrowed. Based on photographic evidence from a live specimen, *Voalavo* has enlarged plantar pads.

Despite comprising a relatively small number of species, terrestrial muridoid nesomyids are morphologically and ecologically exceptionally diverse. Along with eurytopic species and dendrophiles, which are common among terrestrial muridoids, terrestrial muridoid nesomyids include inhabitants of grassy thickets (*Brachyuromys*), rocks (*Petromyscus*) and arid landscapes

(*Steatomys*), as well as animalivorous (*Steatomys opimus*), frugivorous (most commonly) and herbivorous species (*Brachyuromys*).

Most terrestrial muridoid nesomyids have a generalized muridoid body structure without special adaptations to the terrestrial way of life. However, along with ecomorphs common among muridoids, there are also some peculiar forms. Thus, fat mice (*Steatomys*), which at first glance seem to resemble long-tailed "hamsters", are, according the structure of the limbs, in fact, rather short-tailed "gerbils".

Even more unusual is the structure of the Malagasy giant rats (*Hypogeomys antimena*). Because of their long ears, long hind limbs, burrowing habits, and locomotion features, they are sometimes compared to rabbits. In fact, *Hypogeomys* are more similar in body structure to springhares (*Pedetes*, bipedal rodents) than rabbits. However, these rats are quite muridoid. The hind feet of *Hypogeomys* does not differ much in structure from those of the brown rat, but are relatively longer and larger. The same can be said about the tails of these two species: they are approximately the same relative length, but the tail of *Hypogeomys* is relatively thicker and therefore heavier. It serves as a balance when jumping and as a support when the rat sitting on its hind legs. It seems that this unique, originally rattoid species is at the very beginning of the path towards bipedal locomotion. Indeed brief instances of bipedal locomotion in *Hypogeomys* have been observed (Garbutt, 1999)

Ecological strategies of terrestrial muridoid nesomyids: terrestrial (subterranean-terrestrial, subterranean-arboreal-terrestrial, possibly arboreal-terrestrial: **ST**, **STAr**, **TAr**) animalivores (**An** – *Steatomys opimus*), frugivores (**F** – majority), frugivores-herbivores (**FH** – *Hypogeomys*) and herbivores (**H** – *Brachyuromys*).

Ecomorphs of terrestrial muridoid nesomyids. 1) *Rattoids* – 14 species: *Beamys*, *Cricetomys*, *Gymnuromys*, *Megadendromus*, *Nesomys*; **2) *gerbilloid muridoids* –** 8 species: *Steatomys*; **3) *gliridoid muridoids* –** 2 species: *Voalavo*; **4) *arvicoloid muridoids* –** 2 species: *Brachyuromys*; **5) *hypogeomyoids*** –1 species: *Hypogeomys antimena*.

Brachyuromys are blunt-muzzled; other species are normal-muzzled. The absence of sorexoid species among nesomyids is interesting and may reflect the abundance of shrews in mainland Africa and shrew-like tenrecs in Madagascar.

4.5.4.4. Terrestrial muridoids among the birch mice

The birch mice family (*Sminthidae*) includes a single genus, *Sicista*. All 14 species of birch mice have a mouse-like body structure. Although birch mice are excellent climbers and regularly use this ability, all of them are considered here as terrestrial animals, according to the adopted criterion (lack of regularly reproduction on woody or herbaceous vegetation).

A description of the family is given in Section 2.4.4.

The body structure of birch mice combines adaptations to climbing thin branches and jumping. Many climbing mammals are also good jumpers, for example squirrels. However, while jumping serves squirrels mainly to move among branches, birch mice jump on the ground. A sudden jump serves as a means of escape from predators (Fokin, 1978). The birch mice seem to be at the crossroads of two directions of adaptive evolution: adaptation to climbing and adaptation to rapid movement on the ground by jumping. While birch mice have not gone further in either direction, both of these mutually exclusive trends of specialization are pursued by other rodents, including the closest relatives of birch mice. Specialization in climbing with the preservation of the sicistoid body structure is found in nesomyids (*Dendromus* and others), while specialization of sicistoidal ancestors in the direction of fast running led to the appearance of jumping mice (*Zapodidae*) and jerboas (*Dipodidae*).

Ecological strategies of birch mice: terrestrial (subterranean-arboreal-terrestrial: **STAr**) animalivores-frugivores (**AnF**) and frugivores (**F**).

Ecomorph of birch mice: ***normal-muzzled sicistoids*** – all 14 species.

4.5.4.5. Terrestrial muridoids among jumping mice

In the family *Zapodidae* (jumping mice), all 5 species have a mouse-like appearance, and all are terrestrial: *Eozapus setchuanus*, *Napaeozapus insignis* (fig. 9:2) and *Zapus* (3 species).

A description of the family is given in Section 2.4.5.

In body shape, jumping mice occupy an intermediate position between birch mice and jerboas. They are quite mouse-like, but their tail and hind limbs are even longer than those of birch mice. Jumping mice are better adapted than birch mice to living on the ground. Long sudden jumps as a means of escape from predators have been perfected by these rodents. Judging by the structure of the limbs, this is to the detriment of the ability to climb.

Birch mice, jumping mice and jerboas fit surprisingly well along a single ecomorphological line. This line clearly demonstrates how such unusual animals as jerboas could appear from a mouse-like body structure, which is very common among mammals. Moreover, this line is formed by related species, therefore it reveals, if not the phylogeny, then at least adaptive evolution within the superfamily *Dipodoidea*.

Ecological strategies of jumping mice: terrestrial (subterranean-terrestrial) frugivores (**ST/F**).

Ecomorph of jumping mice: *normal-muzzled gerbilloid muridoids* – all 5 species. The assignment of jumping mice to gerbilloid muridoids is debatable. Actually, they bear little resemblance to specialized gerbils, in both appearance and way of life. However, an evolutionary shift in the structure of the hind feet (in comparison with the hind feet of birch mice) brings them morphologically closer to gerbils and even more so to jerboas.

4.5.4.6. Terrestrial muridoids among dormice

In the family *Gliridae* (dormice), 4 species belonging to 2 genera (*Myomimus* and *Selevinia*) have a mouse-like body structure. Although all of them climb well, 3 species (75%) lead a predominantly terrestrial

way of life: the masked mouse-tailed dormouse (*Myomimus personatus*), Setzer's mouse-tailed dormouse (*M. setzeri*), and the desert dormouse (*Selevinia betpakdalaensis*). A fourth muridoid species, *Myomimus roachi*, and most non-muridoid dormice are predominantly arboreal.

Terrestrial muridoid dormice are found in south-western and Central Asia: from eastern Turkey to eastern Kazakhstan. They are found in deserts (desert dormouse), stony semi-deserts, steppes and dry forests. These rodents shelter in burrows, under stones, and under the roots of shrubs. They feed on invertebrates, small vertebrates, and apparently also on fruit and seeds. The desert dormouse is predominantly insectivorous.

Terrestrial muridoid dormice are the size of a mouse. The head and body length is 73–95 mm and the weight is 11–21 g. The fur is soft and coloured grey or reddish brown on the back and sides (in *M. setzeri*) and cream, light grey or white on the underparts. In mouse-tailed dormice, a diffuse, dark stripe runs along the back, and there are indistinct dark rings around the eyes and a dark spot on the upper lip. Both the stripe and the mask may be missing.

The muzzle is of medium length, and the vibrissae are long. The eyes and ears are of medium size. The tail is long, but shorter than the head and body length (about 76–90%). The number of digits is 4/5. The relative length of the hind foot is 17–21%, which means that the hind feet are not elongated or only slightly elongated. The plantar pads of the hind feet and forefeet are of medium size. The desert dormouse has straightened claws.

It can be assumed that the body structure of terrestrial dormice corresponds to the initial stage in the adaptive evolution of *Gliridae*. Terrestrial dormice retained the original structure due to living in arid habitats, where adptation to arboreal locomotion was not favoured.

Ecological strategies of terrestrial muridoid dormice: terrestrial (subterranean-arboreal-terrestrial: **STAr**) animalivores (**An,**

desert dormouse) and animalivores-frugivores (**AnF,** mouse-tailed dormice). *Myomimus personatus* are petrophile.

Ecomorph of terrestrial muridoid dormice: *normal-muzzled gliridoid muridoids* – all 3 species.

4.5.4.7. Terrestrial muridoids among heteromyids

In the family *Heteromyidae* (heteromyids), 26 species belonging to 3 genera have a mouse-like body structure, of which all are predominantly terrestrial: *Heteromys* (spiny pocket mice, all 16 species), *Perognathus* (silky pocket mice, 9 species) and *Chaetodipus hispidus* (hispid pocket mouse). All non-muridoid members of the family are also terrestrial.

A description of the family is given in Section 2.4.7.

Even among the least specialized muridoid heteromyids, the hind feet are clearly adapted for rapid hopping on the ground. This is indicated by the elongated tarsal part, shortened extreme (1st and 5th) digits, small plantar pads, and straightened claws.

Heteromyids constitute a clear ecomorphological line leading from the least specialized rat-like *Heteromys* towards bipedal forms. Moreover, this family provides an amazing example of parallelism with other rodents, especially jerboas (*Dipodoidea*). Thus, *Heteromys* externally resemble jumping mice (*Zapodidae*), *Perognathus* and *Chaetodipus* resemble gerbils, while partly bipedal *Dipodomys* and *Microdipodops* resemble jerboas. However, recent jerboas do not have a "gerbil" stage, and heteromyids do not have a "birch mouse" stage.

Ecological strategies of muridoid heteromyids: terrestrial (subterranean-terrestrial) frugivores (**ST/F**).

Ecomorph of muridoid heteromyids: *normal-muzzled gerbilloid muridoids* – all 26 species.

4.5.4.8. Terrestrial muridoids among spiny rats

In the family *Echimyidae* (spiny rats, or echimyids), 66 species belonging to 17 genera have a mouse-like body structure. Of these, representatives of 6 genera lead a predominantly terrestrial

way of life: *Carterodon sulcidens*, *Hoplomys gymnurus*, muridoid *Mesocapromys* (3 species), *Proechimys* (22), part of *Thrichomys* (3), muridoid *Trinomys* (7). In total, 37 species or 56% of all muridoid echimyids are terrestrial. The remaining muridoid spiny rats lead an arboreal way of life. Among the non-muridoid echimyids, some hutias (*Geocapromys*), as well as *Clyomys*, *Euryzygomatomys*, and *Trinomys* are predominantly terrestrial.

Muridoid hutias (*Capromyinae*) occur only on the island of Cuba. The remaining terrestrial muridoid echimyids are found in various parts of tropical Central and South America. They inhabit forests and savannahs of various types but avoid highlands and deserts. They shelter mainly among dense vegetation, between stones or in burrows. The most fossorial species is *Carterodon sulcidens*. Most echimyids are frugivorous, feeding mainly on fruit, seeds, and insects. Hutias and *Carterodon sulcidens* are predominantly herbivorous.

Terrestrial muridoid spiny rats are fairly uniform in size. Most or all of them can be categorized as medium and large rats. The largest species is possibly the armoured rat (*Hoplomys gymnurus*), which reaches a length of 32 cm and a weight of 0.8 kg; however, some eared hutias (*Mesocapromys auritus*) may be heavier. The head and body length of 49.3 cm indicated in the literature for *Proechimys steerei* is almost certainly an error; the value is far more likely to correspond to the total length of the animal, including the tail.

The pelage of most terrestrial muridoid echimyids is spiny or bristly. The exceptions are the hutias (*Mesocapromys*) and punare (*Thrichomys*). The spiny cover is most developed in the armoured rat (*Hoplomys gymnurus*). The coloration of the upperparts is reddish, greyish or blackish; the underparts are lighter: greyish, yellowish or white. In *Thrichomys*, the eyes are framed by a light border.

The muzzle is of medium length. In herbivorous species it is blunt. The eyes and ears are normally developed, but in hutias

the eyes are relatively small. The tail of all species is shorter than the head and body. Its relative length varies from 50% of the head and body length in fossorial *Carterodon sulcidens* to about 90% in *Thrichomys* and *Trinomys*. Hutias have a prehensile tail. The number of functional digits is 4/5. The structure of the feet is variable. In most species (*Hoplomys*, *Proechimys*, *Trinomys*) the forefeet and hind feet have a versatile structure that allows them both to move on the ground and climb well. They have medium length digits and claws, medium bulged plantar pads and medium length hind foot. However, in *Trinomys* the hind feet are rather narrow. In *Carterodon*, the limbs are adapted to digging and have elongated claws. Species of *Mesocapromys* have soles characteristic of all hutias: granulated, with flat pads. The outer digit of the hind foot is not shortened, while the claws are weakly curved and strong.

Most terrestrial muridoid echimyids have a generalized "rattoid" body structure (*Hoplomys*, *Thrichomys*, *Trinomys*, *Proechimys*). At the same time, rattoid echimyids are quite diverse in their ecological preferences. They are found in a variety of habitats, from wet forests to dry savannahs. Particularly different from other terrestrial muridoid echimyids, both morphologically and ecologically, are the vole-like *Carterodon sulcidens* and hutias. The latter have a body structure that is especially unusual for muridoids, but has much in common with New World porcupines (*Erethizontidae*). Thus, for example, the feet of hutias are surprisingly similar in shape and structural details to the feet of New World porcupines, for example, *Erethison dorsatum*.

The terrestrial muridoid echimyids include petrophiles (e.g. *Thrichomys fosteri*) and dendrophiles (e.g. hutias), and possibly also wetland species (e.g. *Trinomys setosus*). At the same time there are no completely terrestrial species or unique adaptations to terrestrial locomotion that would distinguish terrestrial muridoid echimyids from other members of the family. Nevertheless, certain features are more prevalent among terrestrial species. Thus, terrestrial

muridoid echimyids differ from arboreal ones in the predominance of 1) smaller forms, 2) species with a generalized body structure (rattoids), 3) species with a spiny cover, and 4) frugivorous species. Moreover, all terrestrial echimyids have a tail that is shorter than the head and body.

Ecological strategies of terrestrial muridoid echimyids: terrestrial (probably aquatic-subterranean-terrestrial, subterranean-terrestrial, subterranean-arboreal-terrestrial, and arboreal-terrestrial: **AqST**, **ST**, **STAr**, **TAr**) frugivores (**F,** most) and herbivores (**H,** *Carterodon*, *Mesocapromys*).

Ecomorphs of terrestrial muridoid echimyids: 1) *rattoids* – 33 species: *Hoplomys*, *Thrichomys*, *Trinomys*, *Proechimys*; **2) *capromyoids*** – 3 species: *Mesocapromys*; **3) *arvicoloid muridoids*** – *Carterodon sulcidens*. *Carterodon* and *Mesocapromys* are blunt-muzzled, the rest are normal-muzzled.

4.5.4.9. Terrestrial muridoids among chinchilla rats

In the family *Abrocomidae* (chinchilla rats or abrocomids), 9 species belonging to both genera (*Abrocoma* and *Cuscomys*) have a mouse-like body structure. A predominantly terrestrial way of life is led by 7 muridoid species of the genus *Abrocoma* (78% of all muridoid abrocomids), and probably also the only non-muridoid species of the family, *Abrocoma bolivensis*. Judging by their morphology, species of *Cuscomys* are rather arboreal.

Chinchilla rats (*Abocoma*) inhabit the western, Andean part of South America: in southern Peru, Bolivia, Chile and Argentina. All species except Bennett's chinchilla rat (*Abrocoma bennettii*), which occurs both on the plains and in the mountains, are only found at altitudes above 1800 m. Chinchilla rats inhabit dense shrubs and herbaceous vegetation, often among rocks. In the mountains, they are found up to elevations of 5000 m above the sea level. They are also found in arid regions. Terrestrial chinchilla rats are mainly active on the ground, but also climb trees and shrubs in search

of food. They shelter in hollows between stones, rock crevices and burrows dug by themselves or other animals. They feed mainly on the vegetative parts of plants.

Chinchilla rats are the size of medium rats: the length of the head and body is 16–23 cm, and the weight is approximately 140–300 g. The largest species is *A. bennettii*. The pelage is silky with a thick undercoat. The upperparts are greyish or greyish-brown; the underparts are lighter.

Muridoid chinchilla rats have a blunt muzzle of medium length. The eyes are normally developed. The ears are large and rounded (12–16% of the head and body length), and the vibrissae are long. The tail is covered with dense, short hairs. Its length in relation to the head and body varies between species, from 50 to 70%. The number of digits is 4/5, and all digits, including the outer (5th) digit of the hind foot, are quite short. There are long, coarse hairs on the middle digits of the hind foot. The claws are small. The soles of the feet are granulated, with large, relatively flat pads. The hind foot is short or medium in length (15–18%). The incisors are narrow. The molars grow constantly and have a high crown with a flat and ridged chewing surface.

All chinchilla rats seem to be petrophilous to some extent, and some species, for example, *A. vaccarum*, are especially dependent on rocky and stony habitat. L. Emmons (1999) compares chinchilla rats in an ecological sense to pikas, degus, chinchillas and other inhabitants of rocky and open areas. From the ecomorphological perspective, they have a rattoid body structure, albeit somewhat atypical.

Ecological strategies of muridoid chinchilla rats: terrestrial (subterranean-terrestrial and subterranean-arboreal-terrestrial: **ST**, **STAr**) herbivores (**H**).

Ecomorph of muridoid chinchilla rats: *blunt-muzzled rattoids* – all 7 species. Attribution to the blunt-muzzled category is

somewhat arbitrary, since the muzzles of chinchilla rats are, in fact, intermediate between normal and blunt.

4.5.4.10. Terrestrial muridoids among rodents: summary

Among rodents, muridoid body structure occurs in 1341 species belonging to 268 genera and 9 families (*Muridae*, *Cricetidae*, *Nesomyidae*, *Sminthidae*, *Zapodidae*, *Gliridae*, *Heteromyidae*, *Echimyidae* and *Abrocomidae*). Among these, 994 species (74%) from all families and 188 genera are predominantly terrestrial. The remaining muridoid rodents lead an aquatic, subterranean or arboreal way of life.

Terrestrial muridoid rodents are found throughout the world, including Australia and Madagascar. On different continents, they are represented by different families: in Eurasia, mainly by murids and birch mice; in mainland Africa, by murids and nesomyids; in Madagascar exclusively by nesomyids; in Australia, exclusively by murids; and in the New World mainly by heteromyids, echimyids, and endemic subfamilies of cricetids.

Terrestrial muridoid rodents inhabit various biomes: from deserts to rainforests and from lowlands to alpine meadows. Many species live in anthropogenic landscapes, some in human constructions. Their shelters are mainly burrows and natural hollows in the soil, under stones, tree roots, and fallen trees. Some species build nests on the ground in dense herbaceous vegetation or at the base of a bush or tree (e.g. *Neotoma*). Others are adapted to living among rocks and stones (e.g. *Petromyscus*).

Many terrestrial muridoid rodents forage not only on the ground, but also in water, plant litter, underground or in trees. Apparently, all are capable of swimming, digging and climbing to varying degrees, but different species have their own locomotive preferences and abilities. In this respect, there are hydrophilous (wetland inhabitants), geophilous (fossorial), petrophilous,

herbiphilous (grass-dwelling) and dendrophilous species, along with locomotor generalists, within terrestrial muridoid rodents.

Most terrestrial muridoid rodents feed mainly on seeds, fruit, and insects, but there are also specialized animalivorous and herbivorous species. Animalivores feed on various invertebrates and small vertebrates. Some of the animalivores are specialized in catching and eating particular kinds of animals, such as aquatic organisms, worms or specific insects, such as termites. Animalivorous terrestrial muridoid rodents are found in four families (*Muridae*, *Cricetidae*, *Nesomyidae*, *Gliridae*) and on different continents. Herbivorous terrestrial muridoids are found in five rodent families (*Muridae*, *Cricetidae*, *Nesomyidae*, *Echimyidae* and *Abrocomidae*) and on different continents. Nevertheless, both animalivorous and herbivorous species of terrestrial muridoid rodents are few and sporadically distributed.

Among terrestrial muridoid rodents, there are both very small species, for example, the pygmy mouse (*Mus minutoides*), with a head and body length of approximately 5 cm and a weight of 5 g, and "giants", such as the southern giant poached rat (*Cricetomys ansorgei*), with a head and body length of up to 41 cm and a weight up to 2.8 kg. They have fur of varying density, softness and length. Some species have spines or spine-like bristles on their backs (some *Muridae*, *Cricetidae*, *Heteromyidae*, *Echimyidae*). The fur of many is coloured yellowish, reddish or greyish. The colour of the upperparts varies, depending on the species, from light to almost black; the underparts are lighter, up to white. Some species have light or dark spots or longitudinal stripes on the back.

Some terrestrial muridoid murids (*Arvicanthis*, *Tatera*, *Gerbillus*), New World cricetids (*Sigmodon*), and echimyids (*Thrichomys*) have pale "eyebrows" or light rings around the eyes. A dark facial mask is found in *Echiothrix* (*Muridae*) and the mouse-tailed dormice (*Myomimus*). Terrestrial muridoid rodents often have dark or light longitudinal stripes on their backs. Usually this consists

of one dark stripe, some species have alternating dark and light strips. Sometimes the stripes consist of individual spots. The following rodents have stripes on the back: murids (*Apodemus agrarius*, *Chrotomys*, *Hybomys*, *Lemniscomys*, *Mallomys*, *Pelomys*, *Rhabdomys*), cricetids (some *Peromyscus* and *Reithrodontomys*), nesomyids (*Megadendromus*), birch mice (*Sicista*) jumping mice (*Napaeozapus*, *Zapus*) and mouse-tailed dormice (*Myomimus*). It is noteworthy that most of the striped species are inhabitants of thick herbaceous vegetation.

The muzzle of most terrestrial muridoid rodents has a blunt conical shape and is of medium length. However, in many animalivorous murids and New World cricetids, the muzzle is pointed, and often elongated. A blunt muzzle is characteristic of herbivorous rodents. Such a muzzle is found in some murids, cricetids, nesomyids (*Brachyuromys*) and echimyids. The vibrissae, eyes and ears of most species are of medium size. The sizes of these organs are usually correlated with each other. Thus, in burrowing species, the vibrissae and ears are usually short and the eyes small (e.g. in voles); by contrast, in petrophilous, dendrophilous and xerophilous species, they are usually enlarged (e.g. in gerbils). However, large eyes are rare in terrestrial muridoid rodents. Relatively small eyes are characteristic of fossorial species and, due to allometry, also of very large muridoids, such as hutias.

The relative length of the tail of terrestrial muridoid rodents varies from the minimum for muridoids to 160% of the head and body length in birch mice and jumping mice; but in most species the tail is shorter than or approximately equal to the head and body length. The longest-tailed species are adapted to making long jumps. In many species, the tail has a degree of grasping ability, which is especially developed, for example, in birch mice and hutias. Yet, the tails of terrestrial species do not have the morphological grasping adaptations exhibited by some arboreal muridoid rodents such as *Pogonomys*. In some species, the tail is densely covered with

short hairs (e.g. in abrocomids). Some desert species (*Pachyuromys*, *Zyzomys*) accumulate fat reserves in the tail, which affects the shape of the tail.

