Undervalued habitat or impoverished guild? Exploring the scarcity of living semiaquatic sigmodontine rodents

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Abstract

Sigmodontines (Rodentia: Cricetidae), the largest living radiation of Neotropical rodents (90 genera, 489 species), show about 10% having specializations related to a semiaquatic habitat. In addition, this mode of life is unequally distributed among the several clades which compose the subfamily, concentrated in the Ichthyomyini and in a few large-bodied Oryzomyini. The observed taxonomical and geographical pattern is here discussed in a biogeographical historical context. As working hypothesis is advanced that the risk of predation (exerted by animalivorous fresh-water vertebrates) shaped and limited since the late Miocene the semiaquatic performance of the subfamily. Moreover, by exploring the fossil record can also be argued that during the Pleistocene is registered an important number of amphibious sigmodontines extinctions. Therefore, the scarcity of living semiaquatic sigmodontine rodents can be attributed to a combination of an undervalued habitat (mostly by risk of predation) plus a recent pauperization (by a sum of biological extinctions) of the members of that guild. A shallow comparison of the sigmodontine case against murids suggests that continental waterbodies resulted partially refractory to muroid colonizations.

Undervalued habitat or impoverished guild? Exploring the scarcity of living semiaquatic sigmodontine rodents

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Abstract. Sigmodontines (Rodentia: Cricetidae), the largest living radiation of Neotropical rodents (90 genera, 489 species), show about 10% having specializations related to a semiaquatic habitat. In addition, this mode of life is unequally distributed among the several clades which compose the subfamily, concentrated in the Ichthyomyini and in a few large-bodied Oryzomyini. The observed taxonomical and geographical pattern is here discussed in a biogeographical historical context. As working hypothesis is advanced that the risk of predation (exerted by animalivorous fresh-water vertebrates) shaped and limited since the late Miocene the semiaquatic performance of the subfamily. Moreover, by exploring the fossil record can also be argued that during the Pleistocene is registered an important number of amphibious sigmodontines extinctions. Therefore, the scarcity of living semiaquatic sigmodontine rodents can be attributed to a combination of an undervalued habitat (mostly by risk of predation) plus a recent pauperization (by a sum of biological

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extinctions) of the members of that guild. A shallow comparison of the sigmodontine case against murids suggests that continental waterbodies resulted partially refractory to muroid colonizations.

Key words: Cricetidae, Ichthyomyini, Oryzomyini, South America, Miocene, Predation.

Puerto Madryn, July 15, 2023

Editors-in-Chief

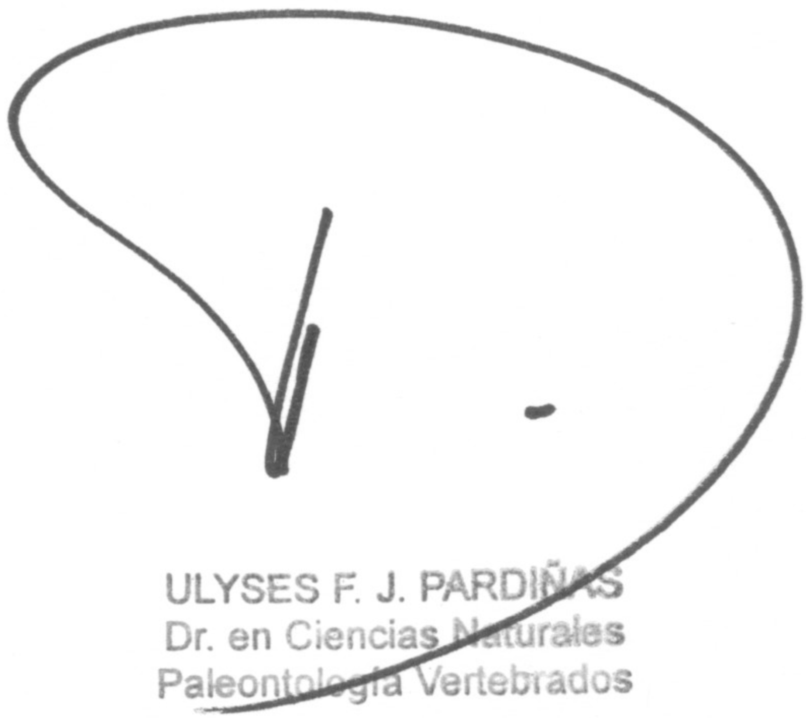
Chris Foote, John Wiley & Sons, UK, cfoote@wiley.com

Dear Dr Foote,

Please find enclosed the manuscript entitled "Undervalued habitat or impoverished guild? Exploring the scarcity of living semiaquatic sigmodontine rodents" (authors: Pardiñas and Cuellar). It has been submitted to your journal for consideration in the category "Nature Notes."

