

Notes on the external morphology, ecology, and origin of *Megalomys desmarestii* (Sigmodontinae, Cricetidae, Rodentia), the extinct giant rat of Martinique Island, Lesser Antilles

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Abstract. The giant rat of Martinique Island, *Megalomys desmarestii* (Fischer, 1829) became extinct at the end of the 19th or the very beginning of the 20th century. Little is known about its habits. The goal of this research was to reconstruct its ecology using the external and craniodental morphological characters of available museum specimens. On the basis of ecomorphological analysis some suggestions are made about the locomotor abilities, ecological strategies, adaptive evolution, and origin of this rodent. It is proposed that *M. desmarestii* foraged mostly on the ground and sheltered in burrows. Its main food was seeds and fruits, including nuts. It was crepuscular rather than strictly nocturnal or diurnal. The general trends of its adaptive evolution were: (1) increasing body size, (2) transition from an arboreal to a terrestrial/subterranean way of life, and (3) adaptation to eating hard-covered fruits. Thus, the ancestor of *M. desmarestii* was probably smaller and had arboreal or semiarboreal habits. The granulated structure of the soles of *M. desmarestii*'s feet supports a close relationship with *Nectomys*.

Key words: *Megalomys*, Sigmodontinae, pilorie, ecomorphology.

INTRODUCTION

The extinct Antillean giant rats of the genus *Megalomys* (Sigmodontinae, Cricetidae) are known from Pleistocene–Holocene fossils, Pre-Columbian midden deposits, and the modern time. They may formerly have occurred on most of the islands of the Lesser Antilles (Alen, 1942; McFarlane & Lundberg, 2002). Four species were described in the genus: *Megalomys desmarestii* (Fischer, 1829) (known only from Martinique), *M. luciae* Forsyth Major, 1901 (known only from Santa Lucia), *M. audreyae* Hopwood, 1926 (known only from Barbuda), and *M. curacensis* Hooijer, 1959 (known only from Curaçao) (McFarlane & Lundberg, 2002; Musser & Carleton, 2005). All species of *Megalomys* are extinct, possibly all due to anthropogenic causes. *Megalomys luciae* lived on St. Lucia Island until at least 1849, and *M. desmarestii* probably survived until 1902 on Martinique (Alen, 1942; McFarlane & Lundberg, 2002). According to Musser & Carleton (2005), a combination of features suggests that the close relatives of *Megalomys* may be sought among certain derived oryzomyines, such as *Oryzomys sensu stricto*, or *Nectomys*.

The last survivor, the giant rat of Martinique or Desmarest's pilorie, *Megalomys desmarestii* (Fig. 1), was the largest species in the genus. It had a head and body length of about 36 cm, and its tail was only slightly shorter (Trouessart, 1885). There are many factors that may potentially have brought about the extinction of the pilorie: hunting and extermination by people, anthropogenic deforestation of the island, and the introduction of cats, dogs, and mongooses. Its final extinction, however, has been attributed to the great volcanic eruption of Monte Pelée in 1902, the slopes of which seem to have been the pilorie's last refuge (Alen, 1942; Nowak, 1991).

Available information on the ecology of *M. desmarestii* is very scarce. It was summarized by Alen (1942) in the two paragraphs reproduced below:

The Martinique musk-rat was first mentioned in literature by Du Tertre in 1654, in his "Histoire Générale des Isles de S. Christophe, de la Guadeloupe, de la Martinique, et Autres dans l'Amérique". He did not know of it from any of the French islands except Martinique, where, he relates, it was commonly eaten by people ... It was said to live in burrows in the ground and against it the colonists waged war on account of its destructive habits in their plantations. In addition to human enemies, the large serpents of Martinique also attacked it. Du Tertre mentions killing a large snake in the stomach of which was one of these rats "almost as big as a cat".

... The late Dr. G. Kinsley Noble, who in 1914 visited Guadeloupe ... was told by Mr. Delphin Duchamp, a former resident of Martinique, that "about five years before the eruption of Mount Pelée [1902] there used to exist in great numbers among the cocoanut plantations along the Rivière Blanche, close to St. Pierre, a species of rat which was black as coal on the back and white as milk below. When adult this creature was some 40 cm long without the tail. I killed many of them,



Fig. 1. Subadult specimen of *Megalomys desmarestii* (MNHN CG 2006-188) mounted with skull. Note a very short rostrum.

for their flesh is very delicate. The negroes call this rat the pilorie. It lives almost entirely in [? among – G.A.] the cocoanut trees but will take to water when driven from shelter.