The structure and relative length of the hind feet vary. In some species, the hind feet are short (e.g. in hamsters); in others they are long, especially in jumping mice (32–35% of head and body length). However, in most species, the hind feet are of medium length, and are either adapted for movement on the ground, or have a versatile structure that allows animals both to run and climb. In many species, the claws of the forefeet are straightened, and in fossorial and rummaging species the claws are elongated (e.g. in *Steatomys*). The plantar pads in many species are small. The number of functional digits is 4/5. The outer digit of the hind foot in many species is partially opposable, but in others it is shortened. In some desert species, such as the silky pocket mice (*Perognathus*), the soles of the hind feet are covered with hair to facilitate movement on the sand.

Terrestrial muridoids are the most diverse group of muridoid rodents, both in terms of the number of species, as well as in body structure and ecology. They are distinguished not so much by their adaptations to the terrestrial way of life proper, but by a clear manifestation of an adaptive radiation in its initial stage. Among them there are 1) wetland inhabitants (among *Muridae* and *Cricetidae*); 2) rummaging species (among *Muridae* and *Cricetidae*); 3) inhabitants of herbaceous vegetation (among *Muridae*, *Cricetidae*, *Nesomyidae*, *Sminthidae*, *Zapodidae*); 4) inhabitants of arid regions (among *Muridae*, *Cricetidae*, *Heteromyidae*); 5) inhabitants of rocks and screes (among *Muridae*, *Cricetidae*, *Nesomyidae*, *Gliridae*, *Echimyidae*, *Abrocomidae*); 6) climbing species that collect a significant part of their food in trees or grass (in almost all families) and 7) ecological generalists that occupy various habitats (almost in all families). Among terrestrial muridoid rodents there are animalivorous, frugivorous (most) and herbivorous species. Different habitats are characterized by certain ecomorphs. At the

same time, representatives of different ecomorphs can occur in the same habitat.

Among terrestrial muridoid rodents, it is difficult to distinguish the animals best adapted to the terrestrial way of life. Formally, species sheltering in herbaceous vegetation can be classified as "completely terrestrial", but morphologically they differ little from their climbing or burrowing relatives. Much clearer adaptation to the terrestrial way of life is manifested in the speed of running. In fact, burrowing but fast-running gerbils are better adapted to terrestrial locomotion than thicket dwellers.

Fast runners include gerbils, some sigmodontines (*Andalgalomys*, *Eligmodontia*, *Salinomys*), all heteromyids, and possibly also New World jumping mice. All of these rodents have long specialized feet and a long tail, which serves as a balancer. Moreover, inhabitants of arid regions predominate among them. This is understandable: in arid areas animals have to cross bare land between patches of vegetation, which is dangerous and requires fast locomotion. Besides, finding food in such habitats requires extensive movement.

Ecological strategies of terrestrial muridoid rodents: terrestrial (aquatic-subterranean-terrestrial, subterranean-terrestrial, possibly completely terrestrial, subterranean-arboreal-terrestrial, and arboreal-terrestrial: **AqST**, **ST**, **T**, **STAr**, **TAr**) animalivores (**An**), animalivores-frugivores (**AnF**), frugivores (**F**, majority), frugivores-herbivores (**FH**) and herbivores (**H**). Thus, terrestrial muridoid rodents use all main terrestrial ecological strategies.

Ecomorphs of terrestrial muridoid rodents: 1) *rattoids* – 567 species (57% of terrestrial muridoid rodents in the families *Muridae*, *Cricetidae*, *Nesomyidae*, *Echimyidae*, *Abrocomidae*); **2) *gliridoid muridoids*** – 218 (22%: *Muridae*, *Cricetidae*, Nesomyidae, *Gliridae*); **3) *gerbilloid muridoids*** – 68 (7%: *Muridae*, *Cricetidae*, *Nesomyidae*, *Zapodidae*, *Heteromyidae*); **4) *arvicoloid muridoids*** – 61 (6%: *Muridae*, *Cricetidae*, *Nesomyidae*, *Echimyidae*); **5) *sorexoids*** – 48 (5%: *Muridae*, *Cricetidae*); **6) *sicistoids*** – 14 (1.4%:

Sminthidae); **7) *deomyoids*** – 11 (1.1%: *Muridae*); **8) *capromyoids*** – 3 (0.3%: *Echimyidae*); **9) *colomyoids*** – 3 (0.3%: *Muridae*); **10) *hypogeomyoids*** – 1 (0.1%: *Nesomyidae*).

Most terrestrial muridoid rodents are normal-muzzled. All sorexoids and deomyoids are sharp-muzzled (in total 59 species; 6%). All arvicoloid muridoids, all capromyoids and some herbivorous rattoids among murids, cricetids and abrocomids (*Hyomys*, *Mallomys*, *Sigmodon* and *Abrocoma*) are blunt-muzzled. In total, there are 91 species of blunt-muzzled, terrestrial muridoid rodents (9%).

Despite the abundance of ecomorphs, rattoids (57%) and gliridoid muridoids (22%) predominate among terrestrial muridoid rodents, though gerbilloid muridoids, arvicoloid muridoids, and sorexoids are as well common. There are also unique ecomorphs: deomyoids, colomyoids and hypogeomioids.

4.5.5. Terrestrial muridoids: summary

Mouse-like body structure occurs in 1927 species of mammals belonging to 334 genera, 23 families and 9 orders. A terrestrial way of life is led by representatives of all 9 orders, 20 families and 318 genera. In total, there are approximately 1478 species of terrestrial muridoid mammal, which represents 77% of all muridoids. The remaining muridoid mammals lead a semi-aquatic, subterranean or arboreal way of life.

Terrestrial muridoid mammals are found throughout the world. Their distribution coincides with the range of muridoids as a whole. Terrestrial muridoids inhabit various biomes: from deserts to rainforests and from lowlands to alpine meadows. Many species live in anthropogenic landscapes, some in human constructions. Their shelters are mainly burrows and natural hollows in the soil, under rocks, tree roots and fallen trees, as well as in dense vegetation and plant litter.

Many terrestrial muridoids forage not only on the ground, but also in water, plant litter and soil, or in trees. Apparently, all are

capable of swimming, digging, and climbing to varying degrees, but different species have their own locomotive preferences and abilities. In this respect, this ecological group of muridoids includes hydrophilous (wetland inhabitants), geophilous (burrowing), petrophilous, herbiphilous (grass dwellers) and dendrophilous species, along with locomotor generalists.

The majority of terrestrial muridoid marsupials, insectivores and tenrecs are predominantly animalivorous, while most terrestrial muridoid rodents are frugivorous; that is, they feed mainly on fruit, seeds, and insects. Among rodents, there are also specialized herbivorous species.

The head and body length and weight of terrestrial muridoids varies from 4 cm and 2 g in the Etruscan shrew (*Suncus etruscus*) to 46 cm in the moonrat (*Echinosorex gymnura*) and 2.8 kg in the poached rat (*Cricetomys ansorgei*). The fur is of varying density, softness and length. Some rodents have spines or spine-like bristles on their backs (some *Muridae*, *Cricetidae*, *Heteromyidae*, *Echimyidae*). The fur of many is coloured yellowish, reddish or greyish. The colour of the upperparts varies, depending on the species, from light to almost black; the underparts are lighter, up to white. Some species have light or dark spots or longitudinal stripes on the back.

Thus, dark rings around the eyes, and sometimes also spots on the muzzle (a "mask"), are found in some marsupials (opossums, dasyurids, bandicoots, mountain pygmy possum), insectivores (moonrat) and rodents (*Echiothrix*, *Myomimus*). The brown four-eyed opossum (*Metachirus nudicaudatus*) and some rodents have light "eyebrows" or light rings around the eyes (some *Muridae*, *Cricetidae*, *Echimyidae*). Much more common in terrestrial muridoids are longitudinal stripes on the back. One or three stripes are found in some opossums (*Monodelphis*), dasyurids (*Murexia*, *Myoictis*, *Phascolosorex*), bandicoots (*Microperoryctes*) and many rodents (in the families *Muridae*, *Cricetidae*, *Nesomyidae Sminthidae*, *Zapodidae* and *Gliridae*). The piebald shrew (*Diplomesodon pulchellus*) and

the Cuban solenodon (*Atopogale cubana*) have variegated colouration: white-grey and yellow-black, respectively.

The muzzle of terrestrial muridoids is of medium length or long. Elongation of the muzzle is achieved either through elongation of the bones of the muzzle or by development of the proboscis in insectivores. In most animalivorous species, the muzzle is pointed; in frugivorous species it is blunt conical; and in herbivorous species it is usually blunt. This is due to differences in the dentition, the structure of the skull, and the development of muscles in different trophomorphs. Nevertheless, some animalivorous muridoids, namely aquatic or carnivorous species, are normal-muzzled. The relative sizes of the vibrissae, eyes, and ears are usually (but not always) correlated with each other. Thus, in burrowing species, the vibrissae and ears can be short and the eyes small, while in petrophilous, dendrophilous and xerophilous species, they are enlarged (e.g., in gerbils). However, large eyes are rare among terrestrial muridoids. Fossorial species and, due to allometry, also very large muridoids such as hutias, have relatively small eyes. Interestingly, in some muridoids, a decrease in the protrusion of the ears above the head is achieved not by a reduction of the auricle, but by a change in its position from vertical to horizontal (e.g. in the white-toothed shrews, *Crocidura*).

The relative length of the tail of terrestrial mouse-like mammals varies from the minimum for muridoids to 160 % of the head and body length in birch mice and jumping mice, but in most species the tail is shorter or approximately equal to the head and body length. In many species, the tail has some degree of grasping ability, which is especially developed in some, opossums and diprotodont marsupials. Among opossums, caenolestids, dasyurids, tenrecs and rodents, there are species in which fat reserves are deposited in the tail. Many of these species live in arid regions. Some shrews have vibrissae on their tails (e.g. the white-toothed shrews).

The structure of the feet of terrestrial muridoid mammals bears the imprint of their origin; nevertheless, common features can also

be traced among unrelated taxa. The hind feet are the most variable, since they are propulsive in muridoids. In some species, the hind feet are short (e.g. in hamsters); in others they are long, especially in jumping mice (32–35% of head and body length). However, in most species, the hind feet are of medium length, and are either adapted for movement on the ground, or have versatile structure that allows animals both to run and climb. In some desert species, such as the silky pocket mice (*Perognathus*), the soles of the hind feet are covered with hair to facilitate movement on the sand.

In comparison with the hind feet, the structure of the forefeet is more uniform; however, the claws are most variable precisely on the digits of the forefeet. Terrestrial muridoids are characterized by straightened claws. In rummaging species, for example, in bandicoots and solenodons, the claws of the forefeet can be significantly elongated.

Among insectivores, tenrecs, and most muridoid marsupials, all limbs are pentadactyl (5/5). However, in bandicoots and diprotodonts, the hind feet are functionally four-toed due to the fusion of the 2nd and 3rd digits. All muridoid rodents have pentadactyl hind feet, while on the forefoot the inner digit is reduced to varying degrees, so they have 4/5 functional digits.

Among some terrestrial muridoids, one of the extreme digits of the hind foot is opposable. In marsupials, this is the hallux, the inner hind foot digit (in opossums, mountain pygmy possums, and musky kangaroos), while in rodents, it is the outer one. Yet, in many terrestrial species, the extreme digits are shortened and are not opposable. Terrestrial muridoids are characterized by flat plantar pads, while the size of pads is variable.

Terrestrial muridoid mammals have different sizes and body structures. This is partly due to the fact that adaptation to the terrestrial way of life goes in different directions, corresponding to the directions of adaptive radiation. Thus, among terrestrial muridoids there are 1) wetland species (among insectivores and

rodents); 2) species that rummage in search of food in the plant litter or in the soil (among marsupials, insectivores, tenrecs and rodents); 3) inhabitants of thick herbaceous vegetation (among marsupials, insectivores and rodents); 4) inhabitants of arid landscapes (among marsupials and rodents); 5) inhabitants of rocks and scree (among rodents); 6) climbing species that collect a significant part of their food in trees or grasses (among marsupials, insectivores and rodents) and 7) ecological generalists that live in multiple habitats. In addition, among the terrestrial muridoids there are animalivorous (in all orders), frugivorous (some marsupials and most rodents) and herbivorous species (some rodents). Different ecological groups are characterized by certain ecomorphs.

Adaptation to a terrestrial way of life is most clearly manifested in the speed of running. Fast runners are found among marsupials and rodents, especially among the inhabitants of arid regions. This is because, in arid areas, animals need to cross bare land between patches of vegetation, which is dangerous and requires fast locomotion. Fast runners usually have specialized long feet and a long tail for balance.

The most unusual among muridoids are the locomotor adaptations of the lutrine opossum (*Lutreolina*) and the brown four-eyed opossum (*Metachirus nudicaudatus*). In both, the forelimbs and hindlimbs are aligned in length; however, in *Lutreolina* this is due to the shortening of the hind limbs, while in *Metachirus* it is due to the lengthening of the forelimbs. The length alignment of the limbs may be associated with the beginning of a change in gait: from a four-legged ricochet to a gallop.

Ecological strategies of terrestrial muridoids. Terrestrial muridoids use all main terrestrial ecological strategies. Among them there are: aquatic-subterranean-terrestrial (**AqST**), subterranean-terrestrial (**ST**), subterranean-arboreal-terrestrial (**STAr**), arboreal-terrestrial (**TAr**), possibly also completely terrestrial (**T**)

animalivores (**An**), animalivores-frugivores (**AnF**), frugivores (**F**), frugivores-herbivores (**FH**) and herbivores (**H**).

Ecomorphs of terrestrial muridoids: 1) *rattoids* – 602 species (marsupials and rodents); **2) *sorexoids* –** 476 (marsupials, insectivores, tenrecs and rodents); **3) *gliridoid muridoids* –** 219 (marsupials and rodents); **4) *gerbilloid muridoids* –** 86 (marsupials and rodents); **5) *arvicoloid muridoids* –** 61 (rodents); **6) *sicistoids* –** 14 (rodents); **7) *deomyoids* –** 11 (rodents); **8) *capromyoids* –** 3 (rodents); **9) *colomyoids* –** 3 (rodents); **10) *lutreolinoids* –** 2 (marsupials); **11) *hypogeomyoids* –** 1 (rodent). The distribution of terrestrial muridoid species by ecomorphs is given in more detail in Table 7.

Among terrestrial muridoid mammals, all three trophomorphs are represented: sharp-muzzled, normal-muzzled, and blunt-muzzled. There are 539 species of sharp-muzzled terrestrial muridoids (36%), 848 (57%) normal-muzzled and 91 (6%) blunt-muzzled ones. However, it should be taken into account that trophomorphs are distributed extremely unevenly among taxa. Sharp-muzzled are predominantly marsupials, insectivores and tenrecs, normal-muzzled are predominantly rodents, and blunt-muzzled are found exclusively among rodents.

It can be seen from the data presented that rattoids and sorexoids predominate among terrestrial muridoids (together 73%), while gliridoid muridoids are also common (15%), and all other ecomorphs are rare. Unique to terrestrial muridoids are gerbilloid muridoids, deomyoids, colomyoids, hypogeomyoids, and lutreolinoids.

4.6. Arboreal muridoids

As with life in the water or underground, a life on plants, in particular trees, provides an alternative to a simple but dangerous existence on the ground. However, if even completely terrestrial mammals can walk in shallow water and use available subterranean shelters without needing to swim or dig, then climbing trees

Table 7. Distribution of terrestrial muridoid species by ecomorphs.
The number of sharp-muzzled/normal-muzzled/blunt-muzzled species is given in parentheses.

Ecomorph	Marsupials	Insectivores	Tenrecs	Rodents	Total species	%
Rattoids	35 (34/1/0)	–	–	567 (0/540/27)	602 (34/541/27)	41
Sorexoids	35 (35/0/0)	373 (373/0/0)	20 (20/0/0)	48 (48/0/0)	476 (476/0/0)	32
Gliridoid muridoids	1 (0/1/0)	–	–	218 (0/218/0)	219 (0/219/0)	15
Gerbilloid muridoids	18 (18/0/0)	–	–	68 (0/68/0)	86 (18/68/0)	6
Arvicoloid muridoids	–	–	–	61 (0/0/61)	61 (0/0/61)	4
Sicistoids	–	–	–	14 (0/14/0)	14 (0/14/0)	1
Deomyoids	–	–	–	11 (11/0/0)	11 (11/0/0)	< 1
Capromyoids	–	–	–	3 (0/0/3)	3 (0/0/3)	< 1
Colomyoids	–	–	–	3 (0/3/0)	3 (0/3/0)	< 1
Lutreolinoids	2 (0/2/0)	–	–	–	2 (0/2/0)	< 1
Hypogeomyoids	-	–	–	1 (0/1/0)	1 (0/1/0)	< 1
Total species	**91** (87/4/0)	**373** (373/0/0)	**20** (20/0/0)	**994** (59/844/91)	**1478** (539/848/91)	**100**

is impossible without specific adaptations. This is both the main challenge and the main advantage of living in trees: in a tree, an animal is out of reach of terrestrial predators that are incapable of climbing. And it is often possible to hide in small hollows or on thin branches to avoid climbing predators, which are usually larger than their potential prey.

Unlike subterranean or aquatic habitats, arboreal habitats provide the same basic food groups as terrestrial habitats: animal food, fruit, seeds and leaves. Nevertheless, the choice of food items, and importantly, the methods required to obtain them are different from the situation on the ground. Since trees, and especially bushes and herbaceous vegetation, are mainly inhabited by small animals, large predators do not have enough prey. Even some medium-sized arboreal carnivores have switched to frugivorous or herbivorous diets (palm civets, binturong, kinkajou, red panda). The feeding conditions in trees are highly favourable for frugivorous species. However, fruit availability is localised and seasonally variable, meaning that frugivorous animals need to be mobile and able to store food. Life in trees is also favourable for leaf-eating species, though searching for palatable leaves requires certain acrobatic abilities and bears little resemblance to grazing on the ground.

The relationship between mammals and plants as a substrate for locomotion and a source of food is variable. Three main strategies can be distinguished. **Arboreal-terrestrial** species (e.g. lynx) feed and shelter both on the ground and in trees (shrubs, herbs), but usually do not raise their offspring in trees. **Terrestrial-arboreal** species (e.g. the pine marten) feed, shelter and raise their offspring in trees, but also feed regularly on the ground. **Completely arboreal** species (such as the flying squirrel) feed, shelter and raise their offspring in trees, descending to the ground only occasionally, for example, to move to a neighbouring tree. Arboreal-terrestrial species are referred to here as terrestrial animals, while terrestrial-arboreal and completely arboreal species are referred to as arboreal.

Thus, **arboreal species** are considered here: 1) species, which ***usually*** **hide and raise offspring on upright plants,** 2) species, for which sheltering are unknown, but they are closest relatives (of the same or the closest genus) of the definitely arboreal species and are morphologically similar to them; and 3) species, which nesting places are unknown, but they definitely forage mostly on the plants. The last two categories are necessary due to the fact that among arboreal mammals there are many species with insufficiently studied or inadequately described ecology. Consequently, species that climb trees (shrubs, grasses) only occasionally, as well as those that arrange shelters in hollows of fallen trees or in stumps, are not considered here to be arboreal.

Arboreal muridoids are found in 7 orders of mammals: among opossums, microbiotheres, dasyuromorphs, diprotodont marsupials, insectivores, afrosoricids, and rodents. That is, in all orders where muridoids are found, with the exception of shrew opossums and bandicoots.

4.6.1. Arboreal muridoids among marsupials

Among marsupials, arboreal muridoids are found in 4 orders: opossums, microbiotheres, dasyuromorphs, and diprotodont marsupials.

4.6.1.1. Arboreal muridoids among opossums

In the order *Didelphimorphia* (opossums), 98 species have a mouse-like body structure. Of these, 63 species belonging to 10 genera lead an arboreal way of life: *Caluromys philander*, *Cryptonanus*, *Didelphis*, *Gracilinanus*, *Hyladelphys*, *Marmosa*, *Marmosops*, part of *Monodelphis* – 2 species (*adusta*, *americana*) or more, *Philander and Tlacuatzin*. Thus, approximately two thirds of muridoid opossums, and indeed of all opossums (64% and 65%, respectively), are arboreal. Almost all non-muridoid opossums also lead the arboreal way

of life (*Caluromys*, *Caluromysiops* and *Glironia*), with the exception of the water opossum.

Arboreal muridoid opossums are found in South, Central and North America, from Canada (Virginian opossum, *Didelphis virginiana*) to the province of Buenos Aires in Argentina (*D. albiventris*). Most species live in tropical South America.

Arboreal muridoid opossums inhabit forests and shrublands (representatives of all ten genera), savannahs (*Cryptonanus*, *Didelphis*, *Gracilinanus*, *Marmosa*, *Monodelphis*, *Tlacuatzin*), grasslands (*Cryptonanus*, *Didelphis*, *Monodelphis*), and marshes and wetlands (*Cryptonanus*, *Didelphis*, *Philander*). Thus, arboreal muridoid opossums are found in different habitats, but mostly in forest, shrubland and savannah. Grasslands are home to small species capable of climbing grass, as well as some large scansorial opossums with wide ecological niches.

Species of *Caluromys*, *Gracilinanus*, *Marmosa*, *and Tlacuatzin* are most highly reliant on trees. Some descend to the ground only to reach another tree, and may be considered completely arboreal (e.g. *Caluromys*). Most arboreal opossums do occasionally feed on terrestrial animals and fallen fruit. Probably least associated with trees are arboreal *Monodelphis*, which do not differ in general body structure from the predominantly terrestrial representatives of the genus.

Most of arboreal opossums are mainly animalivorous, but fruit also plays a significant role in their diet. Many species are omnivorous (animalivorous-frugivorous), but *Caluromys philander* is predominantly fruit eater. The presence of frugivorous forms distinguishes arboreal from terrestrial opossums.

Among arboreal muridoid opossums there are both large (*Caluromys philander*, *Didelphis*, *Philander*) and small species. The head and body length and weight vary from 7 cm and 10 g in small forms (*Hyladelphys*, some *Cryptonanus* and *Gracilinanus*) up to 50 cm and 5 kg in the Virginian opossum. In most species the

fur is soft. Common opossums (*Didelphis*) have long guide hairs protruding from their fur. The colour of the upperparts is usually greyish, yellowish, reddish or brown; the ventral part of the body is usually lighter. Many have dark spots around the eyes, which extend in some species to the muzzle (*Cryptonanus*, *Gracilinanus*, *Hyladelphys*, *Marmosa*, *Marmosops*, *Tlacuatzin*, also some *Didelphis* and *Philander*. In *Caluromys* and *Didelphis*, a dark stripe runs along the middle of the head. *Philander* species have a light spot above the eyes. One species – *Monodelphis americana* – has three longitudinal stripes on the back.