This paper gives a supported investigation into why a successful rodent radiation, the sigmodontines (the biggest Neotropical diversification of terrestrial mammals), failed to provide an appropriate performance colonizing fresh-water habitats.

Thank you in advance for your time and help. Kind regards,



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Neotropics contain four of the largest river basins of the Earth (Amazonas, Orinoco, La Plata and São Francisco), covering about two-thirds of the continent (Ayres & Clutton-Brock, 1992). The most impressive

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and famous, the Amazon River drains about 7,050,000 km^2 (out of the 17,840,000 in the continent) and has more than 1,000 tributaries (Knapp et al., 2021). If there also considered two of the largest wetlands of the world, the Pantanal and Iberá-Ñeembucú (Junk, 2013), the entire region can be categorized as plenty of surface freshwater (Hurlbert et al., 1981; Clapperton, 1993). In sharp contrast with the latter, sigmodontines (Cricetidae: Sigmodontinae), the most speciose and widely distributed group of rodents shows about 10% of its diversity specialized (i.e. with amphibious adaptations) to exploit this kind of habitats (Pardiñas et al., 2017). The intriguing aspect is why this noticeable mammal radiation has such a modest performance in semi aquatic environments? The present note aims to discuss whether sigmodontine colonization of fresh water reflects undervaluation (i.e., the group, for any reason, failed to exploit extensively the habitat), pauperization (i.e., during the past, the group had a greater amphibious diversity today extinguished), or a combination of both.

Two recent compilations (Patton et al., 2005; Pardiñas et al., 2017) containing an exhaustive list of sigmodontine rodents were used as basic data (Appendix 1). Each species was typified as semiaquatic or non-semiaquatic according to a combination of external morphological traits and natural history data. Semiaquatic forms are those showing at least two of the following features (listed in alphabetical order): 1) body pelage composed by two layers, including a wooly underfur and a superficial overfur; 2) continuous comb of stiff hairs along the metatarsal margins and between the digits fringing the sole of the pes; 3) midventral hairs conspicuously longer than hairs on the dorsal and lateral surfaces of the tail; 4) moderately-developed webbing between digits II, III, and IV of the manus; 5) mystacial vibrissae highly developed, numerous, and stiff; 6) nostrils high in the snout, anterolaterally placed and posteriorly enlarged by a small diverticulum flanked by a developed ala nasi ventralis; 7) noticeable small interdigital and metacarpal pedal pads; 8) prismatic cross-section of basal tail; and 9) well-developed interdigital webbing between pedal digits II, III, and IV. The selected external features have been highlighted as indicative of adaptation to aquatic habitats in sigmodontines and other muroids reflecting important activities developed into fresh-water bodies (rivers, streams, lakes, marshes) such as dispersal, foraging, nesting, and reproduction (e.g., Hershkovitz, 1966, 1969; Pine et al., 1981, Voss, 1988; Sierra de Soriano, 1965, 1969; Starrett & Fisler, 1970; Massoia, 1976; Miller & Anderson, 1977; Esher et al., 1978; Kerbis Peterhans & Patterson, 1995; Weksler, 2006; Santori et al., 2008, Rowe et al., 2014).