I am aware of no additional data on the ecology of the pilorie. All later authors just repeat or paraphrase the information cited above (e.g. Nowak, 1991 and internet resources). Given that this is the extent of existing information, what can we learn from it? (1) The pilories were somehow connected with trees, probably feeding on their parts or/and having arboreal habits (“Exist among the cocoanut plantations”, “It lives almost entirely in [? among] the cocoanut trees”). (2) Probably they were partly subterranean (“It was said to live in burrows in the ground.”). (3) Probably they were good swimmers or even semiaquatic (“It ... will take to water when driven from shelter.”). (4) They were plant-eaters, because they caused damage to the coconut plantations. The nature of the damage, which may clarify the diet of the rats, however, is unclear. (5) Snakes were among their natural enemies.

Thus, the available data on the ecology of Desmarest’s pilorie are fragmentary and partly contradictory (in points 1 and 2). Indeed, it is highly unlikely that such a rather large arboreal animal lived also in burrows, and vice versa – a relatively large burrowing species lived in trees. One obvious reason for this doubt is incompatibility of the shape of the claws in arboreal and subterranean animals. Claws should be blunt in burrowers, but sharp in climbers. This contradiction was noted also by Alen (1942), who supplied the corresponding quotation with his own remark ‘in [? among] trees’. The relationship of the pilorie with water also remains uncertain, as does its diet.

On the basis of available data we may create three hypotheses concerning the space utilization strategy of *M. desmarestii*: (1) it was arboreal or semiarboreal; (2) it was partly subterranean; (3) it was semiaquatic. The goal of this article is to test these three hypotheses by evaluating the ecology-dependent morphological characters of *M. desmarestii*. The ecology-dependent morphological characters are those that are connected with an animal’s habits: locomotion, feeding, defence, etc. The choice of these characters was made in a previous study (Miljutin, 1997). Besides, in the course of this work certain features were found that throw light on the origin and evolution of this species.

MATERIAL AND METHODS

As far as I know, only three museums in the world have specimens of *Megalomys desmarestii* in their collections: Natural History Museum in London, National Museum of Natural History in Leiden (1 mounted specimen and 1 skull), and Muséum National d’Histoire Naturelle in Paris (see below for details). I had the opportunity to examine five specimens of *Megalomys desmarestii* stored in the collection of Muséum National d’Histoire Naturelle in Paris (MNHN): three mounted specimens, one ethanol-preserved specimen, and one formalin-preserved specimen (Table 1). The museum has one more mounted specimen of *M. desmarestii*

Table 1. Specimens of *Megalomys desmarestii* examined

| Number and status | Preservation type | Sex | Locality | Date | Collector |
|----------------------|--------------------|--------|---|------|-----------|
| CG 1979-385, syntype | Mounted | Male | Martinique, Antilles | 1826 | M. Plée |
| CG 2006-187, syntype | Mounted | Female | Martinique, Antilles | 1826 | M. Plée |
| CG 2006-188 | Mounted | ? | Martinique, Antilles | ? | ? |
| CG 1996-42 | Ethanol-preserved | Male | 'Des Antilles prob- ably Martinique' | ? | M. Prieur |
| S3-M6-C228 | Formalin-preserved | Male | Martinique | ? | ? |

(reproduced in Nowak, 1991) and one of *M. luciae* in its exposition. Unfortunately, no cleaned skulls or skeletons were available (there are skulls inside the two mounted specimens and the formalin-preserved specimen).

From these specimens photographs and some accessible standard external measurements were taken. These data were compared with analogous data from my database of rodent images, measurements, and morphological descriptions. The ecological meaning of morphological characters was estimated on the basis of similarity or dissimilarity with the characters of rodents with a known specialization. To understand the level and trend of specialization, data from *M. desmarestii* were contrasted with those from an unspecialized rodent – the brown rat, *Rattus norvegicus* (Berkenhout, 1769). The data for the brown rat are from Miljutin (1997). For more details on the choice of characters, terminology, and relevant statistical methods (not used here) see Miljutin (1997, 2008, 2009).