The muzzle is relatively long and pointed. The eyes of *Didelphis* are small, but in other species they are relatively large. The pinnae are of medium length or long (*Gracilinanus*, *Marmosops*, *Tlacuatzin*). The relative length of the tail in arboreal *Monodelphis* is 50–60%. In *Didelphis*, *Philander* and *Tlacuatzin*, the tail is approximately equal to the length of the head and body, and in all other arboreal opossums, the tail is much longer (120–180%). *Gracilinanus emiliae* has the longest tail. In all species, the tail is to some extent prehensile. The hind feet are of medium length, the inner digit of the hind foot is opposable.

Morphological adaptations to the arboreal way of life include a long and prehensile tail, as well as structural features of the feet. Comparison of small opossums, terrestrial *Monodelphis* and arboreal *Marmosa*, shows that the arboreal species (*Marmosa*) has wider hind feet, inner digits that are opposable at a greater angle, and much larger pads on the fore and hind feet.

Arboreal muridoid opossums can be divided into three groups based on their general body structure: generalized muridoids (*Didelphis*, *Philander*), shrew-like muridoids (*Monodelphis*) and specialized tree-climbers (*Caluromys*, *Cryptonanus*, *Gracilinanus*, *Hyladelphys*, *Marmosa*, *Marmosops*, *Tlacuatzin*). Representatives of the latter group are distinguished by a long tail, specialized grasping limbs, and, in many of them, by relatively large eyes and ears.

The first two morphotypes are also common among terrestrial opossums.

Arboreal muridoid opossums differ in the presence of specialized arboreal forms and greater frugivory.

Ecological strategies of arboreal muridoid opossums: arboreal (subterranean-terrestrial-arboreal, terrestrial-arboreal, and completely arboreal: **STAr**, **TAr**, **Ar**) animalivores (**An**), animalivores-frugivores (**AnF**) and frugivores (**F**).

Ecomorphs of arboreal muridoid opossums: 1) *sharp-muzzled gliridoid muridoids* – 48 species: *Caluromys*, *Cryptonanus*, *Gracilinanus*, *Hyladelphys*, *Marmosa*, *Marmosops*, *Tlacuatzin*; **2) *sharp-muzzled rattoids*** – 13 species: *Didelphis*, *Philander*; **3) *sorexoids*** – 2 species: part of *Monodelphis*.

4.6.1.2. Arboreal muridoids among microbiotheres

The only recent member of the order *Microbiotheria*, the monito del monte (*Dromiciops gliridoides*; fig. 4:3), has a mouse-like body structure and leads a predominantly arboreal way of life.

A description of the order is given in Section 2.1.3.

Morphological adaptations to the arboreal way of life include a long and prehensile tail, long digits, enlarged plantar pads, and opposing inner digits on the hind feet.

Ecological strategies of monito: arboreal (**Ar**) animalivore (**An**) or animalivore-frugivore (**AnF**).

Ecomorph of monito: *sharp-muzzled gliridoid muridoid*.

6.6.1.3. Arboreal muridoids among carnivorous marsupials

In the order *Dasyuromorphia* (carnivorous marsupials or dasyuromorphs) muridoid species are found in the family *Dasyuridae* (dasyurids). The arboreal way of life is led by 13 muridoid species belonging to two genera: most *Antechinus* (all but *arktos*, *minimus* and *swainsonii*) and part of *Murexia* (*longicaudata*, *melanurus*, possibly *naso*), which corresponds to 23% of muridoid dasyurids and

18% of all dasyurids. Among non-muridoid dasyurids, members of the genus *Phascogale* and some *Dasyurus* are arboreal.

Arboreal *Antechinus* are mainly found in Eastern Australia, though some species also occur in the northern, southern and south-eastern parts of the mainland. They are absent from Tasmania. Arboreal *Murexia* live on New Guinea and nearby islands. Thus, arboreal muridoid dasyurids are absent from the dry western and central parts of Australia.

All arboreal muridoid dasyurids inhabit various types of forest, but some species of *Antechinus* also live in scrublands and thick herbaceous vegetation. All are animalivores, feeding mainly on insects, other invertebrates, small vertebrates and, to a lesser extent, fruit. There are no completely arboreal species among the muridoid dasyurids.

The head and body length and weight vary from 7 cm and 18 g in some *Antechinus* to 27 cm and 134 g in *Murexia longicaudata*. The fur is short and dense. The colour of the upper parts is greyish or brownish; the underparts are lighter, up to cream or white. There are no stripes or spots. The muzzle is pointed, of medium size or long. The eyes are medium-sized or small. The ears are of medium length. The tail is non-prehensile and varies in relative length from 78% in *Antechinus subtropicus* to 121% in *Murexia naso*. In most species, the tail is approximately equal to the length of the body. The hind feet are of medium length. The inner digit of the hind foot is shortened.

Thus, arboreal muridoid dasyurids have a generalized structure similar to that of related terrestrial forms. Moreover, some species of *Antechinus* and *Murexia* are predominantly terrestrial.

Ecological strategies of arboreal muridoid dasyurids: arboreal (subterranean-terrestrial-arboreal and terrestrial-arboreal: **STAr**, **TAr**) animalivores (**An**).

Ecomorph of arboreal muridoid dasyurids: *sharp-muzzled rattoids* – all 13 species.

4.6.1.4. Arboreal muridoids among diprotodont marsupials

In the order *Diprotodontia*, only 7 species in 3 families have muridoid body structure. Arboreal muridoids are found in two families: among pygmy possums and honey possums; in total, 5 species, belonging to two genera. There are no non-muridoid species in these families.

In the family *Burramyidae* (pygmy possums), a predominantly arboreal way of life is led by all 4 species of *Cercartetus*. They are found in New Guinea, Australia and nearby islands, including Tasmania. Arboreal pygmy possums inhabit forests, scrublands and thick herbaceous vegetation. They nest in tree hollows, cracks, cavities in the ground, rotten stumps, dense vegetation and abandoned bird nests. *Cercartetus* species climb and jump well. They feed on nectar, pollen, plant exudates, seeds, soft fruit and insects.

Externally, pygmy possums resemble mice. The head and body length and weight range from 5 cm and 6 g in the Tasmanian possum (*C. lepidus*) to 11 cm and 43 g in the eastern pygmy possum (*C. nanus*). The fur is thick and soft. The upper parts are brownish or greyish. The underparts are light grey, yellowish or white. There are dark rings around the eyes.

The muzzle is conical and of medium length. The vibrissae are long. The eyes and ears are large. The tail is grasping. In most species, the tail is approximately equal to the head and body length, while in the long-tailed pygmy possum (*C. caudatus*) it is 40% longer. The number of digits is 5/5, but the 2nd and 3rd digits on the hind feet are fused. The hind feet are of medium length. The inner digit of the hind foot is enlarged and opposable. The claws are short, and the pads are large. The papillae of the tip of the tongue are elongated in the form of a brush and used to collect nectar and pollen.

Morphological adaptations to the arboreal way of life include a long and prehensile tail, as well as structural features of the feet, in particular enlarged plantar pads and opposing inner digits on the hind feet.

Ecological strategies of arboreal pygmy possums: arboreal (subterranean-terrestrial-arboreal and terrestrial-arboreal: **STAr**, **TAr**) animalivores-frugivores (**AnF**).

Ecomorph of arboreal pygmy possums: ***normal-muzzled gliridoid muridoids*** – all 4 species.

In the family *Tarsipedidae*, the only representative of the family, the honey possum (*Tarsipes rostratus*; fig. 5:4) is predominantly arboreal.

A description of the family is given in Section 2.1.6.2.

According to the structure of the head, the honey possum has no analogues among other non-flying mammals.

Ecological strategies of the honey possum: arboreal frugivore (nectarivore) (**Ar/F**).

Ecomorph of honey possum: *tarsipedoid*.

4.6.1.5. Arboreal muridoids among marsupials: summary

Among the marsupials, 173 species belonging to 35 genera, 8 families and 6 orders have a mouse-like body structure. About half of these species lead an arboreal way of life: 82 species (47%). They belong to 15 genera, 5 families and 4 orders (*Didelphimorphia*, *Microbiotheria*, *Dasyuromorphia* and *Diprotodontia*). The remaining muridoid marsupials are terrestrial.

Arboreal muridoid marsupials are widespread throughout the range of *Metatheria*, however, there are relatively more of them among New World than Australian marsupials (60% and 27%, respectively). This discrepancy can be explained by the greater aridity and lower forest cover in mainland Australia compared with the Neotropics.

Arboreal muridoid marsupials inhabit various biotopes, but most species are found in forest, shrublands and savannah. Some opossums (*Caluromys*, *Gracilinanus*, *Marmosa*, *Tlacuatzin*) and the honey possum are most dependent on trees, shrubs and thick herbaceous vegetation. Some may descend to the ground only to

move to another plant and may be considered completely arboreal species (e.g. *Caluromys*). Most of arboreal muridoid marsupials still occasionally feed on terrestrial animals and fallen fruit.

Most of arboreal muridoid marsupials are mainly animalivorous, but fruit also forms a significant part of their diet. Many species are omnivorous (animalivorous-frugivorous), while *Caluromys philander* is predominantly fruit eater and the honey possum feeds on nectar and pollen. Arborial and terrestrial muridoid marsupials differ in the greater fruit- and nectar-feeding exhibited by the former.

The head and body length and weight of arboreal muridoid marsupials varies from 5 cm and 6 g in the Tasmanian pygmy possum (*Cercartetus lepidus*) to 50 cm and 5 kg in the Virginia opossum (*Didelphis virginiana*). The fur of most is soft, while the monito del monte (*Dromiciops gliridoides*) has silky fur and the honey possum (*Tarsipes rostratus*) has short, stiff fur. Common opossums (*Didelphis*) have long guide hairs protruding from their fur. The colour of the upper parts is usually greyish, yellowish, reddish or brown; the ventral part of the body is usually lighter, up to white. Many have spots or stripes of various colours.

The most common markings are dark rings around the eyes, which in some species extend to the muzzle. Such a "mask" is present in many opossums (*Cryptonanus*, *Gracilinanus*, *Hyladelphys*, *Marmosa*, *Marmosops*, *Tlacuatzin*, also in some *Didelphis* and *Philander*), the monito del monte and pygmy possums (*Cercartetus*). *Caluromys* and *Didelphis* have a dark stripe along the middle of the head. *Philander* has light spots above the eyes. Longitudinal stripes on the back are only seen in two species of arboreal marsupial, both of which have three dark stripes: the northern three-striped opossum *Monodelphis americana* and the honey possum. The monito del monte has a dark pattern on the back and sides.

The muzzle is of medium length or long, and in most species is pointed. The honey possum has an especially long and thin

muzzle. The eyes and ears of most arboreal muridoid marsupials are medium in size, in some species they are small or large. The relative length of the tail in arboreal *Monodelphis* is 50–60%; in all other species, the tail is approximately equal to or longer than the head and body, up to 180% in Emilia's gracile opossum *Gracilinanus emiliae*. In all species, the tail is to some extent prehensile, though to a lesser extent in dasyurids. In the monito del monte, the base of the tail may be thickened due to the accumulation of fat reserves.

The number of digits is 5/5, but in pygmy possums and honey possums, the 2nd and 3rd digits of the hind foot are fused. The honey possum has elongated digits. The hind feet are of medium length. The inner digit of the hind foot is enlarged and opposable in most species, but in dasyurids this digit is shortened. Most species have enlarged plantar pads, but in the honey possum they are small. The claws are of variable structure. In the honey possum, most of the claws are reduced.

In pygmy possums and honey possums, the papillae of the tip of the tongue are elongated in the form of a brush and used to collect nectar and pollen.

As is the case with terrestrial marsupial muridoids, there are species with both generalized and specialized structure among arboreal forms. The former group includes some opossums and all muridoid arboreal dasyurids. The morphology of the latter group is heterogeneous. Most specialized arboreal species (many opossums, the monito del monte, pygmy possums) have large eyes and ears, long vibrissae, long digits, swollen plantar pads, broad hind feet with an enlarged and opposable hallux, and a prehensile tail. In the honey possum, the limbs have a completely different structure: long narrow hind feet, plantar pads that are not enlarged, and practically no claws for climbing.

Ecological strategies of arboreal muridoid marsupials: arboreal (subterranean-terrestrial-arboreal, terrestrial-arboreal, and completely arboreal: **STAr**, **TAr**, **Ar**) animalivores (**An**),

animalivores-frugivores (**AnF**) and frugivores (**F**, fruit eaters and nectar eaters).

Ecomorphs of arboreal muridoid marsupials: 1) *sharp-muzzled gliridoid muridoids* – 49 species: 48 opossums and *Dromiciops gliridoides*; **2) *normal-muzzled gliridoid muridoids*** – 4 species: *Cercartetus*; **3) *sharp-muzzled rattoids*** – 26 species: 13 opossums and 13 dasyurids; **4) *sorexoids*** – 2 species: part of *Monodelphis*; **5) *tarsipedoids*** – 1 species: *Tarsipes rostratus*.

Rattoids and sorexoids are also common among terrestrial marsupials, while the last ecomorph, tarsipedoid, is unique.

4.6.2. Arboreal muridoids among insectivores

According the definition adopted here there are no reliably arboreal species among the insectivores (*Eulipotyphla*). However, many shrews are good climbers, and nesting above ground has been recorded for at least two species, *Crocidura douceti* and *Suncus megalurus*, with the former also recorded breeding in trees (Burgen & He, 2018). Nevertheless, the regularity of arboreal reproduction in shrews is unclear, and data on space use and locomotion in these animals are very scarce. For this reason, all shrews, with the exception of semi-aquatic species, are considered here as terrestrial, along with other muridoid insectivores.

4.6.3. Arboreal muridoids among afrosoricids

Among the afrosoricids (*Afrosoricida*), 24 species belonging to 4 genera and 2 families have a mouse-like body structure. Among them, at least 3 species of shrew tenrecs (*Microgale*, *Tenrecidae*), or 12.5% of muridoid afrosoricids, are predominantly arboreal: *M. longicaudata*, *M. majori* and *M. principle*. The remaining muridoid afrosoricids lead a semi-aquatic or terrestrial way of life. Among non-muridoid afrosoricids arboreal is the lesser hedgehog tenrec (*Echinops telfair*).

Arboreal muridoid tenrecs are found in the mountainous and most humid eastern part of Madagascar. They inhabit humid forests. Based on observations in captivity, food is collected both on the ground and in the canopy (Jenkins, 2018). There is no information about their nesting behaviour in the wild. They climb and jump well and feed on invertebrates, mainly insects.

Arboreal muridoid tenrecs look like very long-tailed shrews or long-nosed birch mice (*Sicista*). The head and body length is 5–9 cm, the weight 5–14 g. The pelage is short, soft and dense. The muzzle is long, thin and pointed. The eyes are small, while the ears are relatively large (19–26% of head and body length). The tail is very long (170–203%). It is covered with scales and sparse hairs. The tip of the tail is prehensile, with a bare dorsal surface and enlarged scales (Jenkins, 2018). The lesser long-tailed tenrec (*Microgale longicaudata*) has 47 caudal vertebrae, more than twice as many as the shorter-tailed species of *Microgale* (Nowak, 1991). The limbs are pentadactyl (5/5), and the digits are long, ending with claws. The hind feet are long: 22–26%.

Adaptations to the arboreal way of life include a prehensile tail, long digits, and long hind feet that aid jumping.

Arboreal muridoid tenrecs are ecologically similar to small arboreal opossums and marsupial mice, but they have a unique structure. Their head is more shrew-like, they have a very long tail, and their feet resemble those of birch mice. It is possible that the locomotion of arboreal *Microgale* is similar to the locomotion of these rodents.

Ecological strategies of arboreal muridoid afrosoricids: arboreal (subterranean-terrestrial-arboreal) animalivores (**STAr/An**).

Ecomorph of arboreal muridoid afrosoricids: *sorexoids* – all 3 species.

4.6.4. Arboreal muridoids among rodents

Among rodents (*Rodentia*), arboreal mouse-like species occur in 6 families: murids (*Muridae*), cricetids (*Cricetidae*), nesomyids

(*Nesomyidae*), dormice (*Gliridae*), spiny rats (*Echimyidae*) and chinchilla rats (*Abrocomidae*).

4.6.4.1. Arboreal muridoids among murids

Among murids (*Muridae*), 665 species belonging to 131 genera and three subfamilies (*Deomyinae*, *Gerbillinae* and *Murinae*) have a mouse-like body structure. Arboreal muridoids are found only among *Murinae*. Since the necessary data on the ecology of many murid species are insufficient or completely absent, the division of murids into terrestrial and arboreal forms based on the criterion adopted here (whether reproduction regularly takes place on plants) is extremely difficult and inevitably inaccurate. In the absence of certain data, it was necessary to rely on hypothetical estimates from the literarature or on morphological similarity to closely related and definitely terrestrial species.

According to available data, the following muridoid murid taxa can be classified as arboreal (the number in brackets shows the number of species): *Abditomys latidens*, some *Apodemus* (3: *flavicollis*, *sylvaticus*, *uralensis*), some *Apomys* (2: *microdon*, *musculus*), *Batomys* (6), *Carpomys* (2), *Chiromyscus* (3), *Chiruromys* (3), *Coccymys* (3), probably *Dacnomys millardi*, probably *Dephomys* (2), *Diplothrix legata*, *Grammomys* (1 muridoid species), *Haeromys* (3), *Hylomyscus* (11 muridoid species), *Kadarsanomys sodyi*, *Lenothrix canus*, *Leopoldamys* (8), part of *Mallomys* (1), *Melomys* (21), *Micaelamys* (2), *Micromys minutus*, *Niviventer* (15 muridoid species), *Oenomys* (2), *Phloeomys* (2), *Pithecheir* (2), probably *Pithecheirops otion*, *Pogonomelomys* (3), probably *Pogonomys* (5), *Praomys* (probably all 16 species), possibly *Protochromys fellowsi*, part of *Rattus* (15 or more), *Solomys* (4), *Sommeromys macrorhinos*, probably *Taeromys celebensis*, *Thallomys* (2 muridoid species), part of *Uromys* (4 or more), *Vandeleuria* (3) and *Vernaya fulva*.

In total, this approximate list of arboreal muridoid murids includes 155 species belonging to 39 genera. Based on morphological

data, nesting in trees may be assumed in 31 further muridoid murid species, the ecology of which is not well understood. Thus, from 23 to 27% of muridoid murids lead an arboreal way of life. Some of these species may be almost entirely arboreal, but most also regularly forage on the ground. Moreover, many arboreal species nest not only in trees and grass, but also in dense thickets on the ground or in burrows. The remaining muridoid murids lead a semi-aquatic, subterranean or terrestrial way of life.

Among non-muridoid murids, most species are arboreal, with fewer semi-aquatic (*Hydromys*, *Crossomys*) and terrestrial (*Notomys*) species.

Arboreal muridoid murids are widely distributed throughout the Eastern Hemisphere, including Australia, and the black rat was spread by humans around the world. For obvious reasons, they are absent from regions where there are no trees, shrubs or tall, dense herbaceous vegetation, i.e deserts, high altitudes and polar regions.

Arboreal muridoid murids inhabit various habitats where there is woody or tall herbaceous vegetation. Many species live in anthropogenic landscapes, and some even in human buildings. Unlike terrestrial species, arboreal species regularly use shelters located above the ground: in tree hollows or nests constructed on tree branches or on the stems of tall herbaceous plants. In the case of bamboo, nests may be located inside the stem. At the same time, many arboreal muridoid murids also use subterranean shelters: burrows and natural cavities. Many species, maybe all, forage not only in trees, but also on the ground. Most arboreal murids feed mainly on fruit, seeds and insects, but among them there are also herbivorous (leaf-eating) species (*Phloeomys*, *Mallomys*). At the same time, there are apparently no specialized animalivorous species, with the exception of *Sommeromys macrorhinos*.

Arboreal muridoid murids do not differ in size from terrestrial muridoid murids. Among them there are both very small species, for example, the harvest mouse (*Micromys minutus*), with a head

and body length of 5 cm and a weight of 5 g, and the largest representative of the murid family, the southern slender-tailed cloud rat (*Phloeomys cumingi*), which measures up to 48 cm long and weighs more than 2 kg. Arboreal muridoid murids have fur of varying density, softness and length. Some arboreal *Rattus* and *Leopoldamys* have spines or spine-like bristles on their backs. The fur of many is coloured yellowish, brownish or greyish. Spots and stripes are rare. *Phloeomys pallidus* has a facial mask – dark spots around the eyes, sometimes extending to the nose.

In most species, the muzzle is blunt conical in shape and of medium length. However, in the animalivorous *Sommeromys macrorhinos* the muzzle is sharp, and in some herbivorous species it is blunt (*Phloeomys*, *Mallomys*). The eyes are medium or large. The pinnae vary in length from relatively short (such as in *Phloeomys*) to relatively long (such as in the black rat).

The tail of arboreal muridoid murids is approximately equal to or longer than the head and body, up to 188% of the head and body length in *Sommeromys macrorhinos*. There are no short-tailed muridoids among them. The tail serves as a support and balance when climbing and jumping. In addition, it has a degree of grasping ability, which is most pronounced in the genera *Pogonomelomys* and *Pogonomys*. In representatives of these genera, the end of the tail is bent to capture the branches upward. Grip strength is aided by a patch of bare skin (without scales) on the dorsal surface of the tail tip. A similar area of bare skin in the same place is found in *Sommeromys macrorhinos* (Musser and Duden, 2002). The number of functional digits is 4/5. In most species they are equipped with claws; in a few species there is a nail on the 5th and/or 1st digits of the hind feet. One of the extreme digits of the hind foot (1st or, usually, 5th) may be partially opposable.

Morphological adaptations to the arboreal way of life include a long and to some extent prehensile tail, as well as the specialized structure of the limbs. It should be noted that a very long tail is

also characteristic of terrestrial jumping species, such as gerbils. The features of the limbs are more specific. Their structure does vary, but most of arboreal murids are characterized by sharp curved claws, long digits, wide hind feet and large plantar pads. Compared to closely-related terrestrial species, arboreal species have relatively longer limbs (Miljutin, 1997).

Arboreal muridoid murids are not as ecomorphologically diverse as terrestrial species. Nevertheless, among them there are certain ecological groups that differ in some details of morphology. These are 1) arboreal species proper, 2) species that climb herbaceous plants, and 3) species that inhabit bamboo thickets. With respect to the body structure, the majority of arboreal muridoid murids are gliridoid muridoids, and only a few can be classified as rattoids. It is possible that some small, long-tailed species that climb grasses and vines, for example, *Haeromys*, *Vandeleuria* and *Vernaya* (but not *Micromys*), are similar in body structure to the birch mice (*Sicista*), and it might be more correct to classify them as sicistoids, but I do not have enough data to assess this conclusively.

Ecological strategies of arboreal muridoid murids: arboreal (subterranean-terrestrial-arboreal, terrestrial-arboreal, possibly also completely arboreal: **STAr**, **Tar**, **Ar**) animalivores (**An,** *Sommeromys macrorhinos*), frugivores (**F**, majority) and herbivores (**H,** *Phloeomys*, *Mallomys*).