The analyzed data demonstrates that only a few sigmodontines can be considered as semiaquatic (Appendix 1), according to the following detail: 1) all the recognized Ichthyomyini (20 species in 6 genera); 2) a few members of Oryzomyini (15 species belonging to the genera*Amphinectomys* [1 sp.], *Holochilus* [7],*Lundomys* [1], and *Nectomys* [6]). Other 5 genera, including 3 oryzomyines (i.e., *Oryzomys* , *Pseudoryzomys* and*Sigmodontomys*) and 2 akodontines (i.e., *Gyldenstolpia* and*Scapteromys*) have been associated to aquatic habitats (e.g., Hershkovitz, 1966; Ávila-Pires, 1972; Massoia, 1976; Esher et al., 1978; Voss and Myers, 1991; Voss and Carleton, 1993; Pardiñas et al., 2009). However, available data on natural history and morphology contradict the consideration of these forms as semiaquatic. For instance,*Scapteromys* spp. is a well-studied case exemplifying rats with remarkable swimming abilities but spending their vital time in riverine habitats including the construction of galleries, nesting on dry ground, and climbing activities (e.g., Massoia and Fornes 1964, Hershkovitz 1966, Barlow 1969). *Oryzomys palustris* has also demonstrated capacities to face aquatic activities but not so deep morphological adaptations (e.g., Esher et al., 1978; Weksler, 2006). Overall, these sigmodontines are considered here as representing the guild of "waders" according to the definitions provided by Kerbis Peterhans and Patterson (1995: 346); "waders" combine adaptations to live in periodically flooding environments. Although tenuously reputed as semiaquatic (e.g., Pearson, 1951; Hershkovitz, 1970; Bianchini & Delupi, 1993), *Mindomys* (Oryzomyini) and *Neotomys*(Euneomyini) can be discarded as integrating any of the previous categories advanced (see Pardiñas et al. 2015, Brito et al. 2021). Summarizing, semiaquatic mode of life was adopted by 7% and 11% of the living species (n=489) and genera (n=90), respectively, while representing "waders" are 6% and 3%, respectively (Appendix 1). To conclude that it corresponds to a little fraction of the subfamily diversity is straightforward. However, the topic has also an asymmetrical geographic component rather than strictly quantitative. First, most of the ichthyomyine diversity is associated with streams and rivers of Andean and mountain regions in northwestern South

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and Middle America (Voss 1988, 2015a). Second, vast portions of tropical, subtropical, and temperate South American eastern lowland rivers and wetlands are inhabited almost exclusively by a handful of oryzomyines, mostly belonging to *Holochilus* and *Nectomys* (e.g., Hershkovitz, 1955; Bonvicino and Weksler, 2015; Chiquito, 2015; Prado et al., 2021). Finally, the southern portion of the continent lacks any representative of this mode of life, being the southernmost expressions*Holochilus brasiliensis* and the rare *Holochilus lagigliai*both reaching the northern limit of Patagonia (Formoso et al. 2010, Pardiñas et al. 2013; Figure 1).

It is well-known that small mammal adaptation to live in fresh water is challenging due to several factors, including locomotion, thermoregulation, feeding strategy, and risk predation (e.g., Fish 1992, Voss 1988, Fish et al. 2002). In addition, focusing on semiaquatic sigmodontines, some limitations are directly avoided by intrinsic specializations. For example, heat loss is minimized through fur insulation (Santori et al. 2008). In this context, ichthyomyines encompass a variety of morphological features likely representing extreme adaptations to dive, swim, and prey invertebrates in clear and rapid waters (Starrett and Fisler 1970; Voss 1988; Salazar-Bravo et al., 2023). But semiaquatic specializations are not restricted to this tribe because oryzomyine genera connected to the exploitation of fresh waters also bear noticeable traits (e.g. large interdigital webbing, pes enlargement, laterally compressed large tails, dorsally flattened heads, small ears, integumental folds to the close of the nostrils, wool-hairs well developed, etc.; Hershkovitz 1955, Sierra de Soriano 1965, 1969, Massoia 1976). The above demonstrates that both main clades with sigmodontines, Oryzomyalia and Sigmodontalia have been capable to handle the challenge imposed by continental waters. Why so few sigmodontines, in a continent plenty of aquatic resources, adopted this mode of life?

Although the topic is controversial, apparently the history of the sigmodontines started in northern South America through colonization from Central and North America by the latest Miocene (Prevosti et al. 2021, Ronez et al. 2021b and the references cited therein, Candela et al. 2023, Romano et al. 2023). A commonplace biological possibility is that the semiaquatic niche was already occupied by other mammals when sigmodontine radiation begun. This hypothesis (niche saturation; e.g., Northfield et al. 2010, Cassini 2020) directs the attention to mammal groups previously established in South America and currently having semiaquatic representatives such as marsupials and caviomorph rodents. Among the former, the poverty of living forms allied to waters is remarkable, being *Chironectes* the sole exception (Pine et al. 1981, Stein and Patton 2008). Caviomorphs embrace a few but emblematic amphibious taxa such as *Hydrochoerus* and *Myocastor* and others that revealed noticeable dive abilities (*Cuniculus* ; e.g. Patton et al. 2015). More indeed, the paleontological record indicates a Mio-Pleistocene blossom of potentially semiaquatic forms including entire disappear families and subfamilies (e.g., Neoepiblemidae, Potamarchinae; Vucetich et al. 2015, Kerber et al. 2016). However, seems hard to surmise any kind of competition among these groups and ancient sigmodontines, taking in mind the overwhelming body-size differences.