RESULTS

Overall appearance: *Megalomys desmarestii* was a large rat-like rodent with a relatively small head, rather short snout, and a long tail (Fig. 1).

Size: Among the five specimens of *Megalomys desmarestii* examined, three seemed to be adults. Their head and body length exceeded about 1.5 times that of the brown rat, *Rattus norvegicus*. Unfortunately no external measurements of freshly caught specimens of *M. desmarestii* are available. According to Trouessart (1885), the specimen in alcohol (CG 1996-42) had a head and body length (HB) of 36 cm, a tail length (T) of 33 cm, and a hind foot length (HF) of 7.5 cm (including the claw). I remeasured the same specimen (CG 1996-42) and obtained the following values: HB = 325 mm, T = 325 mm, and HF = 67 mm (without the claw). The difference in the value of HB may be explained by greater rigidity of the corpse after more than 120 years of preservation and by the extraction of the skull, which occurred after the animal was measured by Trouessart. The measurements of the tail and hind feet more or less coincided. Of these two sets of measurements (mine and Trouessart's), that of Trouessart is almost certainly more reliable. Other available adult specimens are no longer reliably measurable. However, they seemed to be approximately the same size as the single measured specimen

(CG 1996-42). Therefore, it is more correct to say that these rodents had a head and body length of about 360 mm (as in Nowak, 1991) than ‘up to 360 mm’ as in Alen (1942). These measurements place *M. desmarestii* as a real giant in comparison with most other muroid rodents (Muroidea). It was the largest representative of the New World rats and mice, subfamily Sigmodontinae. While the weight of *M. desmarestii* is unknown, it was probably in the region of 1 kg.

Coverings: The body of *M. desmarestii* was covered with relatively long and harsh fur, while the feet and ears were almost naked. The tail was rather densely covered with short hair; however, also scales may be seen, especially on the tail’s ventral surface.

All specimens that I observed had dark reddish brown upper parts, which is in accordance with the description of Alen (1942). However, Desmarest (1826) describes the species (on the basis of the same specimens) as having a glossy black colour (‘beau noir lustre’). This statement is in accordance with the description made by a former inhabitant of Martinique, Mr. Delphin Duchamp, and related by Alen (1942). This gentleman had seen live or freshly killed pilorie specimens and described them as being ‘black as coal’. From this evidence, it seems likely that the natural colour of the upper parts of *M. desmarestii* was black, while the brown colour now exhibited by museum specimens is a result of fading. Pure black colouration is rare in mammals; most species exhibit some shade of brown or grey. However, this is just one of the peculiarities of this extraordinary species.

Underparts – the chin, throat, and belly – were creamy-white in all specimens except CG 2006-188, which had a brown belly of the same colour as its sides. According to Desmarest (1826), the animal had a chin and throat of pure white (‘blanc pur’). This description is exactly repeated in Latin by Fischer (1829). Duchamp described the pilorie as being ‘white as milk below’ (Alen, 1942). It is notable that both of the contemporary accounts described the pilorie’s underparts as white rather than creamy as they appear in the museum specimens today. It is however very strange that neither Desmarest nor Alen in his own description of the animal (Alen, 1942: 91) mentioned the white belly, even though both type specimens exhibited this feature.

Descriptions of the tail colour are also contradictory. According to Desmarest (1826), the animal had a base to the tail (‘la base de la queue’) that was pure white, while Alen (1942) described it as black at the base, with a white intermediate area and a black tip. As a matter of fact, the tails of the museum specimens that I observed were dark above (the same colour as the back) and lighter beneath. Some specimens had light tips, but no specimens had a white base to the tail. Presumably by ‘la base’ Desmarest meant the ventral part of the tail, not its proximal part.

In Nowak (1991) the colour of *M. desmarestii* is summarized in the following way: ‘The upper parts were glossy black or dark reddish brown. The chin, throat, underparts, and base of the tail were white.’ This description seems to be partly erroneous. The colour of living specimens was almost certainly not reddish brown (as explained above), and the tail was whitish below, not at its base.

Head: The head of *Megalomys desmarestii* was rather rounded with a short and obtuse muzzle. The head seems to have been relatively small, which is in concordance with the large size of the animal. At the same time almost no measurements are available to confirm this statement. Trouessart (1885) recorded the length of the cranium as 7 cm, but did not mention which one of the two skulls available to him at that time he had measured. If it was specimen CG 1996-42, we may divide this value by the head and body length (36 cm) and obtain the relative length of the head as about 19%. For comparison, this value is 20% in the brown rat. Of course the skull measured by Trouessart might have belonged to another much older and perhaps larger specimen.