Ecomorphs of arboreal muridoid murids. 1) ***Sharp-muzzled gliridoid muridoids*** **–** 1 species: *Sommeromys macrorhinos*; **2)** ***normal-muzzled gliridoid muridoids*** – 141 species: part of *Abditomys* (1), part *Apodemus* (3 or more species), part of *Apomys* (2), *Chiromyscus* (3), *Chiruromys* (3), *Coccymys* (3), *Dacnomys* (1), *Dephomys* (2), *Diplothrix* (1), *Grammomys* (1 muridoid species), *Haeromys* (3), *Hylomyscus* (11 muridoid species), *Kadarsanomys* (1), *Lenothrix* (1), *Leopoldamys* (8), *Melomys* (21), *Micaelamys* (2), *Micromys* (1), *Niviventer* (15 muridoid species), *Oenomys* (2), *Pithecheir* (2), *Pithecheirops* (1), *Pogonomelomys* (3), *Pogonomys* (5), *Praomys* (16),

Protochromys (1), part of arboreal *Rattus* (about 13), *Solomys* (4), part of *Taeromys* (1), *Thallomys* (2 muridoid species), part of *Uromys* (4 or more), *Vandeleuria* (3), *Vernaya* (1); **3) *blunt-muzzled gliridoid muridoids*** – 10 species: *Batomys* (6), Carpomys (2), *Phloeomys* (2); **4) *normal-muzzled rattoids*** – 2 species: some arboreal *Rattus*; **5) *blunt-muzzled rattoids*** – 1 species: *Mallomys rothschildi*

4.6.4.2. Arboreal muridoids among cricetids

Among cricetids (*Cricetidae*), 505 species belonging to 93 genera and all 5 subfamilies (*Cricetinae*, *Arvicolinae*, *Neotominae*, *Sigmodontinae*, *Tylomyinae*) have a mouse-like body structure. Arboreal species occur in all subfamilies except *Cricetinae*. As in the case with murids, a scarcity of data on the ecology of many species makes division of terrestrial and arboreal cricetids based on the criterion adopted here (regular reproduction on plants) difficult and inaccurate. In the absence of certain data, it was necessary to rely on hypothetical estimates from the literature or on morphological similarity to closely related and definitely arboreal species.

Among muridoid voles (*Arvicolinae*), only 3 species from the North American genus *Arborimus* (14%) lead an arboreal way of life. They are all subterranean-terrestrial-arboreal (**STAr)** herbivorous (**H)** arvicoloid muridoids.

Among muridoid neotomyines (*Neotominae*), 20 or more species (up to 39) lead an arboreal way of life (16–30%). They belong to 8 genera: muridoid *Habromys* (5 species), *Hodomys* (1) *Isthmomys* (2), *Megadontomys* (3), part of *Neotoma* (3 of 22 muridoid species), *Ochrotomys* (1), part of *Peromyscus* (4 or more of 58 muridoid species), *Xenomys* (1). They are arboreal (subterranean-terrestrial-arboreal and terrestrial-arboreal: **STAr**, **TAr**) frugivorous (**F)** and herbivorous (**H)** gliridoid muridoids (16) and rattoids (4).

Among the muridoid sigmodontines (*Sigmodontinae*), at least 83 species (24%) belonging to 8 genera lead an arboreal way of life: *Cerradomys* (8 species), *Drymoreomys* (1), *Irenomys* (1), muridoid

Oecomys (6), muridoid *Oligoryzomys* (20), *Thomasomys* (44), *Wiedomys* (2), and *Wilfredomys* (1). They are arboreal (subterranean-terrestrial-arboreal, terrestrial-arboreal, possibly also completely arboreal (some *Thomasomys*): **STAr**, **TAr, Ar**), mostly frugivorous (**F**), possibly also herbivorous (**H:** *Wilfredomys*) rodents. According to the structure of the body, they are all gliridoid muridoids.

Among the muridoid tylomyines (*Tylomyinae*), most species are arboreal: probably all 7 species of *Tylomys* (78%). They are subterranean-terrestrial-arboreal, terrestrial-arboreal, possibly also completely arboreal (**STAr**, **TAr, Ar**) frugivorous (**F**) gliridoid muridoids.

Thus, among all muridoid cricetids – 113 species (22%) from 18 genera – are arboreal. Other muridoid cricetids are semi-aquatic, subterranean, or terrestrial. Many non-muridoid cricetids from the New World subfamilies *Neotominae*, *Sigmodontinae*, and *Tylomyinae* are also arboreal.

Arboreal muridoid cricetids are found in North (*Arvicolinae*, *Neotominae*), Central (*Neotominae*, *Sigmodontinae*, *Tylomyinae*) and South America (*Sigmodontinae*, *Tylomyinae*), that is, exclusively in the New World. The absence of arboreal cricetids in the Old World is presumably connected with the occupation of this niche by murids.

Arboreal muridoid cricetids inhabit various biotopes where there is woody or tall herbaceous vegetation. Unlike terrestrial species, arboreal species regularly use shelters located above the ground: tree hollows or nests constructed on tree branches or on the stems of tall herbaceous plants; however, they may also use subterranean shelters – burrows and natural cavities. Many or all species forage not only in trees, but also on the ground. Most arboreal cricetids feed mainly on fruit, seeds and insects, and some species are herbivorous (*Arborimus*, *Neotoma*, *Wilfredomys*). At the same time, there are no specialized animalivorous species among them.

Arboreal muridoid cricetids are similar in size to terrestrial muridoid cricetids. Most species are the size of mice or small rats, and only a few reach the size of large rats. *Tylomys nudicaudus* reaches a length of 27 cm and a weight of 330 g. The fur of most species is soft. The colour of the fur in most is brownish, yellowish, greyish or blackish, while the underparts are lighter. There are no spotted or striped species.

The muzzle, vibrissae, eyes and ears are in most species of medium size or large. Only the tree voles (*Arborimus*) have small eyes. The tail is long or very long in all: from 70% of the head and body length in some *Arborimus* to 160% in *Wiedomys* and *Wilfredomys*. The tail is somewhat prehensile. The forefeet and hind feet are either of versatile structure or adapted for climbing: with long digits, hooked claws, and enlarged digital and plantar pads. The outer digit of the hind foot is to some extent opposable. The hind feet are of medium length or long.

Arboreal muridoid cricetids are much more uniform than terrestrial muridoid cricetids in terms of body shape, as they have a narrower specialization and similar morphological adaptations. Tree voles are somewhat different, because they retain a vole-like appearance. Nevertheless, tree voles have the same trend of morphological specialization as that of other arboreal cricetids.

Morphological adaptations to the arboreal way of life include a long and to some extent prehensile tail, as well as the structure of the limbs. The feet are characterized by sharp curved claws, long digits, wide hind feet and large plantar pads.

Ecological strategies of arboreal muridoid cricetids: arboreal (subterranean-terrestrial-arboreal, terrestrial-arboreal, possibly also completely arboreal: **STAr**, **TAr, Ar**) frugivores (**F**, majority) and herbivores (**H**, *Arborimus*, *Neotoma*, *Wilfredomys*).

Ecomorphs of arboreal muridoid cricetids: 1) *normal-muzzled gliridoid muridoids* – 106 species: part of neotomyines (16 species), all arboreal muridoid sigmodontines (83) and tylomyines

(7); **2) *normal-muzzled rattoids*** – 4 species: some *Neotoma* (3) and *Ochrotomys* (1); **4) *arvicoloid muridoids*** – 3 species: all arboreal muridoid voles (*Arborimus*).

Most arboreal muridoid cricetids have a normal muzzle, but arboreal voles are blunt-muzzled. Unlike terrestrial muridoid cricetids, there are no specialized animalivores among arboreal muridoid cricetids, and gliridoid muridoids predominate.

4.6.4.3. Arboreal muridoids among nesomyids

Among nesomyids (*Nesomyidae*), 47 species belonging to 16 genera and five subfamilies have a mouse-like body structure. Representatives of three subfamilies (*Delanymyinae*, *Dendromurinae*, *Nesomyinae*) and 6 genera lead an arboreal way of life: *Brachytarsomys* (2 species), *Delanymys* (1), *Dendromus* (14), *Dendroprionomys* (1), *Monticolomys* (1) and *Prionomys* (1). In total 20 species, or approximately 43% of all muridoid nesomyid species, are arboreal. The remaining muridoid nesomyids are predominantly terrestrial. Among the non-muridoid nesomyids, only *Eliurus* are arboreal; the remaining species are terrestrial.

Arboreal muridoid nesomyids are found on the island of Madagascar (*Nesomyinae*) and in mainland Africa south of the Sahara Desert (*Delanymyinae*, *Dendromurinae*). They inhabit savannahs, scrublands, swamps and forests. Burrows, dense vegetation, tree hollows and abandoned bird nests serve as shelters. They feed mainly on seeds, fruit and insects. Dollman's tree mouse (*Prionomys batesi*) mainly feeds on ants, and *Dendroprionomys rousseloti* is probably also insectivorous.

Most arboreal muridoid nesomyids are about the size of a mouse. The smallest species, Delany's mouse (*Delanymys brooksi*) and some climbing mice (*Dendromus*), have a head and body length of 5 cm and a weight of 5 g. Only *Brachytarsomys* are size of medium rats. They reach a head and body length of 25 cm and a weight of 350 g. The fur of most species is soft, while in *Dendroprionomys* and

Prionomys it is velvety. The upper parts are yellowish, reddish or greyish; the underparts are lighter, up to white. Some climbing mice have one to three dark stripes along their backs. *Dendroprionomys* and *Prionomys* have dark rings around the eyes, which extend to the nose.

The muzzle, vibrissae, eyes and ears are of medium size. In contrast to other arboreal rodent taxa, there are no large-eyed species. In all species, the tail is long or very long: the relative tail length varies from 104% in *Brachytarsomys albicauda* up to 180% in *Delanymys*. When climbing, the tail wraps around branches and serves as a balancer.

The feet of *Brachytarsomys* have a typical "gliridoid" structure: they are wide, with swollen plantar pads and sharp, curved claws. By contrast, the feet of *Dendromus*, which are adapted to climbing herbaceous plants and thin branches, have a completely different structure: they have very long digits with weakly curved claws, the plantar pads are relatively small, the 5th digit of the manus is reduced to some extent, and the hind feet are long and narrow. The structure of the feet of other arboreal nesomyids apparently falls between these extremes, some resembling more to the former (possibly *Monticolomys*), others more to the latter (*Delanymys*, *Dendroprionomys*, *Prionomys*). In most species, the outer digit of the hind foot is opposable, but in *Prionomys* opposable is the inner digit.

While *Brachytarsomys* are tree climbers, *Dendromus* and related species prefer shrubs, herbaceous plants and vines. All inhabitants of thick herbaceous vegetation are very small and very long-tailed. Climbing mice (*Dendromus*) exhibit a striking morphological similarity to the birch mice (*Sicista*), but *Dendromus* are more adapted to climbing (Dieterlen, 1971; Miljutin, 2006). Arboreal muridoid nesomyids include animalivorous (*Prionomys*), frugivorous (the majority) and herbivorous species (*Brachytarsomys*).

Morphological adaptations to the arboreal way of life include a long and to some extent prehensile tail, as well as the structure of the limbs, which is different for tree-climbers and herb-climbers.

Ecological strategies of arboreal muridoid nesomyids: arboreal (subterranean-terrestrial-arboreal, terrestrial-arboreal, and completely arboreal: **STAr**, **TAr, Ar**) animalivores (**An**, *Prionomys*, possibly *Dendroprionomys*), frugivores (**F**, majority) and frugivores-herbivores (**FH**, *Brachytarsomys*).

Ecomorphs of arboreal muridoid nesomyids: 1) *normal-muzzled sicistoids* – 17 species: *Delanymys*, *Dendromus*, *Dendroprionomys*, *Prionomys*; **2) *gliridoid muridoids*** – 3 species: *Brachytarsomys*, *Monticolomys*.

Most arboreal muridoid nesomyids have normal muzzles, but *Brachytarsomys* are rather blunt-muzzled. The abundance of sicistoids among nesomyids is notable.

4.6.4.4. Arboreal muridoids among dormice

Among the dormice (*Gliridae*), 4 species belonging to 2 genera (*Myomimus* and *Selevinia*) have a mouse-like body structure. All climb well, but only one species can be classified as an arboreal muridoid – Roach's mouse-tailed dormouse *Myomimus roachi*. The remaining muridoid dormice are predominantly terrestrial, while most non-muridoid dormice are arboreal.

Roach's mouse-tailed dormouse is found in the eastern Mediterranean, from south-eastern Bulgaria to western Anatolia in Turkey. These dormice inhabit floodplain thickets, vineyards, vegetable gardens, and hedgerows. During the active period, they nest in tree hollows. They hibernate in burrows. They feed on invertebrates, small vertebrates, fruit and seeds.

Roach's mouse-tailed dormouse is larger than other mouse-tailed dormice. Its head and body length is 9–14 cm, and its weight is 21–70 g. Large variation in weight is associated with seasonal fluctuations. The fur is soft and is brownish grey on the back and sides

and cream or white on the underparts. A diffuse dark stripe runs along the back of some animals. There is no dark mask on the head.

The muzzle is of medium length, and the vibrissae are long. The eyes and ears are of medium size. The tail is long, but shorter than the head and body length: about 80%. The number of digits is 4/5. The hind feet are relatively long (20%) and wide. The plantar pads of the hind feet and forefeet are medium in size, and the claws are curved.

Of all the muridoid dormice, it is Roach's mouse-tailed dormouse that inhabits the most humid climate, which, apparently, explains the arboreal strategy of this particular species.

Ecological strategies of Roach's mouse-tailed dormouse: arboreal (subterranean-terrestrial-arboreal) animalivore-frugivore (**STAr/AnF**).

Ecomorph of Roach's mouse-tailed dormouse: *normal-muzzled gliridoid muridoid*.

4.6.4.5. Arboreal muridoids among spiny rats

Among the spiny rats or echimyids (*Echimyidae*), 66 species belonging to 17 genera have a mouse-like body structure. Of these, representatives of 12 genera lead an arboreal way of life: *Callistomys pictus*, *Capromys pilorides*, muridoid *Dactylomys* (2 species), *Diplomys caniceps*, *Echimys* (3), *Makalata* (3), probably *Olallamys* (2), probably *Pattonomys* (5), muridoid *Phyllomys* (6), probably *Santamartamys rufodorsalis*, part of *Thrichomys* (2: *apereoides*, *inermis*), *Toromys* (2). In total 29 species, or approximately 44% of all species of muridoid spiny rats, are arboreal. The remaining muridoid echimyids are terrestrial. Among the non-muridoid echimyids, the majority of species lead an arboreal way of life.

Arboreal muridoid spiny rats are found in tropical Central and South America. They live mainly in forests and bamboo thickets (*Dactylomys*, *Olallamys*), and less often in savannahs (some *Thrichomys*). They shelter in dense vegetation, tree hollows, rock

crevices and burrows. It is notable, that unlike the sympatric arboreal sigmodontines (*Cricetidae*), most arboreal spiny rats are predominantly herbivorous (folivorous), and only representatives of the least arboreal genus, *Thrichomys*, are definitely frugivorous; that is, they feed mainly on fruit, seeds, and insects.

In size, almost all arboreal muridoid spiny rats belong to the categories of large rats (head and body length >24 cm, most species) and giant rats (>30 cm, *Capromys*, *Dactylomys*, *Diplomys*). Only *Thrichomys* and some *Phyllomys* are somewhat smaller, about the size of medium-sized rats. The largest species of arboreal muridoid echimyids, and muridoids in general, is Desmarest's hutia (*Capromys pilorides*), with a head and body length of up to 62 cm and a weight of up to 7 kg. It is twice as large and several times heavier than other muridoid echimyids.

Unlike the terrestrial muridoid echimyids, many arboreal species have soft fur. Spines or spine-like bristles are found in *Echimys*, *Makalata*, *Pattonomys*, *Phyllomys* and *Toromys*. The coloration of the upperparts is reddish, greyish or blackish, the underparts are lighter: greyish, yellowish, orange or white. The painted tree rat (*Callistomys pictus*) is black and white, while the white-faced spiny tree rat (*Echimys chrysurus*) has a white stripe down the middle of the head, and the tip of the tail is also white. In the Amazonian bamboo rat (*Dactylomys dactylinus*), a similar stripe on the head is yellowish in colour and extends to the back of the head. In *Thrichomys*, the eyes are framed with a light border.

The muzzle is of medium length and in many herbivorous species is blunt. The eyes and ears are normally developed, but the eyes of the hutia are relatively small. The length of the tail in relation to the head and body varies from 50% in Desmarest's hutia to 160% in *Olallamys*. In all species except the hutia, the length of the tail is more than 70%, and in about half of the species the tail is longer than the head and body. The tail has a degree of grasping ability.

The number of digits is 4/5. The feet have variable structure. In most species, the forefeet and hind feet have a "gliridoid" structure: swollen plantar pads and sharp, curved claws. *Thrichomys* have versatile ("rattoid") feet, while those of "bamboo rats" (*Dactylomys*, *Olallamys*) and hutia are different. Bamboo rats have particularly long middle digits and flat soles. *Dactylomys* have nails instead of claws on all digits, while in *Olallamys* claws are retained. Desmarest's hutia have feet that are similar to those of other hutias: with granulated soles, flat pads, relatively short digits, and strong curved claws.

In general, species with "gliridoid" appearance predominate among arboreal muridoid echimyids: with grasping feet and a long, somewhat prehensile tail. Punares (*Thrichomys*) have a generalized ("rattoid") body structure. Indeed punares, along with Desmarest's hutia, are least associated with woody vegetation.

Quite different from other species are the "bamboo rats" – *Dactylomys* and *Olallamys*. The unusual structure of their feet is apparently associated with a need to climb the smooth trunks and branches of bamboo, where swollen plantar pads and hook-like claws would be redundant. These animals climb like monkeys – by grasping branches with long digits. In this respect, they are similar to the birch mice and other "herb-climbers"; therefore, here, they are conditionally classified as sicistoids.

Desmarest's hutia differs from other arboreal echimyids even more by virtue of its large size, heavy body structure, relatively short tail, unusual feet and way of life. At the same time, Desmarest's hutia is very similar to other the hutias, and, with the exception of the pelage, also to porcupines, especially those from the New World (*Erethizontidae*). The similarity in the structure of the feet between hutias and eretizontids is striking. Not only does the foot shape match, but also the granulated surface of the soles.

Arboreal and terrestrial muridoid echimyids differ in the predominance among the former of large forms, species with gliridoid body structure, long-tailed species, and a smaller proportion

of species with spiny cover. Arboreal echimyids also comprise an abundance of large, herbivorous forms. Moreover, in this respect, arboreal muridoid echimyids differ from all other arboreal muridoids. The reason for this seems to be the advanced specialization of echimyids reflecting the antiquity of this group in comparison, for example, with *Muridae*.

Ecological strategies of arboreal muridoid echimyids: punares (*Thrichomys*) are arboreal (subterranean-terrestrial-arboreal) frugivores (**STAr/F**), all other species are terrestrial-arboreal (**TAr,** *Capromys*) or (almost) completely arboreal (**Ar,** most) frugivores-herbivores (**FH**) and herbivores (**H**).

Ecomorphs of arboreal muridoid echimyids: 1) *blunt-muzzled gliridoid muridoids* – *22* species: *Callistomys* (1 species), *Diplomys* (1), *Echimys* (3) *Makalata* (3), *Pattonomy* (5) *Phyllomys* (6), *Santamartamys* (1) *Toromys* (2); **2) *blunt-muzzled sicistoids*** – 4 species: *Dactylomys*, *Olallamys*; **3) *normal-muzzled rattoids*** – 2 species: *Thrichomys*; **4) *capromyoids*** – *Capromys pylorides*.

4.6.4.6. Arboreal muridoids among chinchilla rats

Among the chinchilla rats or abrocomids (*Abrocomidae*), 9 species belonging to both genera (*Abrocoma* and *Cuscomys*) have a mouse-like body structure. A predominantly arboreal way of life is probably led by representatives of the genus *Cuscomys* (2 species: *C. ashaninka* and *C. oblativa*). This assumption is based solely on morphological characters, since the ecology of these species is unknown. Available data are restricted to one dead specimen of *C. ashaninka* and ancient bone remains and photographs of a living specimen of *C. oblativa*. All other abrocomids lead a predominantly terrestrial way of life.

Two known modern specimens of *Cuscomys* and ancient skeletal remains of *C. oblativa* have been found in southern Peru, in the mountains at altitudes of approximately 2400 and 3370 m. They seem to inhabit forests. Based on morphological features and

observations of a living specimen of *C. oblativa*, these rodents are good climbers and feed mainly on leaves.

The head and body length of the only known specimen of *Cuscomys ashaninka* is almost 35 cm, and the weight is 910 g. The second species of *Cuscomys*, C. *oblativa*, is approximately the same size, but the exact size of this rodent is unknown. The upperparts are grey or brownish-grey, the underparts slightly lighter. The specimen of *C. ashaninka* has a white muzzle tip, a white stripe down the middle of the head, and a white tail tip. The only purported specimen of *C. oblativa*, caught alive and photographed, had similar colouration.

The muzzle is of medium length and appears blunt. The eyes are normally developed. The ears are of medium length (in *C. ashaninka* 11% of the head and body length). The vibrissae are long. The tail is densely covered with short hair. Its relative length in *C. ashaninka* is 76%. The number of digits is 4/5, and the inner digit of the forefoot is completely absent. The hind feet are wide, and their relative length in *C. ashaninka* is 19%. The outer digit of the hind foot is long. Long coarse hair grows on the middle digits of the hind foot. The claws are strong and hook-shaped. The soles of the feet are granulated, with relatively flat pads. The molars are high-crowned, and their chewing surface is flat and ridged.

L. Emmons (Emmons, 1999) justifiably compares the appearance of *Cuscomys* to that of the giant herbivorous *Muridae* and the painted tree rat (*Callistomys pictus*, *Echimyidae*). In terms of foot structure, *Cuscomys* are especially similar to some arboreal echimyids.

Ecological strategies of *Cuscomys*: probably arboreal (subterranean-terrestrial-arboreal or terrestrial-arboreal: **STAr**, **TAr**) herbivores (**H**).

Ecomorph of *Cuscomys*: *blunt-muzzled gliridoid muridoids* – both species. Attribution to the blunt-muzzled category is arbitrary,

since in fact the muzzle of *Cuscomys* has intermediate structure between normal-muzzled and blunt-muzzled forms.

4.6.4.7. Arboreal muridoids among rodents: summary

Among rodents, muridoid body structure occurs in 1341 species belonging to 268 genera and 9 families. Of these, about 320 species (24%) from 77 genera and 6 families (*Muridae*, *Cricetidae*, *Nesomyidae*, *Gliridae*, *Echimyidae* and *Abrocomidae*) are predominantly arboreal. The remaining muridoid rodents lead an aquatic, subterranean or terrestrial way of life.