A second plausible explanation on the poverty of semiaquatic sigmodontines is simply time. The temporal window of the first main sigmodontine dichotomy (i.e., the separation between Oryzomyalia and Sigmodontalia) is estimated from molecular-based phylogenies in about 8 MA (Parada et al. 2021). Although the oldest fossils are markedly younger (about 5.7 MA; see Candela et al. 2023, Romano et al. 2023), we can suspect a bias regarding the paleontological record from suitable areas in northern South America (see Ronez et al. 2023 for a synthesis). Was the evolutionary time insufficient to allow a more diverse adaptation to the aquatic niche? This question has not an easy answer. However, it can be partially falsified by the ichthyomyines. If an entire clade had the time to evolve a definite array of semiaquatic adaptations is hard to understand why this process was not more widespread. However, even when Oryzomyini seems to be one of the first tribes to split (around 6 MA according to Parada et al. 2021), the subclade containing semiaquatic forms (clade D) emerges later (Percequillo et al. 2021). This temporal contrast between the two main groups of amphibious sigmodontines could be partially explanatory of the also important differential specialization level showed by them. To complicate the overall picture, evolutionary rates are supposed to be faster among animalivorous than in herbivorous muroids (Maestri et al. 2017).

In a fruitful discussion about body size and aquatic environments, Wolff and Guthrie (1985) selected the risk predation as a main worldwide explanation of larger bodies characterizing semiaquatic mammals. In one

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hand, predation can be posed as the limiting factor that shaped the Sigmodontinae evolutionary quantitative performance in continental waters. Although rarely documented, occasional ingestion by fishes of sigmodontine individuals fallen to waters seems widespread (e.g., Mann Fischer 1978, Pardiñas et al., 2004; Vitule et al. 2015). On the other hand, fresh water Neotropical fish assemblages are noticeably rich (just the Amazon basin embraces >3000 species described; Junk 2007) and include a large variety of voracious kinds capable to exercise potential predatory control (e.g., several piranhas Serrasalmidae, electric eel *Electrophorus electricus* , etc.; Reis et al. 2016). But waterbodies are not only plagued of predatory fishes since the guild of animalivorous predators also embraces a large diversity of turtles, caimans, snakes, and even mammals. Although still scarcely known, fossil assemblages from Late Miocene-Pliocene deposits in northern South America are eloquent about an important paleodiversity of predatory fishes and reptiles (e.g., Carrillo-Briceño et al. 2019, Cadena et al. 2020).

There is enough evidence to advance a working hypothesis capable to provide an explanation integrating several of the topics raised above. By the late Miocene, paleogeographic reconstructions indicate a northern South America plenty of salty and fresh waterbodies (e.g., Lundberg et al. 1998, McDermott 2021 and the references cited therein) and this was the physical territory faced by earliest sigmodontines (Ronez et al. 2021b). Lineages diversified in lowlands were limited to exploit continental waters mostly by non-mammal predators including a large variety of fishes and reptiles recorded as fossils (e.g., Sánchez-Villagra et al. 2010). An ancient clade that had the chance to colonize the growing Andean ranges was capable to produce an entire group (Ichthyomyini) devoted of shallow and clear rivers and streams mostly free of predatory animals (Reis et al. 2016). At the same time that ichthyomyines begun its noticeable radiation a few oryzomyine lowland lineages started to occupy pounds and marshes with a comparatively lower risk of predation. They evolved following a tendency to increase body-size as a co-evolutionary response to avoid predation and herbivorous specialization (Wolff and Guthrie 1985).

But there is another non-excluding and exciting possibility in order to explain semiaquatic living sigmodontines scarcity: extinctions. The paleontological record for the subfamily is still mostly conformed by disperse pieces and is more than insufficient to obtain a pale vision of their past. However, even biased to southern South America and, therefore, scarcely representing tropical and subtropical past areas (Pardiñas et al. 2003, Ronez et al. 2023), there are several indications of a greater diversity of preterit semiaquatic forms. Since fossils are not much than isolated molars and cranial fragments it is clear that morphological similarities are the base of our conjectures about extinct taxa connection with fresh waters.