The vibrissae seemed normally developed but not long – the longest vibrissae were about the length of the head. The eyes were probably relatively small: about 1/4 of the distance between the anterior (inner) edge of the eye and the opening of the acoustic canal of the ear. The ear pinna was well developed but not large: about 1/2 of the distance between the anterior edge of the eye and the ear opening.

Tail: The relative length of the tail in specimen CG 1996-42 was 92%. This is longer than in an unspecialized rodent like the brown rat (79%). The tail was oval in cross-section.

Forelimbs: The forefoot of *M. desmarestii* (Fig. 2) was about two times smaller than the hind foot. This is a typical proportion for most rat-like rodents. The forefoot was of medium length compared with the overall body length and was partially covered with short hair above and completely bare below. The skin on the ventral side of the palm had a granulated structure. Like in all Muroidea, the



Fig. 2. Forefoot of *Megalomys desmarestii* (MNHN CG 1996-42). The epidermis is partly destroyed.

forefoot had only four functional digits. The first digit, the pollex, was reduced to the size of a pad and covered by a nail, while digits 2–4 terminated with claws. The claws were well developed, of moderate length, slightly curved, and with relatively blunt tips. The edges of the claw's dorsal plate demonstrated a tendency to join on the ventral side – the edges came close to each other at the base of the claw. The digital pads were weakly developed and not prominent. There were five well developed interdigital and metacarpal pads. This is a typical number for rodents, but the structure of the pads was remarkable. Most of the pad's surface was covered with the same type of skin as was present between the pads, but every pad also had a smooth and probably tough region on its tip.

Hind limbs: In the single measured specimen (CG 1996-42) the length of the hind foot relative to the length of the head and body was 18.6%. This is a moderate value, close to that of the brown rat (18.7%). Like the forefeet, the hind feet were partly covered with short hair above and were completely bare below. In the hind foot the granulation on the ventral surface was even more obvious than in the forefoot (Fig. 3). The hind foot had five digits. They terminated with claws. The claws were well developed, of moderate length, and were more curved than those on the forefoot, with relatively blunt tips. The convergence of the edges of the claw dorsal plate on the ventral side was less obvious than in the forefoot or was missing altogether. The digital pads were of moderate size and were better developed than those on the forefoot digits. There were six interdigital and metatarsal pads. They had the same peculiar structure as those on the forefoot: each resembled a large granulose cushion with a smooth and tough 'cap' on its tip.

Skull and dentition: Unfortunately I have not seen the cranium of any *Megalomys desmarestii* specimen. Therefore the description below is based on the drawings in Trouessart (1885) and its redrawn copy in Hall (1981) (Fig. 4). The skull appeared noteworthy in many ways. It was strongly built with prominent ridges. The zygomatic arches were wide and strong. The roof of the cranium had prominent



Fig. 3. Hind foot of *Megalomys desmarestii* (MNHN CG 1996-42).

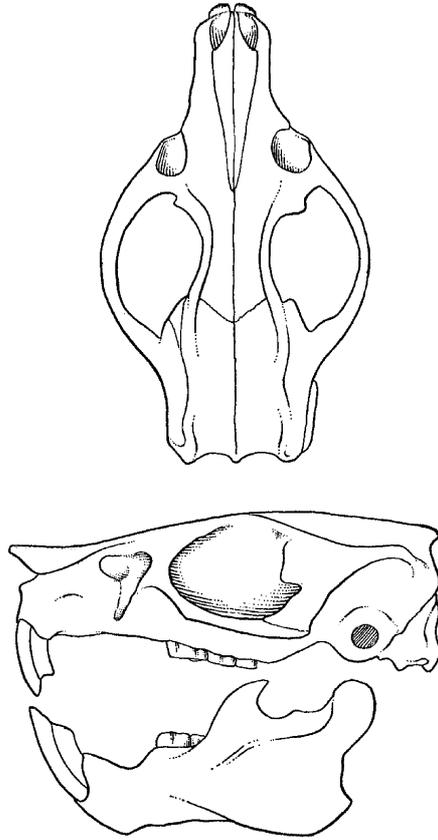


Fig. 4. Skull of *Megalomys desmarestii* (from Hall, 1981: 625; redrawn from Trouessart, 1885).

frontal, temporal, and sagittal ridges. The last is unusual among murid rodents. Another curious trait was the upwardly bent anterior part of the nasal bones. The mandibula was robustly built with a reduced angular process. The molar teeth of *M. desmarestii* were typical of Cricetinae – brachyodont and bunolo-phodont – while its incisors were remarkably deep in the anterior–posterior direction, but not very broad.