Arboreal muridoid rodents are found throughout the world, including Australia and Madagascar. They are absent in areas where there are no trees, shrubs or tall, dense herbaceous vegetation: in deserts, highlands and polar regions. On different continents, arboreal muridoid rodents are represented by different families. In Eurasia, they are represented mainly by murids, in mainland Africa by murids and nesomyids, in Madagascar exclusively by nesomyids, in Australia exclusively by murids, and in the New World mainly by echimyids and the endemic subfamilies of cricetids (sigmodontines in the broad sense).

Arboreal muridoid rodents inhabit various biotopes where there is woody or tall herbaceous vegetation. Many species live in anthropogenic landscapes, some in human buildings. Unlike terrestrial species, arboreal species regularly use shelters located above the ground: tree hollows or nests on the branches of tree and bushes, or on the stems of tall herbaceous plants. In the case of bamboo, the nest can also be located inside the stem. At the same time, many arboreal muridoid rodents also use subterranean or ground shelters: burrows, natural cavities, dense thickets. Many species, perhaps all, forage not only in trees, but also on the ground.

Most of arboreal rodents feed mainly on fruit, seeds, and insects, but some species are animalivorous or herbivorous. The proportion of herbivorous species is especially high among arboreal echimyids.

At the same time, specialized animalivorous species are very rare among arboreal muridoid rodents; apparently there are only three such species: one murid (*Sommeromys macrorhinos*) and two nesomyids (*Prionomys batesi* and *Dendroprionomys rousseloti*).

Arboreal muridoid rodents are as varied in size as terrestrial muridoid rodents. There are both very small species, for example, a harvest mouse (*Micromys minutus*) with a head and body length of 5 cm and a weight of 5 g, and the largest muridoid, Desmarest's hutia (*Capromys pilorides*), with a head and body length of up to 62 cm and a weight up to 7 kg. The fur is of varying density, softness and length. Some arboreal murids (*Rattus*, *Leopoldamys*) and some echimyids have spines or spine-like bristles on their backs. The colour of the fur in most is reddish, yellowish, greyish or blackish, with lighter underparts. Some species have light or dark spots or longitudinal stripes on the back. In many long-tailed species, the distal part of the tail is white or pink.

In punares (*Thrichomys*, *Echimyidae*), the eyes are framed with a light border. *Phloeomys pallidus* (*Muridae*), *Dendroprionomys* and *Prionomys* (*Nesomyidae*) have a facial mask – dark rings around the eyes, which may extend to the muzzle. Striped species among arboreal muridoid rodents are rare. One or three longitudinal dorsal stripes are found in climbing mice (*Dendromus*) and the Bolivian bamboo rat (*Dactylomys bolivensis*, *Echimyidae*). An indistinct dorsal stripe is also seen in some Roach's mouse-tailed dormice (*Myomimus roachi*). Among the echimyids and abrocomids, there are somewhat variegated species: the painted tree rat (*Callistomys pictus*) has black and white colouration, while in the white-faced spiny tree rat (*Echimys chrysurus*) and in the *Cuscomys* a white stripe runs along the middle of the head. The Amazonian bamboo rat (*Dactylomys dactylinus*) has a similar stripe, but it is a yellowish colour.

The muzzle of most arboreal muridoid rodents is blunt conical in shape and of medium length. In the animalivorous *Sommeromys macrorhinos* (*Muridae*), the muzzle is sharp, and in herbivorous

species it is blunt (in arboreal voles, abrocomids, in some murids, nesomyids and echimyids). The vibrissae are of medium length or long. The eyes are mostly of medium size or large. Arboreal voles and hutia have relatively small eyes. The length of the ears varies from relatively short to relatively long.

Tail length in relation to head and body length varies from 50% in Desmarest's hutia to 188% in *Sommeromys macrorhinos*. Desmarest's hutia is the only relatively short-tailed species. In all other arboreal muridoid rodents, the length of the tail is more than 70%, and in many it exceeds the length of the body. The tail serves as a support and balancer when climbing and jumping. In addition, it has a degree of grasping ability, which is probably most developed in murids from the genera *Pogonomelomys*, *Pogonomys* and *Sommeromys*. In these rodents, the grasping ability of the tail is manifested morphologically in a patch of bare skin (without scales) on the dorsal surface of the tail tip. No species accumulate fat in the tail.

The number of functional digits is 4/5. The hind feet are of medium length or long. One of the extreme digits of the hind foot, usually the outer one, may be partially opposable. In some echimyids, the opposition of digits is different (see Section 2.4.8). The forefeet and hind feet of arboreal muridoid rodents can be of versatile ("rattoid") structure, but usually they are adapted for climbing in one way or another. The most common adaptation is a "gliridoid" foot: wide, with swollen plantar pads, and sharp, curved claws. However, herb-climbing *Dendromus* and bamboo-dwelling echimyids (*Dactylomys*, *Olallamys*) have a "sicistoid" foot structure: the plantar pads are either reduced or flattened, and the digits are very long with short straightened or even reduced claws. Desmarest's hutia has an exceptional foot structure, in which flattened plantar pads are combined with relatively short digits and strong curved claws.

In contrast to terrestrial muridoid rodents, no arboreal rodents exhibit reduced dentition, which is apparently due to the absence of animalivorous species feeding on soft prey.

Arboreal muridoid rodents are also more uniform in terms of body shape, since they have a narrower specialization and similar morphological adaptations. However, their climbing adaptations may vary. Plant-dwelling species can be divided into tree-climbers (the majority), herb-climbers (e.g. *Dendromus*) and bamboo dwellers (e.g. *Dactylomys*). If the tree-climbers are represented mainly by gliridoid muridoids and rattoids, then among the species climbing herbaceous vegetation or bamboo there are sicistoids – animals with long digits and flat plantar pads. The grass-dwelling sicistoids are very small and have very long tails, while the "bamboo rats" can be very large. Arboreal voles and hutias differ morphologically from typical arboreal muridoid rodents, resembling related terrestrial species: voles and hutias, respectively.

Ecological strategies of arboreal muridoid rodents: arboreal (subterranean-terrestrial-arboreal, terrestrial-arboreal, and completely arboreal: **STAr**, **TAr**, **Ar**) animalivores (**An,** *Sommeromys*, *Prionomys*, possibly *Dendroprionomys*), animaliviores-frugivores (**AnF**), frugivores (**F**, majority), frugivores-herbivores (**FH**) and herbivores (**H,** some murids and cricetids, many echimyids). Thus, arboreal muridoid rodents utilize all possible ecological strategies connected with living on plants.

Ecomorphs of arboreal muridoid rodents: 1) *gliridoid muridoids* – 286 species (89% of arboreal muridoid rodents: in the families *Muridae*, *Cricetidae*, *Nesomyidae*, *Gliridae*, *Echimyidae*, *Abrocomidae*); **2) *sicistoids*** – 21 (7%: *Nesomyidae*, *Echimyidae*); **3) *rattoids*** – 9 (2.8%: *Muridae*, *Cricetidae*, *Echimyidae*); **4) *arvicoloid muridoids*** – 3 (0.9%: *Cricetidae*); **5) *capromyoids*** – 1 (0.3%: *Echimyidae*).

The majority of arboreal muridoid rodents are normal-muzzled: 274 species (86%). The only definitely sharp-muzzled species is the animalivorous *Sommeromys macrorhinos* (*Muridae*). There are large number of nearly blunt-muzzled and blunt-muzzled species. They are found among herbivorous murids, cricetids, nesomyids,

abrocomids, and especially echimyids. In total, there are 45 species of blunt-muzzled arboreal muridoid rodents (14%). They occur among the gliridoid muridoids, rattoids, sicistoids, arvicoloid muridoids and capromyoids; that is, in combination with all locomorphs of arboreal muridoid rodents.

Arboreal rodents differ from terrestrial muridoid rodents in the predominance of gliridoid forms (89%). The presence of blunt-muzzled sicistoids is unique.

4.6.5. Arboreal muridoids: summary

Mouse-like body structure occurs in 1927 species of mammal belonging to 334 genera, 23 families and 9 orders. Of them, 405 species (21%) from 93 genera, 12 families and 6 orders (*Didelphimorphia*, *Microbiotheria*, *Dasyuromorphia*, *Diprotodontia*, *Afrosoricida* and *Rodentia*) are predominantly arboreal. The remaining muridoid mammals lead a semi-aquatic, subterranean or terrestrial way of life.

Arboreal muridoids are found throughout the world, including Australia and Madagascar. They are absent in areas where there are no trees, shrubs or tall, dense herbaceous vegetation: in deserts, highlands and polar regions. Arboreal muridoids inhabit various biotopes where there is woody or tall herbaceous vegetation. Many species live in anthropogenic landscapes, some in human buildings.

Unlike terrestrial species, arboreal muridoids regularly use shelters located above the ground: tree hollows or nests on the branches of trees or bushes, or on the stems of tall herbaceous plants. In the case of bamboo, the nest can also be located inside the stem. At the same time, many arboreal muridoids also use subterranean or ground shelters: burrows, natural cavities and dense thickets. Many species gather food both in trees and on the ground. However, it is possible, that some species descend to the ground only in order to move to another plant and can be considered completely arboreal.

Most arboreal muridoid marsupials and tenrecs are animalivorous, but fruit also forms a significant part of the diet of the former. Most arboreal rodents feed mainly on fruit, seeds, and insects, but there are also herbivorous species among them, while animalivorous species are extremely rare. The honey possum (*Tarsipes rostratus*) has a trophic specialization unique to muridoids – it feeds predominantly on nectar and pollen. Pygmy possums (*Cercartetus*) are also somewhat nectarivorous, but are less specialized.

Arboreal muridoids are as varied in size as terrestrial ones. Among them are both very small species, for example, the Tasmanian pygmy possum (*Cercartetus lepidus*) and harvest mouse (*Micromys minutus*), with a head and body length of 5 cm and a weight of 5–6 g, and the largest muridoid, Desmarest's hutia (*Capromys pilorides*), with a head and body length up to 62 cm and a weight up to 7 kg. The fur is of varying density, softness and length. Some arboreal mice (*Rattus*, *Leopoldamys*) and echimyids have spines or spine-like bristles on their backs. The colour of the fur in most is reddish, yellowish, greyish or blackish, with lighter underparts. Some species have light or dark spots or longitudinal stripes on the back or head. In many long-tailed species, the distal part of the tail is white or pink.

Of the variants of fur pattern, dark rings around the eyes are most common in arboreal muridoids. In some species, the dark colour extends to the muzzle. Such facial masks occur in many opossums, the monito del monte (*Dromiciops gliridoides*), pygmy possums and some rodents: *Phloeomys pallidus* (*Muridae*), *Dendroprionomys* and *Prionomys* (*Nesomyidae*). Opossums of the genera *Caluromys* and *Didelphis* have a dark stripe down the middle of the head. Opossums of the genus *Philander* have a light spot above the eyes. In punares (*Thrichomys*, *Echimyidae*), the eyes are framed with a light border.

Striped species are rare among arboreal muridoids. One or three longitudinal stripes on the back, are seen in climbing mice

(*Dendromus*, *Nesomyidae*), the Bolivian bamboo rat (*Dactylomys bolivensis*, *Echimyidae*), some specimens of Roach's mouse-tailed dormice (*Myomimus roachi*), the opossum *Monodelphis americana* and the honey possum.

Among the New World arboreal muridoids there are some variegated species. Thus, the monito del monte has a dark pattern on the back and sides, while the white-faced spiny tree rat (*Echimys chrysurus*, *Echimyidae*) and species of *Cuscomys* (*Abrocomidae*) have a white stripe along the middle of the head. The Amazonian bamboo rat (*Dactylomys dactylinus*, *Echimyidae*) has the same stripe, but it is yellowish in colour. The painted tree rat (*Callistomys pictus*, *Echimyidae*) has particularly bright black and white coloration.

The muzzle of arboreal muridoid marsupials and tenrecs is of medium length or long and usually pointed. The honey possum has an especially long, thin muzzle. In most muridoid rodents, the muzzle is blunt conical and of medium length, but in the animalivorous *Sommeromys macrorhinos* (*Muridae*), the muzzle is sharp, and in herbivorous rodents it is blunt (in arboreal voles, abrocomids, in some murids, nesomyids and echimyids). The vibrissae are predominantly of medium length or long. The eyes and ears of most are medium-sized or large, in some species they are small. The length of the ears varies from relatively short to relatively long.

Among arboreal muridoids, only opossums of the genus *Monodelphis* and Desmarest's hutia have relatively short tails. In all other species, the relative length of the tail is more than 70%, and in many it exceeds the length of the body, often significantly. The longest tails are those of long-tailed tenrecs (*Microgale longicaudata* and *M. principula*) – 200% or more.

The tail serves as a support and balancer when climbing and jumping. In addition, it has a certain grasping ability, which is most developed in arboreal muridoid marsupials (with the exception of dasyurids), tenrecs and some rodents. In arboreal muridoid tenrecs and some murids (*Pogonomelomys*, *Pogonomys* and *Sommeromys*),

the grasping ability of the tail is manifested morphologically in a patch of bare skin (without scales) on the dorsal surface of the tip of the tail. In the monito del monte, the base of the tail may be thickened due to the accumulation of fat reserves.

In tenrecs and in most muridoid marsupials all limbs are pentadactyl (5/5). The exceptions are the pygmy possums and the honey possum, in which the hind foot is functionally four-toed due to the fusion of the 2nd and 3rd digits. All muridoid rodents have pentadactyl hind feet, while on the forefoot the inner digit is reduced to varying degrees, such that they have 4/5 functional digits. Many arboreal muridoids have elongated digits. The majority of arboreal muridoids have short, hooked claws, but the honey possum and New World bamboo rats (*Dactylomys*, *Echimyidae*) have nails on all or almost all digits.

In most arboreal muridoids, one of the extreme digits is opposable to some extent. In marsupials, this is the inner digit, while in rodents it is usually the outer digit. In some echimyids, the opposition is different (see Section 2.4.8). However, a clear opposition comparable to that of primates exists only among marsupial muridoids. Arboreal muridoids are characterized by large swollen plantar pads, but in species that climb herbaceous vegetation or bamboo, the pads are either small or large but flat.

The hind feet of arboreal muridoids are of medium length or long. The forefeet and hind feet can be of versatile ("rattoid") structure, but they are usually adapted for climbing. The most common are "gliridoid" foot: wide, with swollen plantar pads and sharp, curved claws. However, herb-climbers (*Tarsipes*, *Dendromus* etc.) and bamboo-climbers (*Dactylomys*, *Olallamys*) have a "sicistoid" foot: the plantar pads are either reduced or flattened, and the digits are very long, with short, straightened, or even reduced claws. Desmarest's hutia has an exceptional foot structure, in which flattened plantar pads are combined with relatively short digits and strong

curved claws. Terrestrial hutias and New World porcupines (*Erethizontidae*) have similar foot structure.

Plant-dwelling muridoids can be divided into tree-climbers (the majority), herb-climbers (e.g. *Dendromus*) and bamboo dwellers (e.g. *Dactylomys*). If the tree-climbers are represented mainly by gliridoid muridoids and rattoids, then among the species that climb herbaceous vegetation or bamboo there are sicistoids – animals with long digits and flat plantar pads. The grass-dwelling sicistoids are very small and have very long tails, while the "bamboo rats" can be very large. The honey possum also has a sicistoid body structure, as perhaps do long-tailed tenrecs; however, based on the structure of the head, they are assigned here to other ecomorphs. Arboreal voles and hutias differ morphologically from typical arboreal muridoid rodents. They resemble related terrestrial species: voles and hutias, respectively.

Ecological strategies of arboreal muridoids: arboreal (subterranean-terrestrial-arboreal, terrestrial-arboreal, and completely arboreal: **STAr**, **TAr**, **Ar**) animalivores (**An**), animaliviores-frugivores (**AnF**), frugivores (**F**: granivores, fruit-eaters, nectarivores), frugivores-herbivores (**FH**) and herbivores (**H**). Thus, arboreal muridoids utilize all possible ecological strategies connected with living on plants.

Ecomorphs of arboreal muridoids: 1) ***gliridoid muridoids*** – 339 species: 53 marsupials and 286 rodents; **2)** ***rattoids*** – 35 species: 26 marsupials and 9 rodents; **3)** ***sicistoids*** – 21 species of rodents; **4)** ***sorexoids*** – 5 species: 2 marsupials and 3 tenrecs; **5)** ***arvicoloid muridoids*** – 3 species of rodents; **6)** ***capromyoids*** – 1 species of rodent: Desmarest's hutia; **7)** ***tarsipedoids*** – 1 species of marsupial: honey possum. The distribution of arboreal muridoid species by ecomorph is given in more detail in Table 8.

Table 8. Distribution of arboreal muridoid species by ecomorphs. The number of sharp-muzzled/normal-muzzled/blunt-muzzled species is given in parentheses.

Ecomorph	**Marsupials**	**Tenrecs**	**Rodents**	**Total species**	**%**
Gliridoid muridoids	53 (49/4/0)	–	286 (1/249/36)	339 (50/253/36)	84
Rattoids	26 (26/0/0)	–	9 (0/8/1)	35 (26/8/1)	9
Sicistoids	–	–	21 (0/17/4)	21 (0/17/4)	5
Sorexoids	2 (2/0/0)	3 (3/0/0)	-	5 (5/0/0)	1
Arvicoloid muridoids	–	–	3 (0/0/3)	3 (0/0/3)	< 1
Capromyoids	–	–	1 (0/0/1)	1 (0/0/1)	< 1
Tarsipedoids	1 (1/0/0)	–	–	1 (1/0/0)	< 1
Total species	**82** (78/4/0)	**3** (3/0/0)	**320** (1/274/45)	**405** (82/278/45)	**–**
%	**20**	**one**	**79**	**–**	**100**

Among arboreal muridoids, normal-muzzled species predominate. In total, there are 82 species of sharp-muzzled arboreal muridoids (20%), 278 species of normal-muzzled arboreal muridoids (69%), and 45 species of blunt-muzzled arboreal muridoids (11%). Actually, this ratio of **trophomorps** reflects not a law of nature, but the current status of the contemporary muridoid fauna: the normal-muzzled species prevail just because rodents currently predominate among muridoids. By contrast, the ratio of the most common **locomorphs** of arboreal muridoids, is similar both in marsupials and rodents.

In contrast to the terrestrial muridoids, gliridoid muridoids predominate among the arboreal species (84%), while rattoids relatively common (9%), and all other ecomorphs are rare. Unique to arboreal muridoids are blunt-muzzled sicistoids and tarsipedoids.

However, the only representative of tarsipedoids, the honey possum, can also be considered an unusual sharp-muzzled sicistoid.

4.7. Ecomorphological diversity of muridoids: summary

4.7.1. Ecological groups of muridoids: taxonomic composition and appearance

Mouse-like mammals were divided here into four ecological groups: semi-aquatic, subterranean, terrestrial and arboreal. Let us compare these groups with each other, starting with how they are distributed among orders (Table 9).

Table 9. Taxonomic composition and number of species in ecological groups of muridoids.

Order	Aquatic	Subterranean	Terrestrial	Arboreal	Total species	%
Didelphimorphia	–	–	35	63	**98**	**5**
Paucituberculata	–	–	7	–	**7**	**< 1**
Microbiotheria	–	–	–	1	**1**	**< 1**
Dasyuromorphia	–	–	43	13	**56**	**3**
Peramelemorphia	–	–	4	–	**4**	**< 1**
Diprotodontia	–	–	2	5	**7**	**< 1**
Eulipotyphla	16	–	373	–	**389**	**20**
Afrosoricida	1	–	20	3	**24**	**1**
Rodentia	23	4	994	320	**1341**	**70**
Total species	**40**	**4**	**1478**	**405**	**1927**	–
%	**2**	**< 1**	**77**	**21**	–	**100**

Table 9 shows that terrestrial and arboreal species predominate among mouse-like mammals (respectively 77% and 21%), while there are very few semi-aquatic and especially subterranean species. Terrestrial species are represented in 8 orders out of nine, arboreal

species in 6 orders, semi-aquatic species in three orders, and subterranean species in a single order. All ecological groups are found only among rodents – the most species rich order of mammals.

Terrestrial muridoids are not only the most numerous, but also the most widespread ecological group of the four. Terrestrial species occupy habitats where other muridoids cannot live, for example, deserts and highlands. Arboreal muridoids are also widespread, but their distribution is limited by the presence of woody or dense herbaceous vegetation. The relatively small numbers of semi-aquatic and subterranean muridoid species are less widely distributed.

Terrestrial and arboreal muridoids do not differ in size. Both groups cover the entire size range – from very small "mice" to "giant rats". Even among semi-aquatic muridoids there are species the size of mice and rats. Nonetheless, sometimes the way of life imposes restrictions on body size. Thus, species moving in the plant litter and climbing in herbaceous vegetation, for example, shrews and harvest mice, are very small.

The way of life is to some extent reflected in the character and even the colour of the fur. Thus, all semi-aquatic muridoids have thick pelage, hard vibrissae, and some have a fringe of hard hair on their feet. Shrews, as well as shrew-like tenrecs and rodents (soricoids), are characterized by short velvety fur, which, in many cases, is grey or black. A spiny cover is found in both terrestrial and arboreal muridoids, but more frequently among the terrestrial species. The most frequent fur coloration patterns for both terrestrial and arboreal muridoids are a dark facial mask and longitudinal stripes, but these patterns are not evenly distributed. The "mask" is more common in arboreal species, and the stripes are especially common in species – both terrestrial and climbing – inhabiting herbaceous vegetation.

Nevertheless, the patterns mentioned above are not unique to particular ecological groups. The same is true of other morphological traits. Actually, it is possible to talk only about trait states that

are typical of a particular group. For example, a long tail is typical of arboreal species, but some arboreal species are not long-tailed. Moreover, very long tails are also found in some terrestrial species.

There is no exact correspondence between the ecology and morphological features of species for a number of reasons. Firstly, a change in way of life occurs gradually in the process of evolution, so many species have an intermediate structure; moreover, their way of life may also be intermediate, for example, between terrestrial and arboreal. Secondly, morphological features change more slowly than ecology, and even more so than the behaviour of animals. Thirdly, with a change in way of life, some morphological features may not change at all if they do not interfere with life in new conditions. Finally, the same trait state may be useful for different ways of life. For example, a long tail is needed for both climbing and jumping on the ground. In addition, it should be remembered that even within the same ecological group, specialization proceeds in different directions. Terrestrial animals, for example, can have very different appearance; that is, they can be represented by different life forms.

Since comparison of the four ecological groups of muridoids on the basis of separate morphological traits does not yield very clear results, it may be more informative to compare the groups in terms of the presence and frequency of species with a certain set of adaptive traits. The set of adaptive traits is nothing but an ecomorph. The ecomorphological structure of the ecological groups of muridoids is shown in Table 10.

Table 10 shows that terrestrial muridoids are represented by the largest number of ecomorphs – 11 out of thirteen, arboreal muridoids are represented by 7, semi-aquatic by 2 and subterranean by 1 ecomorph. It may seem that the more species in the group, the more ecomorphs it contains. This is partly true, but the terrestrial environment also provides more opportunities for specialization than others.

Table 10. Distribution of species by ecomorph in ecological groups of muridoids. (The names of ecomorphs are explained on pp. 94-96)

Ecomorph	Aquatic	Subterranean	Terrestrial	Arboreal	Total species	%
Rattoids	–	4	602	35	**641**	**33**
Gliridoid muridoids	–	–	219	339	**558**	**29**
Sorexoids	–	–	476	5	**481**	**25**
Gerbilloid muridoids	–	–	86	–	**86**	**4**
Arvicoloid muridoids	5	–	61	3	**69**	**3**
Hydromyoid muridoids	35	–	–	–	**35**	**2**
Sicistoids	–	–	14	21	**35**	**2**
Deomyoids	–	–	11	–	**11**	**< 1**
Capromyoids	–	–	3	1	**4**	**< 1**
Colomyoids	–	–	3	–	**3**	**< 1**
Lutreolinoids	–	–	2	–	**2**	**< 1**
Hypogeomyoids	–	–	1	–	**1**	**< 1**
Tarsipedoidss	–	–	-	1	**1**	**< 1**
Total species	**40**	**4**	**1478**	**405**	**1927**	–
%	**2**	**< 1**	**77**	**21**	–	**100**

Approximately half of the muridoid ecomorphs are versatile to varying degrees. Essentially, only hydromyoid muridoids can be unambiguously associated with the semi-aquatic way of life and gerbilloid muridoids with the terrestrial way of life. However, there are ecomorphs that are typical for particular ecological groups of muridoids. Thus, for aquatic muridoids, it is hydromyoid muridoids; terrestrial species are characterized by rattoids, sorexoids,

gerbilloid muridoids, arvicoloid muridoids, and hypogeomyoids; and arboreal muridoids are characterized by gliridoid muridoids.

Thus, although it is impossible to determine with absolute certainty the ecological strategy of an unknown species on the basis of its morphological characters, it can be done with a certain degree of probability, and sometimes with a very high degree.

4.7.2. Life forms of muridoids: taxonomic composition and evolution

Among the muridoids, 13 ecomorphs were identified here, some of which are represented by two or three versions of the muzzle structure (trophomorphs). Let us consider the taxonomic composition of these ecomorphs (Table 11).

Table 11 shows that the majority of muridoid species (87%) belong to only three ecomorphs: rattoids (33%), gliridoid muridoids (29%), and sorexoids (25%). All other ecomorphs are much rarer. This same ratio can be seen within rodents and marsupials, while sorexoids predominate among insectivores. Among muridoids in general, normal-muzzled species predominate (60%), while a third of species are sharp-muzzled (33%), and 7% are blunt-muzzled. However, these values vary greatly between taxa: marsupials, insectivores, and tenrecs are mostly sharp-muzzled, while 85% of rodents are normal-muzzled. Blunt-muzzled species are found only among rodents. These differences are associated with the greater herbivory of rodents.

Looking at Table 11, one may gain the false impression that certain ecomorphs are associated with certain taxa, or, to put it another way: there are no life forms, there are only taxa. For example, the muridoid *Eulipotyphla* (insectivores), a species-rich group, consists predominantly (95%) of shrew-like (sorexoid) species, mostly shrews. However, despite the undoubted imprint of origin on the external appearance of muridoid insectivores, they are shrew-like (sorexoid) not because they belong to the order *Eulipotyphla*, but

Table 11. Taxonomic composition of muridoid ecomorphs. The number of sharp-muzzled/normal-muzzled/blunt-muzzled species is given in parentheses. (The names of ecomorphs are explained on pp. 94-96)

Ecomorph	Marsupials	Insectivores	Afrosoricids	Rodents	Total species	%
Rattoids	61 (60/1/0)	–	–	580 (0/552/28)	**641** (60/553/28)	**33**
Gliridoid muridoids	54 (50/4/0)	–	–	504 (1/467/36)	**558** (51/471/36)	**29**
Sorexoids	37 (37/0/0)	373 (373/0/0)	23 (23/0/0)	48 (48/0/0)	**481** (481/0/0)	**25**
Gerbilloid muridoids	18 (18/0/0)	–	–	68 (0/68/0)	**86** (18/68/0)	**4**
Arvicoloid muridoids	–	–	–	69 (0/0/69)	**69** (0/0/6 9)	**3**
Hydromyoid muridoids	–	16 (16/0/0)	1 (0/1/0)	18 (0/18/0)	**35** (16/19/0)	**2**
Sicistoids	–	–	–	35 (0/31/4)	**35** (0/31/4)	**2**
Deomyoids	–	–	–	11 (11/0/0)	**11** (11/0/0)	**< 1**
Capromyoids	–	–	–	4 (0/0/4)	**4** (0/0/4)	**< 1**
Colomyoids	–	–	–	3 (0/3/0)	**3** (0/3/0)	**< 1**
Lutreolinoids	2 (0/2/0)	–	–	–	**2** (0/2/0)	**< 1**
Hypogeomyoids	–	–	–	1 (0/1/0)	**1** (0/1/0)	**< 1**
Tarsipedoids	1 (1/0/0)	–	–	–	**1** (1/0/0)	**< 1**
Total species	**173** (166/7/0)	**389** (389/0/0)	**24** (23/1/0)	**1341** (60/1140/141)	**1927** (638/1148/141)	–
%	**9**	**20**	**1**	**70**	–	**100**

because they lead a certain way of life. This is easy to verify. After all, shrew-like mammals are present not only in all families of insectivores, but also among opossums, caenolestids, carnivorous marsupials, tenrecs, murids and cricetids. That is, in 6 orders and 10 families of mammals. They are present even in such phylogenetically distant taxa as marsupials and placentals. In this case, we are dealing not with a primitive morphological construction, but with a highly specialized form. All these phylogenetically different, but externally similar animals are connected not by kinship, but by a way of life. They belong to the same life form.

Moreover, it is easy to see that a change in the way of life of muridoid insectivores drastically changes their appearance, giving rise to other life forms, such as desmans, moles or hedgehogs. For greater persuasiveness, nature repeated the adaptive evolution of insectivores, taking as a "control group" afrosoricids. The results of the parallel evolution of insectivores and afrosoricids turned out to be so similar that for almost two hundred years these animals were combined in a single order *Insectivora*. They would be still there if not for DNA studies, which showed that insectivores and afrosoricids belong to phylogenetically distant clades: *Laurasiatheria* and *Afrotheria*, respectively.

As mentioned above, ecomorphs are not discrete: in the process of evolution, they gradually transform into each other. But in what direction and in what order? Let us consider each ecomorph separately. Comments on ecomorphs given below are intentionally limited to muridoid structure; the post-muridoid stage of adaptive evolution will be discussed in the next chapter.

Rattoids (rat-like) are the most numerous and least specialized group of muridoids. Most rattoids are the most primitive muridoids in an evolutionary sense and fulfil the role of ancestral body structure for all other ecomorphs. However, judging by the structure of their feet and prehensile tail, rattoid opossums and diprotodont marsupials acquired a rattoid appearance secondarily,

having passed through the gliridoid stage during the course of evolution. Among rattoids there are subterranean, terrestrial and arboreal species. They might be sharp-muzzled, normal-muzzled, and blunt-muzzled. *Taxonomic composition*: 641 species of marsupials and rodents – *Didelphidae* (27), *Dasyuridae* (33), *Hypsiprymnodontidae* (1), *Muridae* (306), *Cricetidae* (218), *Nesomyidae* (14), *Echimyidae* (35), *Abrocomidae* (7).

Gliridoid muridoids (dormouse-like) are the most common ecomorph among scansorial and arboreal muridoids. They probably originated from rattoids, which is supported by the abundance of transitional forms. Gliridoid muridoids, in turn, could serve as the basis for some secondary rattoids (e.g. opossums) and those sicistoids that have large but flat plantar pads, such as sicistoid echimyids. That is, the adaptive evolution of gliridoid muridoids can go in several directions, including the return to rattoid structure. Gliridoid muridoids may be sharp-muzzled, normal-muzzled, and blunt-muzzled. *Taxonomic composition*: 558 species of marsupials and rodents: *Didelphidae* (48), *Microbiotheriidae* (1), *Burramyidae* (5), (*Muridae* (248), *Cricetidae* (223), *Nesomyidae* (5), *Gliridae* (4), *Echimyidae* (22), *Abrocomidae* (2).

Sorexoids (shrew-like), on one hand, seem rather uniform in body structure; on the other hand, this very numerous and poorly studied group may conceal interesting combinations of characters. In terms of locomotion, sorexoids are closest to rattoids and probably formed in the course of rattoids adaptating to rummaging for invertebrates in plant litter and soil. They can also be considered as a separate group of sharp-muzzled rattoids. Sorexoids gave rise to sharp-muzzled hydromyoid muridoids. It is possible that some sharp-muzzled rattoids and sharp-muzzled gliridoids also passed through the sorexoid stage. Sorexoids are predominantly terrestrial, but there are also a few arboreal species. *Taxonomic composition*: 481 species of marsupials, insectivores, tenrecs and rodents – *Didelphidae* (19), *Caenolestidae* (7), *Dasyuridae* (5), *Peramelidae* (4),

Erinaceidae (3), *Soricidae* (361), *Talpidae* (7), *Solenodontidae* (2), *Tenrecidae* (23), *Muridae* (28), *Cricetidae* (20).

Gerbilloid muridoids (gerbil-like) probably arose during the adaptation of rattoid, possibly also sicistoid, ancestors to living among the sparse vegetation of arid regions. Intermediate forms between rattoids and gerbilloid muridoids are common. Further specialization of gerbilloid muridoids goes beyond muridoid body structure. This is an exclusively terrestrial ecomorph. Gerbilloid muridoid dasyurids are sharp-muzzled, the rest are normal-muzzled. *Taxonomic composition*: 86 species of marsupials and rodents – *Dasyuridae* (18), *Muridae* (23), *Cricetidae* (6), *Nesomyidae* (8), *Zapodidae* (5), *Heteromyidae* (26).

Arvicoloid muridoids (vole-like) probably arose during the adaptation of rattoid ancestors to a fossorial and herbivorous way of life. They can also be considered as a separate group of blunt-muzzled rattoids. In terms of locomotion, arvicoloid muridoids are heterogeneous: they include semi-aquatic, subterranean-terrestrial, petrophilous, and even arboreal species. *Taxonomic composition*: 69 species of rodents – *Muridae* (45), *Cricetidae* (21), *Nesomyidae* (2), *Echimyidae* (1).

Hydromyoid muridoids ("water rats") are adapted to a semi-aquatic way of life. They are of two origins. Hydromyoid rodents are clearly descended from terrestrial semi-aquatic rattoids resembling the brown rat in body structure, which is supported by the presence of transitional forms, while the ancestors of hydromyoid shrews certainly had a sorexoid body structure. Further specialization of hydromyoid muridoids goes beyond the muridoid structure. Shrews are sharp-muzzled, the rest are normal-muzzled. *Taxonomic composition*: 35 species of insectivores, afrosoricids and rodents – *Soricidae* (16), *Potamogalidae* (1), *Muridae* (4), *Cricetidae* (14).

Sicistoids ("birch-mouse-like") arose as a result of an adaptation to climbing thin and smooth branches with the help of long digits, in which circumstances claws become redundant. They appear to

have dual origins: from herbaceous vegetation-dwelling rattoids (e.g. birch mice) and from arboreal gliridoid muridoids (echimyids). The terrestrial sicistoids clearly gave rise to an evolutionary lineage leading to jumping mice, referred to here as gerbilloid muridoids, and further beyond the muridoid structure. Among the sicistoids there are terrestrial and arboreal species. They are normal-muzzled and blunt-muzzled (echimyids). *Taxonomic composition*: 35 species of rodents – *Nesomyidae* (17), *Sminthidae* (14), *Echimyidae* (4).

Deomyoids (similar to *Deomys*) are long-legged muridoids, with a thin muzzle. They are probably descended from rattoid ancestors, but this is the most enigmatic ecomorph and requires further study. Currently, data on the ecology of deomyoids are very scarce. They are terrestrial. *Taxonomic composition*: 11 species of *Muridae* (*Deomys*, *Leptomys*, *Malacomys*, *Paraleptomys*).

Capromyoids (hutia-like) are herbivorous, terrestrial and arboreal rodents that have emerged in island environment, in the absence of large predators. They differ sharply in appearance from all other muridoids and only slightly from non-muridoid hutias. Judging by the rarity and isolation of hutias, this is a dead-end line of evolution. Blunt-muzzled. *Taxonomic composition*: 4 species of *Echimyidae* (all muridoid hutias, *Capromyinae*).

Colomyoids (similar to *Colomys*) are muridoids adapted to obtaining animal food in shallow water. They may represent an intermediate link between rattoids and hydromyoid muridoids. Normal-muzzled. *Taxonomic composition*: 3 species of *Muridae* (*Colomys*, *Xeromys*, *Parahydromys*).

Lutreolinoids (similar to *Lutreolina*). This ecomorph includes only lutrine opossums, which are distinguished by their weasel-like appearance: short legs and a long body. They are probably descended from rattoid ancestors. Lutreolinoids demonstrate an evolutionary shift towards greater carnivory and to a change of locomotion. They are predominantly terrestrial and carnivorous. Normal-muzzled. *Taxonomic composition*: 2 species of *Didelphidae* (*Lutreolina*).

Hypogeomyoids (similar to *Hypogeomys*). This ecomorph includes only the Malagasy giant rat. It can also be considered an unusual rattoid with long, large hind feet and a thickened tail. Presumably it is in the initial stage of transition toward bipedal locomotion. This rodent leads a terrestrial way of life, is frugivorous and normal-muzzled. *Taxonomic composition*: 1 species of *Nesomyidae* (*Hypogeomys antimena*).

Tarsipedoids (similar to *Tarsipes*). This ecomorph includes only the honey possum. It can also be considered an unusual sharp-muzzled sicistoid that switched to feeding on nectar. Its ancestors may have had the appearance of modern pygmy possums (*Burramyidae*) and were rattoid or gliridoid muridoid. Judging by the very narrow specialization, it is a dead-end evolutionary line. *Taxonomic composition*: 1 species of *Tarsipedidae* (*Tarsipes rostratus*).

4.7.3. Ecomorphological structure of taxa

In the previous sections of this chapter, separate ecological groups of mouse-like mammals were considered, and as a result the descriptions of many families were divided into parts. Below, those parts are joined to show a holistic picture of the ecomorphological diversity of all 23 mammalian families that contain muridoid species.

Opossums (*Didelphidae*)

The family includes 103 species, of which 98 (95%) are muridoids. Among the muridoids there are 35 terrestrial and 63 arboreal species (36% and 64%, respectively).

Ecological strategies of muridoid opossums: subterranean-terrestrial (**ST**), subterranean-terrestrial-arboreal (**STAr**), terrestrial-arboreal (**TAr**) and completely arboreal (**Ar**) animalivores (**An**), animaliviores-frugivores (**AnF**), and frugivores (**F**).

Ecomorphs of muridoid opossums: 1) *sharp-muzzled gliridoid muridoids* – 48 species; **2) *sharp-muzzled rattoids*** – 27 species; **3) *sorexoids*** – 21 species; **4) *lutreolinoids*** – 2 species (*Lutreolina*).

Caenolestids (*Caenolestidae*)
All 7 species of the family are subterranean-terrestrial (**ST**) animalivorous (**An**) ***sorexoids.***

Microbiotherids (*Microbiotheriidae*)
The only species of the family, the monito del monte (*Dromiciops gliridoides*), is an arboreal (**Ar**) animalivorous (**An**) or animalivorous-frugivorous (**AnF**) ***sharp-muzzled gliridoid muridoid***.

Carnivorous marsupials or dasyurids (*Dasyuridae*)
The family includes 74 species, of which 56 (76%) are muridoids. Among the muridoids there are 43 terrestrial and 13 arboreal forms (77% and 23%, respectively).
Ecological strategies of muridoid dasyurids: subterranean-terrestrial (**ST**), subterranean-terrestrial-arboreal (**STAr**) and terrestrial-arboreal (**TAr**) animalivores (**An**).

Ecomorphs of terrestrial muridoid dasyurids: 1) *sharp-muzzled rattoids* – 33 species; **2) *sharp-muzzled gerbilloid muridoids*** – 18 species; **3) *sorexoids*** – 5 species.

Bandicoots (Peramelidae)
The family includes 20 species, of which 4 species of mouse bandicoots (*Microperoryctes*; 20%) are muridoids. All muridoid species are subterranean-terrestrial (**ST**) animalivorous-frugivorous (**AnF**) ***sorexoids***.

Pygmy possums (*Burramyidae*)
All 5 species in the family have a mouse-like body structure. One species is terrestrial (*Burramys parvus*); the others are arboreal (20% and 80%, respectively). They are subterranean-terrestrial (**ST**), subterranean-terrestrial-arboreal (**STAr**) and terrestrial-arboreal (**TAr**) animalivorous-frugivorous (**AnF**) ***normal-muzzled gliridoid muridoids.***

Honey possums (*Tarsipedidae*)
The only species in the family, the honey possum (*Tarsipes rostratus*), is an arboreal, predominantly nectarivorous (**Ar/F**) mammal. It is separated here into its own ecomorph – ***tarsipedoid*.**

Musky rat-kangaroos (*Hypsiprymnodontidae*)
The only species in the family, the musky kangaroo (*Hypsiprymnodon moschatus*), is a subterranean-arboreal-terrestrial (**STAr)** frugivorous (**F)** ***normal-muzzled rattoid*.**

Hedgehogs (*Erinaceidae*)
The family includes 26 species, of which 3 (12%) are muridoids. All three species are subterranean-terrestrial (**ST)** animalivorous (**An)** or animalivorous-frugivorous (**AnF)** ***sorexoids*.**

Shrews (*Soricidae*)
The family includes 448 species, of which 377 (84%) are muridoids. Among muridoid shrews there are 16 semi-aquatic and 361 terrestrial species (4% and 96%, respectively).

Muridoid shrews are aquatic-subterranean-terrestrial (**AqST)**, subterranean-terrestrial (**ST)** and subterranean-arboreal- terrestrial (**STAr)** animalivorous (**An)**, less often animalivorous-frugivorous (**AnF)** ***sharp-muzzled hydromyoid muridoids*** (16 species) and ***sorexoids*** (361 species).

Moles (*Talpidae*)
The family includes 54 species, of which 7 species of shrew moles (*Uropsilus*; 13%) are muridoids. All muridoid species are subterranean-terrestrial (**ST**) animalivorous (**An**) ***sorexoids*.**

Solenodons (*Solenodontidae*)
Both species of solenodons are subterranean-terrestrial (**ST)** animalivorous (**An)** ***sorexoids*.**

Tenrecs (*Tenrecidae*)
The family includes 31 species, of which 23 (74%) are muridoids. Among muridoid tenrecs, there are 20 terrestrial and 3 arboreal species (87% and 13%, respectively). They are subterranean-terrestrial (**ST)** and subterranean-terrestrial-arboreal (**STAr)** animalivorous (**An)** ***sorexoids.***

Otter shrews (*Potamogalidae*)
The family includes 3 species, one of which has a mouse-like body structure – the Nimba otter shrew (*Micropotamogale lamottei*; 33%). It is a semi-aquatic (**AqST)** animalivorous (**An)** ***normal-muzzled hydromyoid muridoid.***

Murids (*Muridae*)
The family includes 816 species, of which 665 (81%) are muridoids. Among the muridoids there are 4 semi-aquatic, 1 subterranean, 505 terrestrial and 155 arboreal species (0.6%, 0.2%, 76% and 23%, respectively).

Ecological strategies of muridoid murids: aquatic-subterranean-terrestrial (**AqST)**, subterranean-terrestrial (**ST)**, subterranean-terrestrial-arboreal (**STAr)**, terrestrial-arboreal (**TAr)** possibly also completely arboreal (**Ar)** animalivores (**An)**, frugivores (**F** – majority) and herbivores (**H)**.

Ecomorphs of muridoid murids: 1) ***rattoids*** **–** 303 species; **2)** ***gliridoid muridoids*** – 248 species; **3)** ***arvicoloid muridoids*** – 45 species; **4)** ***sorexoids*** – 28 species; **5)** ***gerbilloid muridoids*** – 23 species; **6)** ***deomyoids*** – 11 species; **7)** ***hydromyoid muridoids*** – 4 species; **8)** ***colomyoids*** – 3 species. Most muridoid murids are normal-muzzled. One gerbilloid muridoid, all sorexoids and all deomyoids are sharp muzzled. Six rattoids and 10 gliridoid muridoids are blunt muzzled.

Cricetids (*Cricetidae*)

The family includes 765 species, of which 505 (66%) are muridoids. Among the muridoids there are 14 semi-aquatic, 3 subterranean, 370 terrestrial and 113 arboreal species (3%, 1%, 73% and 22%, respectively).

Ecological strategies of muridoid cricetids: possibly aquatic-subterranean (**AqS),** aquatic-subterranean-terrestrial (**AqST),** subterranean-terrestrial (**ST**), possibly completely terrestrial (**T**), subterranean-terrestrial-arboreal (**STAr**), terrestrial-arboreal (**TAr**), possibly completely arboreal (**Ar**) animalivores (**An**), frugivores (**F** – majority) and herbivores (**H**).

Ecomorphs of muridoid cricetids: 1) *gliridoid muridoids* – 223 species; **2) *rattoids*** – 221 species; **3) *arvicoloid muridoids*** – 21 species; **4) *sorexoids*** – 20 species; **5) *hydromyoid muridoids*** – 14 species: **6) *gerbilloid muridoids*** – 6 species. Most species of muridoid cricetids are normal-muzzled. Animalivorous sigmodontines (20 species) are sharp muzzled. Thirty-one species are blunt muzzled (all voles and some sigmodontines).

Nesomyidae (*Nesomyidae*)

The family includes 68 species, of which 47 (69%) are muridoids. Among the muridoids there are 27 terrestrial and 20 arboreal species (57% and 43%, respectively).

Ecological strategies of muridoid nesomyids: subterranean-terrestrial (**ST**), subterranean-terrestrial-arboreal (**STAr**), terrestrial-arboreal (**TAr**) and completely arboreal (**Ar**) animalivores (**An**), frugivores (**F** – majority), frugivores-herbivores (**FH**) and herbivores (**H**).

Ecomorphs of muridoid nesomyids: 1) *sicistoids* – 17 species; **2) *rattoids*** – 14 species; **3) *gerbilloid muridoids*** – 8 species; **4) *gliridoid muridoids*** – 5 species; **5) *arvicoloid muridoids*** – 2 species; **6) *hypogeomioids*** – 1 species. Most species of muridoid nesomyids

are normal-muzzled. There are no sharp-muzzled species; 4 species are blunt-muzzled (*Brachytarsomys*, *Brachyuromys*).