DISCUSSION

Ecological meaning of body characters

Megalomys desmarestii had mouse-like body proportions typical of hundreds of other rodent species and many marsupial and insectivore mammals (Miljutin, 1992a). Earlier I described animals of this body construction (= life form, = ecomorph) as ‘muridoids’ (Miljutin, 1992b). Such a widespread distribution of

the muridoid design may be explained by its antiquity and universality. Indeed, it is the most lizard-like body construction among mammals, with the resemblance to reptiles stressed by the scaly tails. The first mammals as well as the first rodents were probably muridoids (see skeleton reconstructions of *Morganucodon* and *Paramys* in Carroll, 1988). The universality of the muridoid construction in mammals is comparable with that of the lizard construction in reptiles. Among muridoid rodents there are semiaquatic (*Nectomys*, Cricetidae), subterranean (*Nesokia*, Muridae), subterranean–terrestrial (*Hypogeomys*, Nesomyidae), arboreal (*Uromys*, Muridae), animalivorous (*Selevinia*, Gliridae), frugivorous (*Apodemus*, Muridae), and herbivorous (*Phloeomys*, Muridae) species (see Miljutin, 2009 for an explanation of these terms). At the same time muridoids usually do not demonstrate extreme ecological specialization. Most of them are generalists rather than specialists. Thus, the general construction of the pilorie's body does not tell us very much about its habits, except that it did not have extreme locomotor specialization.

The size of *Megalomys desmarestii* was extraordinarily large. Among 310 genera in the rodent superfamily Muroidea (Musser & Carleton, 2005) about 250 genera have a mouse-like body construction (are muridoids). Of these 250 genera, the length of the head and body exceeds 30 cm in representatives of only 14 genera (i.e., about 6%) (after data from Nowak, 1991). Thus, the great size of Desmarest's pilorie is really rather uncommon. Since it was the largest member of its subfamily (Sigmodontinae), it is parsimonious to assume that this species evolved from an ancestor of lesser size. This raises the question of why an increase in size should have occurred, or even if it did not occur, why was *M. desmarestii* so large? I suspect that its great size was in some way connected with its island distribution.

Of 14 genera of 'giant rats' only 3 have a predominantly mainland distribution (*Bandicota*, *Cricetomys*, *Rhizomys*), 9 genera have an exclusively island distribution, while in the remaining 2 genera (*Hydromys*, *Uromys*) most species have an exclusively island distribution. It is notable that among 11 mainly insular genera of giant rats, 64% are found in the Australian region (*Hydromys*, *Hyomys*, *Mallomys*, *Papagomys*, *Solomys*, *Uromys*, *Xenuromys*). Others inhabit the Philippines (*Bullimus*, *Phloeomys*), Madagascar (*Hypogeomys*), and the Antilles (*Megalomys*).

There are thousands of islands on the planet and about one thousand species of mice and rats (in the morphological sense). Why are giant rats concentrated in the Australian region? I suppose that the reason is the lack of large mammalian predators. If an animal is approximately as large as its natural enemies, there is likely to be selective pressure towards increasing size during the course of evolution. Examples of this antipredator evolutionary strategy can be seen among large herbivorous mammals (buffalo, rhinoceros, elephants). For rodents this strategy is not normally appropriate, because carnivorous mammals are generally much larger than most rodents. In an insular environment the situation may be different, and in the absence of large carnivores, large size may become advantageous for rodents.

Megalomys desmarestii evolved in an environment that completely lacked mammalian predators (Morgan & Woods, 1986). Moreover, Martinique had no large diurnal birds of prey or large owls that specialized on mammalian prey (Raffaele et al., 2003). The only enemies of the pilorie were non-specialist birds of prey and snakes. For this reason, a large body size might have reduced the frequency and success of attacks from raptors on adult pilories. While birds are able to tear their prey, snakes need to be able to swallow their prey whole. Thus prey size is of great importance for snakes. The large size of adult pilories did not completely defend them against predation by snakes, but it perhaps provided defense against predation by smaller species of snakes and by young individuals of larger snakes.