Birch mice (*Sminthidae*)
All 14 species in the family are subterranean-arboreal-terrestrial **(STAr)** animalivorous-frugivorous **(AnF)** and frugivorous **(F)** ***normal-muzzled sicistoids.***

Jumping mice (*Zapodidae*)
All 5 species in the family are subterranean-terrestrial **(ST)** frugivorous **(F)** ***normal-muzzled gerbilloid muridoids.***

Dormice (*Gliridae*)
The family includes 29 species, of which 4 (14%) are muridoids. Among the muridoids, there are 3 terrestrial and 1 arboreal species (75% and 25%, respectively). They are subterranean-terrestrial-arboreal **(STAr)** animalivorous (**An**, *Selevinia*) and animalivorous-frugivorous (**AnF**, *Myomimus*) ***normal-muzzled gliridoid muridoids.***

Heteromyids (*Heteromyidae*)
The family includes 66 species, of which 26 (39%) are muridoids. All muridoid species are subterranean-terrestrial **(ST)** frugivorous **(F)** ***normal-muzzled gerbilloid muridoids.***

Spiny rats (*Echimyidae*)
The family includes 99 species, of which 66 (67%) are muridoids. Among the muridoids, there are 37 terrestrial and 29 arboreal species, respectively (56% and 44%).

Ecological strategies of muridoid echimyids: aquatic-subterranean-terrestrial **(AqST)**, subterranean-terrestrial **(ST)**, subterranean-terrestrial-arboreal **(STAr)**, terrestrial-arboreal **(TAr)**, possibly

completely arboreal (**Ar)** frugivores (**F),** frugivores-herbivores (**FH)** and herbivores (**H**).

Ecomorphs of muridoid echimyids: 1) ***normal-muzzled rat-toids*** – 35 species; **2)** ***blunt-muzzled gliridoid muridoids*** – *22* species; **3)** ***capromyoids*** – 4 species; **4)** ***blunt-muzzled sicistoids*** – 4 species; **5)** ***arvicoloid muridoids*** – 1 species (*Carterodon sulcidens*).

Chinchilla rats (*Abrocomidae*)

The family includes 10 species, of which 9 (90%) are muridoids. Among muridoids there are 7 terrestrial and 2 arboreal species (78% and 22%, respectively).

Ecological strategies of muridoid abocomids: subterranean-terrestrial (**ST)**, subterranean-terrestrial-arboreal (**STAr)**, possibly also terrestrial-arboreal (**TAr)** herbivores (**H)**.

Ecomorphs of muridoid abrocomids: 1) ***blunt-muzzled*** (?) ***rat-toids*** – 7 species (*Abrocoma*); **2)** ***blunt-muzzled*** (?) ***gliridoid muri-doids*** – 2 species (*Cuscomys*).

5. EVOLUTIONARY FATE OF MURIDOIDS

As was discussed at the beginning of the book, muridoids are probably the most ancient life form among mammals. If this is true, they gave rise to all other mammalian life forms, including both those that currently exist and those that existed in the past. Of course, they did not give rise *directly* to all, but rather to all secondary ecomorphs, which may then have given rise to tertiary, quaternary, quinary, etc. life forms.

How did it happen and why? Fortunately, the recent fauna contains so many muridoid species and their probable ecomorphological descendants that it is possible to trace the evolution of muridoids even without resorting to paleontological data. Let us first consider the very first stage in the transformation of muridoids into other ecomorphs, and then what happened next.

5.1. Muridoids are changing their appearance

Let us remember that it is locomotion that makes an animal muridoid, namely, the use of a four-legged ricochet as a fast gait (run), in which the hind legs are the propulsive legs, and the front legs serve only for landing. In such animals, the hind legs are much longer than the front ones, and the tail serves as a balancer, so it is also long. A change of the gait in the course of evolution inevitably

changes the appearance of an animal. We will now consider how this happens.

Among recent mammals, muridoids are found in 23 families. Of these, 8 families consist exclusively of muridoids (Caenolestidae Microbiotheriidae Burramyidae, Tarsipedidae, Hypsiprymnodontidae, Solenodontidae, Sminthidae, Zapodidae). This is unsurprising, because these are the families that comprise few species, from 1 to 14. The remaining 15 families are interesting in that they include, in addition to muridoids, also related non-muridoid species. Often, muridoid and non-muridoid species are found even within the same genus. If we want to identify life forms that have descended from a muridoid ancestor, then examining non-muridoid species in otherwise muridoid families and genera is a good place to start.

What were the exact characters that did not fit the definition of muridoids in their closest non-muridoid relatives? These characters are listed in Table 12.

Of course, morphological characters change in the course of evolution, not in isolation, but in a functional complex with other characters. For example, with the shortening of the tail, the hind foot usually also shortens and its structure changes. Particular characters can only serve as an indicator of these changes.

The remarkable thing about the caracters listed in Table 12 is that the same changes occur independently in different families. The second important point is that all these changes are adaptive in nature. In other words, in different families, species adapt to the same environmental conditions, in the same way. In the course of adaptive evolution, muridoids have transformed not just into other ecomorphs, but into very particular ecomorphs, and these ecomorphs are repeated in different families and orders.

It is noteworthy that among many formal "non-muridoids", the original muridoid structure remains clearly visible. For example, a gerbil with a tufted tail may otherwise not differ in appearance

Table 12. Non-muridoid characters in species from muridoid families

Character	Taxa
Spiny armour	***Erinaceidae*** (*Erinaceinae*), ***Tenrecidae*** (*Echinops*, *Setifer*)
Vertically flattened tail	***Talpidae*** (*Desmana*), ***Potamogalidae*** (*Potamogale*), ***Cricetidae*** (*Ondatra*)
Short tail	non-muridoid ***Peramelidae***, ***Erinaceidae*** and ***Talpidae***, ***Soricidae*** (in 6 genera), ***Tenrecidae*** (*Oryzorictes*), ***Muridae*** (*Leimacomys*) ***Cricetidae*** (many hamsters and voles, 6 genera of *Sigmodontine*), ***Nesomyidae*** (*Mystromys*, *Saccostomus*, *Malacothrix*), ***Echimyidae*** (4 genera)
Tufted tail	***Dasyuridae*** (in 5 genera), ***Muridae*** (in 20 genera), ***Cricetidae*** (in 20 genera), ***Nesomyidae*** (*Eliurus*, *Mactotarsomys*), ***Gliridae*** (*Eliomys*, *Chaetocauda*), ***Heteromyidae*** (in 8 genera), ***Abrocomidae*** (*Abrocoma bolivensis*)
Bushy tail	***Didelphidae*** (*Cauromys*, *Glironia*); ***Dasyuridae*** (*Dasyurus*, *Sarcophilus*, part of *Myoictis*), ***Muridae*** (*Crateromys*, *Lophiomys*), ***Cricetidae*** (*Neotoma cinerea*), ***Nesomyidae*** (*Nesomys lambertoni*), ***Gliridae*** (most species), ***Echimyidae*** (part of *Isothrix*, *Mesocapromys melanurus*, *Mysateles*)

Character	Taxa
Webbing between digits	***Didelphidae*** (*Chironectes*), ***Soricidae*** **(***Nectogale*), ***Talpidae*** (*Desmana*, *Galemys*), ***Tenrecidae*** (*Microgale mergulus*), ***Potamogalidae*** (*Micropotamogale ruwenzorii*), ***Muridae*** (*Hydromys*, *Crossomys*), ***Cricetidae*** (*Rheomys*, *Lundomys*, *Holochilus*, *Amfinectomys*, *Nectomys*), ***Echimyidae*** (*myocastor*)
Forelimbs modified for digging	***Soricidae*** (*Surdisorex*), ***Talpidae*** (most species), ***Cricetidae*** (*Geoxus*, *Paynomys*)
Shortened hind limbs due to transition to trotting	***Erinaceidae*** (*Erinaceinae*), ***Tenrecidae*** (*Tenrecinae*), ***Muridae*** (*Lophiomys*) ***Cricetidae*** (hamsters, voles), ***Nesomyidae*** (*Mystromys*, *Saccostomus*, *Malacothrix*)
Elongated forelimbs due to transition to galloping	***Dasyuridae*** (*Antechinomys*, *Dasyurus*, *Sarcophilus*); in kultarr (*Antechinomys laniger*) both pairs of limbs are elongated
Elongated hind limbs due to transition to bipedal locomotion	***Muridae*** (*Notomys*), ***Heteromyidae*** (*Dipodomys*, *Microdipodops*)

from a closely related gerbil without a tuft. At the same time, other "non-muridoids" have completely lost their resemblance to muridoids, for example, hedgehogs. Such a difference can be explained by the stage of adaptive evolution of these species, but ultimately the main reason lies in the preservation or change of the original type of locomotion. Similarity to muridoids is preserved in those species that have retained the fast gait inherent in muridoids – a four-legged ricochet – and this similarity disappears in the case of transition to other types of locomotion: swimming, digging, climbing, and running by trot or gallop.

Muridoid structure is lost especially quickly in the course of transition to a subterranean way of life. It is not by chance that there are so few subterranean forms among muridoids. The original muridoid structure changes to a lesser extent during transition to the aquatic and, especially, to the arboreal way of life. This is because the muridoid body structure, up to a certain level of specialization, is suitable for a semi-aquatic or climbing way of life and does not require significant restructuring.

The situation is more complicated with terrestrial specialization. Although most muridoids are predominantly terrestrial, they are, with rare exceptions, not adapted to a completely terrestrial way of life. Movement on the ground surface, especially in the open, is very dangerous for a small animal. In the course of adaptive evolution, the problem of safe movement on the ground has been solved in muridoid families in two different ways: 1) by changing the gait to a faster one and 2) by forming protective armour. Both ways lead to a change of ecomorph. Thus, hopping mice (*Notomys*) as well as kangaroo rats (*Dipodomys*) and kangaroo mice (*Microdipodops*) switched to a bipedal ricochet, and the kultarr (*Antechinomys laniger*, *Dasyuridae*), judging by its body structure, to a semi-paired gallop. Hedgehogs and hedgehog-like tenrecs acquired a protective armour of spines. They also changed their gait, but to a slower one, since they could afford it.

5.2. Non-muridoid ecomorphs in muridoid families

Which ecomorphs can be seen among non-muridoid species within muridoid families? Below is a preliminary list of these ecomorphs along with a brief description. Ecomorphs are grouped in the list according to their preferred habitats: aquatic, subterranean, terrestrial and arboreal. The taxonomic composition of these ecomorphs is shown in Table 13.

"Water rats" (hydromyoids) are morphologically adapted to a semi-aquatic way of life and an animalivorous diet. They differ from "muridoid hydromyoids" by webbing between the digits. A typical representative is the Australian water rat or rakali (*Hydromys chrysogaster*). However, the presence of webbing does not always indicate a higher level of specialization – such highly specialized semi-aquatic species as the muskrat and otter shrew do without webbing. This, as well as the phylogenetic proximity and morphological similarity of many muridoid and non-muridoid hydromyoids, allows us to consider them also as variants of the same ecomorph. In the ecomorphological sense, the ancestors of hydromyoids could have been rattoids or hydromyoid muridoids. Hydromyoids occur in 6 muridoid families among marsupials, insectivores, afrosoricids, and rodents.

Hydromys chrysogaster

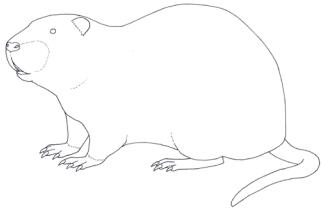
"Desmans" (desmanoids). This group includes the Pyrenean desman (*Galemys pyrenaicus*) and Russian desman (*Desmana moschata*). Unlike hydromyoids, in desmans, not only the hind limbs, but also the forelimbs are adapted for swimming, and the muzzle is very long. Desmans are clearly of sorexoid origin.

Desmana moschata

"Otters" (lutroids). The only representative of this ecomorph among muridoid families is the giant otter shrew (*Potamogale velox*). It differs markedly in body shape from hydromyoids and resembles a small otter, rather than a rat. This body structure is associated with swimming mostly by fluctuation of the tail and trunk rather than the hind limbs. The hind feet of the otter shrew are relatively short and without webbing. The ecomorphological origin of the otter shrew is unclear, but it may have had a muridoid origin.

Potamogale velox

"Beavers" (castoroids). This group includes two representatives of muridoid families: muskrat (*Ondatra zibethicus*) and coypu (*Myocastor coypus*), which differ in body shape from muridoids only in a vertically flat tail (muskrat) or the presence of webbing (coypu). Both species are undoubtedly more specialized than the semi-aquatic arvicoloid muridoids, but still differ only slightly from them, especially in the case of the muskrat. On the other hand, they have a clear ecomorphological resemblance to beavers that have completely lost their muridoid appearance. The muridoid origin of the muskrat and coypu is obvious. They belong to two different families of rodents.



Myocastor coypus

"Moles" (talpoids) are animalivorous species with forelimbs that are modified for digging to an extent that prevents locomotion with the quadrupedal ricochet characteristic of muridoids. Typical representatives are moles of the genus *Talpa*. Talpoids apparently originated from shrew-like (sorexoid) ancestors – transitional forms are found in all muridoid families where there are talpoids. There are 4 such families among insectivores, afrosoricids, and rodents.

Talpa stankovici

"Mole-rats" (spalacoids) are herbivorous subterranean species, with a cylindrical body, short legs and wide incisors, some with forelimbs modified for digging. A typical representative is the greater blind mole-rat (*Spalax microphthalmus*). Among muridoid families, spalacoids are found only in two genera of cricetids, more precisely, in the subfamily of voles. They are the long-clawed vole (*Prometheomys schaposchnikowi*) and the mole voles (*Ellobius*). These animals are clearly descended from arvicoloid ancestors. In the ecomorphological sense, a transitional form between arvicoloids and spalacoids is the mountain water vole (*Arvicola monticola*).

Ellobius tancrei

"Short-tailed shrews" (sorexoids). This group includes shrews and similar species that do not meet the formal definition of muridoid due to their short tails. It is possible that this is a transitional group between the sorexoids and the "hedgehogs" (gymnures) or the "moles" (shrews). "Short-tailed shrews" occur in two muridoid families among insectivores.

Surdisorex norae

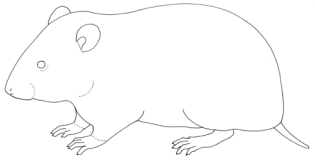
"Badgers" (melesoids) are species that are morphologically adapted to rumagging in plant litter and soil, and movement on the ground surface. They are characterized by a long snout and elongated front claws. Among muridoid families, melesoids are found in 6 genera of bandicoots and 2 genera of tenrecs (*Hemicentetes*, *Tenrec*). Unlike true badgers, bandicoots and tenrecs are clearly sorexoid in origin. With larger size, it becomes more convenient for shrew-like animals to forage on the soil surface rather than within it. Bandicoots and similar tenrecs can be distinguished into an ecomorph of a lower rank – ***"bandicoots" (perameloids).*** Among the muridoids, the moonrat (*Echinosorex gymnura*) and the solenodons (*Solenodontidae*) are most similar to "bandicoots". At the same time, both bandicoots and melesoid tenrecs display an ecomorphological similarity to hedgehogs. Moreover, the tailless tenrec (*Tenrec ecaudatus*) and the streaked tenrecs (*Hemicentetes*) have spines, while spiny bandicoots (*Echymipera*) are covered in spine-like bristles. "Badgers" occur in two muridoid families among marsupials and afrosoricids.

Isodon macrourus

"Hedgehogs" (erinaceoids) are animalivorous or omnivorous species covered with a spiny armour. A typical representative is the European hedgehog (*Erinaceus europaeus*). The evolutionary transition from "shrews" to "bandicoots" and then to "hedgehogs" is well demonstrated by recent tenrecs. Unlike all previously mentioned ecomorphs, the appearance of "hedgehogs" is determined not only by the peculiarities of locomotion and feeding, but primarily by the defence strategy. That is, "hedgehogs" are partly a protectomorph, similar in their defensive strategy to the herbivorous ecomorph of "porcupines". Ecomorphological "hedgehogs" are represented in two muridoid families among insectivores and afrosoricids.

Atelerix sclateri

"Hamsters" (cricetoids) are most similar to typical muridoids (to normal-muzzled rattoids). In body shape, they differ from muridoids in their shortened hind legs and tail. These peculiarities are associated with living in dense vegetation, where running in search of food and away from enemies is not necessary and even not always possible. Among true hamsters (*Cricetinae*), relatively slow locomotion is compensated by aggressiveness. A typical representative is the common hamster (*Cricetus cricetus*). The muridoid origin of "hamsters" is clear. Cricetoids occur in three muridoid families among rodents.



Cricetus cricetus

"Voles" (arvicoloids) are species that are morphologically adapted to herbivory, living among herbaceous vegetation and digging burrows. They have a broad head with a blunt muzzle, usually small eyes, backward-pointing ears, a short tail, short legs, and straightened claws. Typical representatives are voles of the genus *Microtus*. Arvicoloids are clearly of muridoid origin. The transitional form is arvicoloid muridoids. Arvicoloids occur in two muridoid families among rodents.

Microtus paradoxus

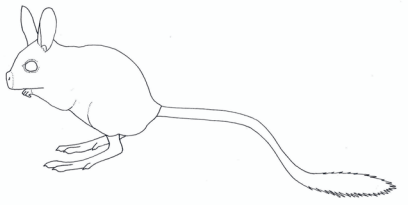
"Short-tailed hutias" (capromyoids). The least understood group that unites part of the hutias – large herbivorous rodents. The short-tailed hutias are similar to the other hutias classified here as muridoids and "squirrels" (see below). In an ecomorphological sense, "hutias" may be the predecessors of "porcupines". Capromyoids are found in only one muridoid family among rodents (*Echimyidae*).

Geocapromys brownii

"Gerbils" (gerbilloids) are species that are adapted to rapid movement on the ground with a four-legged ricochet. They have relatively long, narrow hind feet, with shortened extreme digits or all digits. They differ from gerbilloid muridoids only by the presence of a tuft at the end of the tail. Typical representatives are gerbils of the genus *Meriones*. Judging by the numerous transitional forms, they are of rattoid origin. Gerbilloids are found in 5 muridoid families among marsupials and rodents.

Meriones tamariscinus

"Jerboas" (dipodoids) are bipedal species. Typical representatives are jerboas of the genus *Allactaga*. Dipodoids are probably gerbilloid in origin. They occur in two muridoid families among rodents.



Allactaga major

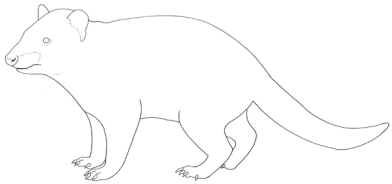
"Jumping shrews" (elephantuloids) are species that are adapted to movement by a semi-paired gallop, with elongated hind and forelimbs. Typical representatives are the elephant shrews (*Elephantulus*). The only representative of this ecomorph in muridoid families is the kultarr (*Antechinomys laniger*, *Dasyuridae*). The ancestors of the elephantuloids were probably gerbilloid muridoids or gerbilloids.

Antechinomys laniger

"Weasels" (musteloids) have a weasel-like body structure. Unlike muridoids, their fore limbs and hindlimbs are aligned in length, the neck is noticeable, and the tail is bushy. Typical representatives are weasels (*Mustela*). Musteloids are found in only one muridoid family, among dasyurid marsupials (*Dasyuridae*) of the genus *Dasyurus* (quolls). In the least specialized species of *Dasyurus*, the muridoid origin is obvious. The lutrine opossums (*Lutreolina*) have a body structure that is transitional between muridoid and musteloid.

Dasyurus maculatus

"Hyenas" (hyenoids) are species that are morphologically adapted to running and eating carrion. The only representative of this ecomorph in muridoid families is the Tasmanian devil (*Sarcophilus harrisii*). It bears little resemblance to a hyena, but is somewhat more like another scavenger, the wolverine. The origin of the marsupial devil is not directly muridoid – it went through a more complex path of adaptive evolution.



Sarcophilus harrisii

"Cuscuses" (phalangeroids). This group includes species that are adapted to climbing with the help of grasping limbs and a long bushy and tapering tail, often prehensile. A typical representative is the spotted cuscus (*Spilocuscus maculatus*). In muridoid families, this group includes some specialized arboreal opossums (part of *Caluromys*, *Glironia venusta*). They are clearly of muridoid origin.

Caluromys lanatus

"Dormice" (gliridoids) are species that are morphologically adapted for both climbing and movement on the ground, with a long, tufted tail. A typical representative is the garden dormouse (*Eliomys quercinus*). "Dormice" from muridoid families are clearly of muridoid origin. The transitional form is gliridoid muridoids. They are found in 7 muridoid families among marsupials and rodents.

Eliomys quercinus

"Squirrels" (sciuroids) are species that are morphologically adapted to climbing, mainly with the help of claws and a long bushy tail. A typical representative is the red squirrel (*Sciurus vulgaris*). Most of the "squirrels" from the muridoid families are clearly of muridoid origin. Sciuroids are found in 5 muridoid families among marsupials and rodents.

Glis glis

Table 13. Non-muridoid ecomorphs in muridoid families and their taxonomic composition

Ecomorph	**Taxa** (in brackets are given a number of orders/families/genera)
"Water rats" (hydromyoids)	**Didelphimorphia:** ***Didelphidae*** (*Chironectes*); **Eulipotyphla:** ***Soricidae*** (*Nectogale*), **Afrosoricida:** ***Tenrecidae*** (*Microgale mergulus*), ***Potamogalidae*** (*Micropotamogale ruwenzorii*); **Rodentia:** ***Muridae*** (*Hydromys*, *Crossomys*), ***Cricetidae*** (5 genera); (4/6/11)
"Desmans" (desmanoids)	**Eulipotyphla:** ***Talpidae*** (*Desmana*, *Galemys*); (1/1/2)
"Otters" (lutroids)	**Afrosoricida:** ***Potamogalidae*** (*Potamogale*); (1/1/1)
"Beavers" (castoroids)	**Rodentia:** ***Cricetidae*** (*Ondatra*), ***Echimyidae*** (*Myocastor*); (1/2/2)
"Moles" (talpoids)	**Eulipotyphla:** ***Soricidae*** (*Surdisorex*) ***Talpidae*** (17 genera); **Afrosoricida:** ***Tenrecidae*** (*Oryzorictes*); **Rodentia:** ***Cricetidae*** (*Blarinomys*, *Geoxus*, *Notiomys*); (3/4/22)
"Mole-rats" (spalacoids)	**Rodentia:** ***Cricetidae*** (*Ellobius*, *Prometheomys*); (1/1/2)
"Short-tailed shrews" (sorexoids)	**Eulipotyphla:** ***Erinaceidae*** (3 genera of gymnures), ***Soricidae*** (7 genera); (1/2/10)
"Badgers" (melesoids)	**Peramelemorphia:** ***Peramelidae*** (6 genera); **Afrosoricida:** ***Tenrecidae*** (*Hemicentetes*, *Tenrec*); (2/2/8)
"Hedgehogs" (erinaceoids)	**Eulipotyphla:** ***Erinaceidae*** (5 genera: all *Erinaceinae*); **Afrosoricida:** ***Tenrecidae*** (*Echinops*, *Setifer*); (2/2/7)
"Hamsters" (cricetoids)	**Rodentia:** ***Muridae*** (*Leimacomys*, *Lophiomys*), ***Cricetidae*** (6 genera: most *Cricetinae*, *Galenomys*), ***Nesomyidae*** (*Mystromys*, *Saccostomus*, *Malacothrix*); (1/3/11)

"Voles" (arvicoloids)	**Rodentia: *Cricetidae*** (28 genera: most *Arvicolinae*, *Paynomys*, *Punomys*), ***Echimyidae*** (*Clyomys*, *Euryzygomatomys*); (1/2/30)
"Short-tailed hutias" (capromyoids)	**Rodentia: *Echimyidae*** (*Plagiodontia*, *Geocapromys*); (1/1/2)
"Gerbils" (gerbilloids)	**Dasyuromorphia: *Dasyuridae*** (*Dasycercus*, *Dasyuroides*, *Sminthopsis longicaudata*); **Rodentia: *Muridae*** (8 genera of gerbils), ***Cricetidae*** (4 genera of *Sigmodontine*), ***Nesomyidae*** (*Mactotarsomys*), ***Heteromyidae*** (*Perognathus alticola*, part of *Chaetodipus*); (2/5/18)
"Jerboas" (dipodoids)	**Rodentia: *Muridae*** (*Notomys*), ***Heteromyidae*** (*Dipodomys*, *Microdipodops*); (1/2/3)
"Jumping shrews" (elephantuloids)	**Dasyuromorphia: *Dasyuridae*** (*Antechinomys laniger*); (1/1/1)
"Weasels" (musteloids)	**Dasyuromorphia: *Dasyuridae*** (*Dasyurus*, part of *Myoictis*); (1/1/2)
"Hyenas" (hyenoids)	**Dasyuromorphia: *Dasyuridae*** (*Sarcophilus*); (1/1/1)
"Cuscuses" (phalangeroids)	**Didelphimorphia: *Didelphidae*** (*Caluromys*, *Glironia venusta*); (1/1/2)
«Dormice" (gliridoids)	**Dasyuromorphia: *Dasyuridae*** (*Phascogale*); **Rodentia: *Muridae*** (14 genera), ***Cricetidae*** (16 genera), ***Nesomyidae*** (*Eliurus*), ***Gliridae*** (*Eliomys*, *Chaetocauda*), ***Echimyidae*** (8 genera), ***Abrocomidae*** (*Abrocoma bolivensis*); (2/7/44)
"Squirrels" (sciuroids)	**Rodentia: *Muridae*** (*Crateromys*), ***Cricetidae*** (*Neotoma cinerea*), ***Gliridae*** (7 genera), ***Echimyidae*** (*Mesocapromys melanurus*, *Mysateles*, part of *Isothrix*); (1/4/12)

Muridoid families with non-muridoid species are found in 6 orders. At the order level, the most widely represented are "water rats" (4 orders). They are followed by "moles" (3 orders). At the level of families, the most widely represented are "dormice" (7 families out of 15), non-muridoid "water rats" (6 families), "gerbils", and "squirrels" (5 families each). At the level of genera, "dormice" are the most widespread – they occur in 44 genera of muridoid families (out of 190), "voles" are in second place (30 genera), and "moles" are in third place (22 genera). Other common ecomorphs are "gerbils" (17 genera), "squirrels" (13 genera), "water rats" (11 genera) and "hamsters" (11 genera).

From the ecomorphological perspective, the levels of order and family are the most indicative, since they reflect adaptive evolution (including parallel and convergent evolution) rather than phylogeny, while the latter may prevail at the level of genus. For example, the similarity of 17 genera of true moles among themselves can be explained by their kinship, but this does not explain their similarity to mole-like rodents from the subfamily *Sigmodontine*. If we summarize the data from the previous paragraph, we find that at the level of orders and families, the most widely represented are "water rats" (4 orders / 6 families), "moles" (3/4), "gerbils" (2/5), "dormice" (2/7), and "squirrels" (2/5). It is immediately apparent that these most common non-muridoid ecomorphs correspond to the main directions of adaptive evolution: towards living in water, underground, on the ground surface, and on plants.

Most non-muridoid ecomorphs from the muridoid families probably descended directly from muridoids (**secondary ecomorphs)**, while some others had intermediate stages (**tertiary ecomorphs)**. There are only two tertiary ecomorphs in muridoid families: "hedgehogs" and "hyenas". "Hedgehogs", judging by the transitional forms, have passed the stage of "bandicoots" in the process of evolution, and the Tasmanian devil may have passed the stage of "weasel".

It should be remembered that one high-ranking ecomorph can include species that not only have different phylogenetic origin, but also different ecomorphological origin. Thus, for example, quolls or "marsupial martens" (*Dasyurus*) are, judging by their body structure, most likely of muridoid origin, while true martens (*Martes*), which belong to the same ectomorph, "weasels", have taken a longer path of adaptive evolution. Such differences in the ecomorphological origin of species within the same ecomorph is reflected by body structure and can serve as a criterion for distinguishing subdivisions within ecomorphs. An example is the "bandicoots" inside the "badgers".

5.3. Non-muridoid ecomorphs from muridoid families among mammals in general

In the previous section, the non-muridoid ecomorphs from muridoid families, that is, in those families that include muridoids, were tentatively outlined and described. From the names of these ecomorphs alone, it is clear that they are also found in other families of mammals. We may consider in which orders and families they occur, and how diverse is their taxonomic composition (Table 14).

Table 14 shows that the 20 non-muridoid ecomorphs under consideration are found in 13 orders (46%) and 58 families (36%) of mammals: in both families of monotremes, in 5 orders and 10 families of marsupials, in 3 families of insectivores, in all three families of afrosoricids, in the only family of elephant shrews, in 25 families of rodents, in both families of tree shrews, in three families of primates and in 8 families of carnivores.

These figures indicate that non-muridoid ecomorphs found in muridoid families are also widespread outside the latters. Moreover, 37 non-muridoid families and 4 orders of mammals (monotremes, marsupial moles, elephant shrews, tree shrews) consist exclusively of these ecomorphs. Since most of the considered ecomorphs are of direct muridoid origin, it is possible that the muridoids were also

Table 14. Non-muridoid ecomorphs from muridoid families among mammals in general. (Within each order the non-muridoid families are placed at the end of the list. The composition of muridoid families is specified in Table 13)

Ecomorph	**Taxa** (in brackets are given a number of orders/families)
"Water rats" (hydro myoids)	**Didelphimorphia:** *Didelphidae*, **Eulipotyphla:** *Soricidae*; **Afrosoricida:** *Tenrecidae*, *Potamogalidae*; **Rodentia:** *Muridae*, *Cricetidae*; (4/6)
"Desmans" (desmanoids)	**Monotremata:** *Ornithorhynchidae*; **Eulipotyphla:** ***Talpidae*** (*Desmana*, *Galemys*); (2/2)
"Otters" (lutroids)	**Afrosoricida:** *Potamogalidae*; **Carnivores:** *Viverridae* (*Cynogale*), *Mustelidae* (*Lutrinae* except sea otter); (2/3)
"Beavers" (castoroids)	**Rodentia:** *Cricetidae*, *Echimyidae*, *Castoridae*; (1/3)
"Moles" (talpoids)	**Notoryctemorphia:** *Notoryctidae*; **Eulipotyphla:** *Soricidae*, *Talpidae*; **Afrosoricida:** *Tenrecidae*, *Chrysochloridae*; **Rodentia:** *Cricetidae*; (4/6)
"Mole-rats" (spalacoids)	**Rodentia:** *Cricetidae*, *Spalacidae*, *Aplodontiidae*, *Geomyidae*, *Heterocephalidae*, *Bathyergidae*, *Ctenomyidae*, part of *Octodontidae* (*Spalacopus*) (1/8)
"Short-tailed shrews" (sorexoids)	**Eulipotyphla:** *Erinaceidae*, *Soricidae*
"Badgers" (melesoids)	**Peramelemorphia:** *Chairopodidae*, *Peramelidae*, *Thylacomyidae*; **Afrosoricida:** *Tenrecidae*; **Carnivora:** *Herpestidae* (*Crossarchus*), *Eupleridae* (*Eupleres*), *Mustelidae* (*Melogale*, *Melinae*), *Mephitidae* (*Conepatus*, *Mephitis*, *Mydaus*); (3/8)
"Hedgehogs" (erinaceoids)	**Monotremata:** *Tachyglossidae*; **Eulipotyphla:** *Erinaceidae*; **Afrosoricida:** *Tenrecidae*; (3/3)
"Hamsters" (cricetoids)	**Rodentia:** *Muridae*, *Cricetidae*, *Nesomyidae*; (1/3)
"Voles" (arvicoloids)	**Rodentia:** *Cricetidae*, *Echimyidae*, *Thryonomyidae*, part of *Octodontidae* (*Aconaemys*); (1/4)

"Short-tailed hutias" (capromyoids)	**Rodentia:** *Echimyidae*, *Dinomyidae* (*Dinomys brankickii*); (1/2)
"Gerbils" (gerbilloids)	**Dasyuromorphia:** *Dasyuridae*; **Rodentia:** *Muridae*, *Cricetidae*, *Nesomyidae*, *Heteromyidae*, part of *Octodontidae*; (2/6)
"Jerboas" (dipodoids)	**Diprotodontia:** *Potoroidae*, most of the *Macropodidae*; **Rodentia:** *Muridae*, *Heteromyidae*, *Dipodidae*, *Pedetidae*; (2/6)
"Jumping shrews" (elephantuloids)	**Dasyuromorphia:** *Dasyuridae*; **Macroscelidea:** *Macroscelididae*; (2/2)
"Weasels" (musteloids)	**Dasyuromorphia:** *Dasyuridae*; **Carnivora:** *Nandiniidae*, *Herpestidae*, *Eupleridae*, *Viverridae*, *Mustelidae*, *Procyonidae* (*Bassaruscus*, *Bassaricyon*), *Mephitidae* (*Spilogale*); (2/8)
"Hyenas" (hyenoids)	**Dasyuromorphia:** *Dasyuridae*; **Carnivora:** *Hyaenidae* (*Hyaena*, *Crocuta*), *Mustelidae* (*Gulo*); (2/1)
"Cuscuses" (phalangeroids)	**Didelphimorphia:** *Didelphidae*; **Diprotodontia:** *Phalangeridae* (*Ailuropinae*, *Phalangerinae*), *Pseudocheiridae* (*Pseudocheirinae*, *Pseudochiropsinae*); (2/3)
"Dormice" (gliridoids)	**Dasyuromorphia:** *Dasyuridae*; **Rodentia:** *Muridae*, *Cricetidae*, *Nesomyidae*, *Gliridae*, *Echimyidae*, *Abrocomidae*, *Calomyscidae*, *Platacanthomyidae*, part of *Octodontidae*; **Scandentia:** *Ptilocercidae*; (3/11)
"Squirrels" (sciuroids)	**Diprotodontia:** *Phalangeridae* (*Trichosurinae*), *Pseudocheiridae* (*Hemibelideinae*), *Petauridae*, *Acrobatidae*; **Rodentia:** *Muridae*, *Cricetidae*, *Gliridae*, *Echimyidae*, part of *Sciuridae* (chipmunks, squirrels, flying squirrels), *Zenkerellidae*, *Anomaluridae*, *Diatomyidae*, *Petromuridae*; **Scandentia:** *Tupaiidae*, **Primates:** *Cheirogaleidae*, *Daubentoniidae*, *Galagidae*; (4/17)

present in some of the families that do not currently contain them. "In some families", because the same ecomorph can have a different origin not only in the phylogenetic, but also in the ecomorphological, sense, as was shown above in the example of quolls and martens.

Only three of the 20 ecomorphs listed in Table 14 are unique to muridoid families. These are "water rats", "short-tailed shrews" and "hamsters". All of them are only slightly different from muridoids. "Hamsters", for example, are essentially "short-tailed rattoids". Both "hamsters" and "short-tailed shrews" are probably transitional forms between muridoids and other ecomorphs ("voles", "moles" and "hedgehogs"). The adaptive evolution of "water rats" does not seem to have gone any further.

5.4. At the summit of mammalian specialization

A comprehensive survey of all mammalian life forms is beyond the scope of this study, but it is difficult to resist the temptation to take at least a cursory glance at the ecomorphological diversity of mammals in general.

We have already discussed muridoids, as well as non-muridoid ecomorphs found in the same families as muridoids (Table 15). The following list includes mammals that differ ecomorphologically from all forms so far mentioned.

Aquatic: whales and dolphins; sirens; pinnipeds, sea otter; capybaras; hippopotamids.

Subterranean: fairy armadillos (*Chlamyphorinae*)

Terrestrial: wombats; aardvark; terrestrial pangolins (*Pholidota*); terrestrial armadillos; giant anteater; terrestrial monkeys (e.g. baboons); pikas and hares; many rodents (of the families *Sciuridae*, *Ctenodactylidae*, *Hystricidae*, *Erethizontidae*, *Caviidae*, *Dasyproctidae*, *Cuniculidae*, *Chinchillidae*); many carnivores: fossa

(*Cryptoprocta ferox*), some civets (*Civetictis*, *Viverra*), felids, canids, aardwolf (*Proteles cristatus*), raccoons, coatis (*Nasua*, *Nasuella*), bears; hyraxes; elephants; artiodactyls; tapirs, rhinoceroses, equids.

Arboreal: koalas, tree kangaroos; arboreal pangolins; arboreal anteaters, sloths; most primates; colugos (*Dermoptera*); most New World porcupines (*Erethizontidae*); part of carnivores: some viverrids (e.g. binturong), Asiatic linsangs (*Prionodontidae*), kinkajou (*Potos flavus*), red panda.

Flying: bats.

This list represents taxa, not ecomorphs. However, thanks to the distribution of taxa according to their ecological strategies, ecomorphologically similar forms happen to be nearby, making it easier to notice their similarities. For example, the similarities between pinnipeds and sea otters, capybaras and hippos, koalas and sloths.

It turned out to be much easier to separate specialized taxa according to ecological strategies, than it was for muridoids. However, even among specialists, there are species that are "inconvenient" for classification, for example, raccoons. They can sleep both in a tree hollow and in a burrow, and can collect food in water, on the ground and in trees.

A detailed analysis of non-muridoid ecomorphs is a task for future research.

5.5. The role of muridoids in the adaptive evolution of mammals

The results of this study of muridoids confirm that the evolution of mammals does not proceed chaotically, but in certain directions. These are exactly the directions that Henry Osborn identified more than a hundred years ago in his article "The law of adaptive radiation" (Osborn, 1902). In a slightly modified form, these directions have been

described here as an adaptation to living 1) in water, 2) underground, 3) on the ground, 4) in trees, and feeding on 5) other animals, 6) the generative parts of plants or 7) the vegetative parts of plants.

Why does adaptive evolution proceed in these main directions? That is because there are no other locomotor and feeding opportunities for mammals on our planet. Therefore, any taxon can actually or potentially evolve only in the seven main directions listed above.

Not only is the choice of substrates and food the same for all taxa, during transition to a new environment or a new feeding strategy, representatives of different taxa face the same problems. These problems can be solved in different ways, but the number of options is not infinite. Therefore, the same morphological solutions are inevitably repeated in different phylogenetic lineages, as well as combinations of these solutions, that is, ecomorphs.

Ecomorphs are usually the result of specialization, sometimes very narrow specialization. This is not the case with muridoids. Muridoids lack a narrow morphological specialization, and the range of ecological specialization is unusually wide. Muridoids are the only mammalian ecomorph that has mastered all seven major trends of ecological specialization. Among them there are aquatic, subterranean, terrestrial, arboreal, animalivorous, frugivorous, and herbivorous forms. Consequently, **muridoids are not only the most ancient, but also the most versatile mammalian ecomorph.**

A consequence of the ecological versatility of the muridoids is that their further evolution is possible only towards more narrow specialization, which often leads to the loss of muridoid structure. There are many transitional forms from the muridoids to other ecomorphs, but I don't know any cases of evolution in the opposite direction. Of course, despecialization occurs in nature, but the result of it is not a muridoid. Squirrels, for example, descended during evolution to the ground (Steppan et al., 2004), but ground squirrels, and not rats, emerged from this transition. Some examples of transitional forms between muridoids and other ecomorphs are shown in Figure 11.

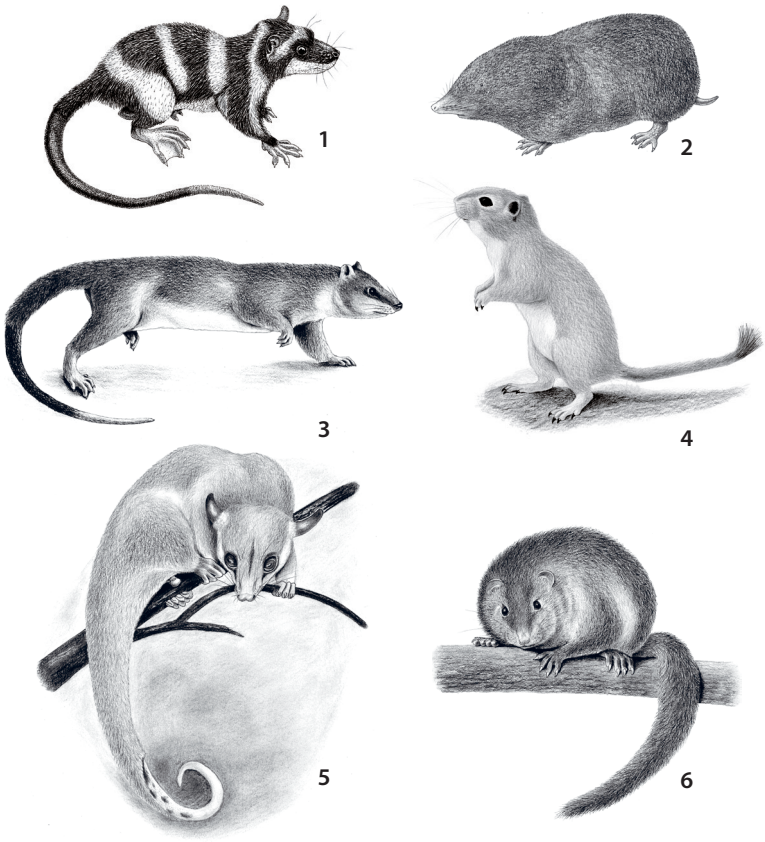


Fig. 11. Visible evolution: some transitional forms between muridoids and other ecomorphs.
1 – The water opossum (*Chironectes minimus*, Didelphidae) is a non-muridoid with obvious muridoid origin; 2 – the Chinese mole shrew (*Anourosorex squamipes*, Soricidae) is a shrew on its way to becoming a "mole"; 3 – the lutrine opossum (*Lutreolina crassicaudata*, Didelphidae) in the morphological sense is no longer quite a "rat," but not yet a "mongoose"; 4 – the great gerbil (*Rhombomys opimus*, Muridae) has a tuft on its tail, which makes jumping more manoeuvrable; otherwise it has a muridoid body structure; 5 – the brown-eared woolly opossum (*Caluromys lanatus*, Didelphidae) is on the way from a "rat" to "cuscus" morphology; 6 – the Panay cloud rat (*Crateromys heaneyi*) looks like a squirrel, but taxonomically it is a rat – a member of the family Muridae.

The primitive structure of muridoids, along with their great ecological diversity and the abundance of transitional forms to other ecomorphs, indicate a special role of muridoids in the evolution of mammals. Analogous to the process of development of an organism, in which all the diversity of specialized cells is generated by stem cells, the ecomorphological diversity of mammals has apparently been generated by muridoids. **Muridoids represent the original ecomorph from which all other life forms of mammals developed in the course of evolution, either directly or through intermediate stages.** Having given rise to new life forms, muridoids not only persisted, but continue to flourish today, as well as they did in the distant Mesozoic.

CONCLUSIONS. THE MEANING AND SIGNIFICANCE OF THE MOUSE-LIKE BODY STRUCTURE IN MAMMALS

Below are some thoughts that I consider important to highlight.

The essence of mouse-like body structure. Animals with a mouse-like body structure, many of which we call rats and mice in everyday speech, are a **life form** (ecomorph). Since there is no biologically meaningful difference between "rats" and "mice", these names were replaced here by the umbrella term **"muridoids"**.

The meaning of mouse-like body structure. A muridoid is made a muridoid by its locomotion – the use of a four-legged ricochet as a fast gait (run), in which the hind legs are the propulsive legs, and the front legs serve only for landing. In animals that move with a four-legged ricochet, the hind limbs are much longer than the front ones. In addition, this gait requires a balancer in the form of a long tail. This ratio of limbs and tail gives us a mouse-like body structure.

In addition to the gait, the distinctive appearance of muridoids is also determined by the presence of many primitive traits in the body structure, for example, a scaly tail. These traits were inherited from mammals that lived in the Mesozoic, and perhaps their reptilian ancestors. Muridoids are probably the most ancient ecomorph of mammals. Thus, the **mouse-like structure of the body**

is explained by a type of locomotion, as well as by the ancient origin of their morphological traits.

Abundance of muridoids and their significance in nature. Mouse-like body structure occurs in approximately 1927 species of mammals (31%) belonging to 334 genera, 23 families and 9 orders. Consequently, about a third of all mammal species are muridoids. This is the most common life form of recent mammals in terms of the number of species, and probably also by the number of individuals. Muridoids are distributed on all continents except Antarctica and on many islands. They are found almost everywhere where there are terrestrial flightless mammals: from arctic tundra to tropical rainforests, and from lowlands to highlands.

In many habitats, muridoids are represented by a large number of species and individuals. The prosperity of this life form is explained by the exceptional ecological plasticity of muridoids, which is based on the absence of a narrow locomotor specialization. Most of them regularly use several media and surfaces for locomotion (water, soil, ground surface, plants). Muridoids are the only mammalian ecomorph that has mastered all seven major trends of ecological specialization. Among them there are aquatic, subterranean, terrestrial, arboreal, animalivorous, frugivorous and herbivorous forms. At the same time, they retain their mouse-like body structure. Thus, **muridoids are the most common life form of mammals and the most versatile in an ecological sense.** Due to their abundance and ubiquity, muridoids undoubtedly play an important role in ecosystems.

Significance of muridoids in the evolution of mammals. Muridoid body structure has existed for millions of years and continues to dominate among mammals today. However, persistence in time is combined in muridoids with amazing evolutionary plasticity. After all, it was apparently the **muridoids that gave rise to all of the current and extinct life forms of mammals,** either directly or through intermediate stages of morphogenesis.

Despite giving rise to many new life forms, the muridoids not only managed to persist, but continue to flourish today. It seems that in case of a mass extinction of mammals, muridoids would be the last to hang on; or perhaps the ones that survive…

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