The shaggy fur of *M. desmarestii* lacked the thick soft underfur typical of semiaquatic rodents. The moderate length and thickness of its vibrissae suggest that the animal did not have semiaquatic or arboreal habits, because semiaquatic rodents have relatively short and bristly vibrissae while arboreal rodents have long and thin vibrissae. The relatively small size of the pilorie's head also suggests that it did not have arboreal habits, since arboreal species usually have larger heads than their non-arboreal relatives of comparable size (Miljutin, 1997). Small eyes and ears hint that the animal was not strictly nocturnal.

The tail of the pilorie was remarkably long: about the same length as its head and body combined. This is unusual both for burrowing and unspecialized rodents, but typical of semiarboreal and arboreal species. There are no traces of specialization in aquatic locomotion in the tail's cross-section or in its covering.

The structure of forefoot claws is important in determining both burrowing and climbing ability. The relatively blunt tips of the pilorie's forefoot claws, the slight convergence of the claws' dorsal plate edges, and the weak development of the digital pads are clear indications of non-arboreal habits. However, these characters hint at a slight subterranean specialization. The claws and the digital pads of the hind foot seem to be less specialized than those of the forefoot. This is typical of fossorial species, because the hind feet are less engaged in digging.

The morphology of the interdigital and metapodial pads of the pilorie's front and hind feet is very intriguing. They can be described as being both large and small. They are large in their whole size, but small if only their smooth 'cap' is considered. I explain this condition as a transitional state between the large pad of a foot adapted to climbing and the small pad of a foot adapted to burrowing. If correct, the same transition might be expected among other rodent taxa that are passing the same transition. Indeed, I found the same foot pad structure for example in ground squirrels, *Spermophilus* (Sciuridae), the greater bandicoot rat, *Bandicota indica* (Muridae), and greater long-tailed hamster, *Tscherskia triton* (Cricetidae). The ground squirrels obviously evolved from an arboreal ancestor (Steppan et al., 2004), while the ancestor of bandicoot rats was probably also more arboreal,

because bandicoot rats, along with *Nesokia*, are the most specialized burrowers in their family, and perhaps the least arboreal. The long-tailed hamster retains an ancestral mouse-like body construction, which is associated with better climbing ability than that of hamster-like species. If this reasoning is correct, the ancestor of *M. desmarestii* should have exhibited more arboreal habits than its descendant.

Another interesting feature of the pilorie's feet was the granulated structure of the skin on the soles. This feature is not uncommon among rodents and occurs in various taxa, including for example the house mouse, *Mus musculus*. Because it may be present in rodents with different habits, I propose that it is connected more with ancestry than locomotion. Such skin structure is a reflection of the scales of the reptilian stage of mammalian evolution. However, most rodents have a more or less smooth skin on the soles of their feet, and the remains of scales persist only on the tail and digits. If the granulated pattern of the soles is just an ancestral state, we can assume that the ancestor of the pilorie and its nearest contemporary relatives is also likely to possess this feature. Indeed, it is notable that *Nectomys squamipes*, which is regarded as a close relative of *Megalomys* (Musser & Carleton, 2005), exhibits the same granulated structure on the soles of its feet. This peculiarity is even reflected in the specific name of its Latin binomial: *Nectomys 'squamipes'*.

Ecological meaning of craniodental characters

The robustly built skull of the pilorie with well-developed ridges was presumably associated with strong masticatory muscles. The presence of a sagittal crest indicates strong development of the *temporalis* muscle, which is responsible for powerful biting and clenching of teeth. Buno-lophodont molars are typical of frugivorous rodents, whose diets consist mainly of fruits and seeds. Strong deep incisors in combination with a sagittal crest suggest adaptation for breaking hard material, probably the shells of nuts. The incisors of the pilorie seem to have been not especially wide, thus not adapted for digging.

CONCLUSIONS

On the basis of morphological data relating to *Megalomys desmarestii* discussed above, some conclusions may be drawn about its locomotor abilities, ecological strategies, adaptive evolution, and origin.

Swimming ability: There is no doubt that the pilorie could swim like all other quadrupedal mammals. There are even eye-witness accounts describing its use of water to escape from predators (Alen, 1942). At the same time, it did not possess particular morphological adaptations to a semiaquatic life.

Burrowing ability: Certain morphological characters indicate a slight adaptation for digging: blunt tips of the claws, slight convergence of the claw dorsal plate edges, weak development of the digital pads, and structural reduction and increased toughness of the interdigital and metapodial pads.

Running ability: The pilorie certainly ran by bounds like all other rodents with a mouse-like body construction (Gambaryan, 1974; Hildebrand, 1989). This means that it was not a quick runner and needed underground or arboreal shelters to escape predators.

Climbing ability: The data relating to the climbing ability of the pilorie are somewhat contradictory. Its relatively small head, moderate vibrissae, blunt claws, and small digital pads are indicative of poor climbing ability. At the same time its long tail and the outlines of the interdigital and metapodial pads hint at arboreal habits. Perhaps the most likely explanation is that the pilorie was indeed a relatively poor climber and that its arboreal characters were inherited from its arboreal ancestor. These ancestral characters perhaps persisted due to low selective pressure in the island environment.

Substrate utilization strategy: In summary, the substrate utilization strategy of *Megalomys desmarestii* was obviously terrestrial/subterranean, which means that it mostly foraged on the ground and sheltered in burrows (see Miljutin, 2009 for an explanation of these terms).

Feeding strategy: On the basis of skull and dental morphology, it seems most likely that the main food of the pilorie was seeds and fruits, including nuts. It probably also consumed a small amount of animal food (invertebrates and small vertebrates) and green matter (leaves, stems, and roots).

Defence strategy: When attacked by a predator, the pilorie probably ran away and escaped to its burrow, or perhaps more rarely to a tree or to water. However, when facing certain critical situations, this large rodent with powerful jaws was probably able to defend itself by biting.

Circadian activity: In common with the majority of rodents, the pilorie was probably most active in darkness; however, its relatively small eyes and short vibrissae suggest that it was crepuscular with some diurnal activity rather than strictly nocturnal.

Trends of adaptive evolution: If the arguments presented in the Discussion are correct, the general trends of the pilorie's adaptive evolution were: (1) increasing body size, (2) transition from an arboreal to a terrestrial/subterranean way of life, and (3) adaptation to eating hard-covered fruits.

Origin: The granulated structure of the soles of the pilorie serve as an additional feature that suggests a close relationship with *Nectomys*. On the basis of external morphology it seems likely that the ancestor of *M. desmarestii* was smaller and exhibited arboreal or semiarboreal habits.

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**Märkmed Martinique'i saare (Väikesed Antillid)
väljasurnud hiidroti *Megalomys desmarestii*
(Sigmodontinae, Cricetidae, Rodentia) välismorfoloogia,
ökoloogia ja põlvnemise kohta**

Andrei Miljutin

Martinique'i saare hiidrott *Megalomys desmarestii* (Fischer, 1829) suri välja 19. sajandi lõpul või 20. sajandi algul. Teadmised tema eluviisi kohta on väga puudulikud. Antud uurimuse eesmärgiks on selle liigi ökoloogia rekonstrueerimine muuseumikogudes säilinud isendite morfoloogiliste tunnuste põhjal. Ökomorfoloogilise analüüsi tulemusena on tehtud oletusi selle närilise lokomotoorsete võimete, ökoloogiliste strateegiate, adaptiivse evolutsiooni ja põlvnemise kohta. On oletatud, et *M. desmarestii* toitunud põhiliselt maapinnal ja varjas end urgudes. Tema peamiseks toiduks olid seemned ja viljad, sealhulgas pähklid. Ta oli aktiivne pigem videvikus kui öösel või päeval. *M. desmarestii* adaptiivse evolutsiooni peamiseks suundadeks olid: 1) keha mõõtmete suurenemine, 2) üleminek puupealselt eluviisilt pinnasepealsele/pinnasisesele eluviisile ja 3) kohastumine kõva kestaga viljade söömiseks. Lähtudes nendest oletustest, pidi *M. desmarestii* eellane olema suuruselt väiksem ja puupealse eluviisiga. *M. desmarestii* jalataldade granuleeritud struktuur toetab arvamust tema sugulusest *Nectomys*'tega.