Discarding +*Megalomys* , a Caribbean oryzomyines extinguished in historical times and dubiously associated to aquatic environments (see Miljutin 2010 for a detailed analysis), at least other 6 fossil genera deserve attention (Figure 2). +*Reigomys primigenus* , originally described as a species of *Holochilus* (see Steppan 1996), is an enigmatic oryzomyine from the Pleistocene deposits of Tarija basin, Bolivia (Hoffstetter 1973, Pardinas and Barbiere 2018). +*Noronhomys vespuccii* , another large oryzomyine endemic of Noronha Island (Brazil) was described as a Quaternary form allied also to *Holochilus* (Carleton and Olson 1999). +*Carletonomys cailoi* , a giant oryzomyine from Buenos Aires Province (Argentina) Pleistocene sediments, was associated to *Holochilus* and*Lundomys* (Pardinas 2008). A still undescribed also giant oryzomyine, probably a new genus closely related to *Lundomys* , is represented by a hemimaxillary unearthed from Late Pleistocene deposits in southernmost Santa Fe Province (Argentina). Finally, the enigmatic +*Ichthyurodon ameghinoi* , originally described as a Pleistocene Phyllotini (Steppan and Pardinas 1998) was reinterpreted as a specialized Oryzomyini allied to *Lundomys* (Barbiere 2019). If these genera represent semiaquatic sigmodontines, a plausible hypothesis based on craniodental morphology, bearing-sediments, associated fossil taxa, and phylogeny (Carleton and Olson 1999, Machado et al. 2013), the present unbalanced faunal scenario (semiaquatic versus terrestrial sigmodontines) could be tempered.

Any working hypothesis has the risk to be discarded by speculative, more in times when science is signed by a marked quantitative tendency. In this context, concomitant evidences could bring additional support. A past richest diversity of semiaquatic sigmodontines is not only limited to extinct taxa but also to more ample geographical ranges. Selected noticeable examples are the Quaternary occurrence of *Lundomys*registered from Minas Gerais in Brazil (Voss and Carleton 1993) to southern Buenos Aires Province in Argentina (Pardinas and Teta 2011). Its widespread past range (covering more than 15 degrees of latitude) contrast with its current geographic distribution restricted to less than 10 recording localities in Uruguay and southernmost Brazil (Voss 2015b, Brandao and Fegies 2017). Large populations belonging to *Holochilus* have been recorded in Holocene deposits (Nuapua locality) of southern Bolivian Chaco (Pardinas and Galliari 1998) where today is neither *Holochilus* nor permanent water (Coltorti et al. 2012). Extensive occurrence of the same genus is also recorded along the Patagonian Rivers Limay and Negro as testify Holocene material from archaeological sites (e.g. Fernandez et al. 2011, Pardinas and Teta 2011). Finally, the progressive loss of wetlands and associated mammals during the last thousands of years was recurrent in western Argentina (Lopez and Chiavazza 2021; Figure 2).

Up to this point and aimed to extract any biological worldwide signature from the discussed topic seems relevant to compare sigmodontine semiaquatic performance against other groups of muroids. The single grossly equivalent subfamily, judged on richness and geographical diversity is Murinae (Muridae), including about 145 genera and 656 species (Denys et al. 2017). This amazing muroid radiation, characterized by a long history traced by confident fossils at least to 12 Ma (Kimura et al. 2021) and developed on four continents (i.e., Africa, Asia, Australia, and Europe) embraces very few members adapted to fresh waters. Even considering jointly amphibious and "waders," less of 10 genera can be highlighted (e.g., *Colomys* ,*Crossomys* , *Dasymys* , *Hydromys* , *Nilopegamys* ,*Waiomys* ; Helgen 2005, Rowe et al. 2014). Taken uncritically these numbers, to note that this is a poorer situation that the scenario showed by sigmodontines is obvious. To observe that changing the framework the semiaquatic performance achieved by the sigmodontines looks successful invites to further explorations. To conclude that continental waterbodies resulted partially refractory to muroid colonization seems indisputable.

The contemporary scarcity of semiaquatic sigmodontines seems the result of a combination of an underexploited habitat (due to risk predation) plus a pauperization process. Interestingly, even from fossil or current record is Oryzomyini the single lineage to develop semiaquatic specializations within the clade Oryzomyalia (a group currently comprising 12 tribes; Pardinas et al. 2021). Ronez et al. (2021a) also pointed out the uniqueness of oryzomyines in colonizing islands partially highlighting their capacity to face marine barriers. Both issues reinforce the idea that not all the tribes have the same evolutionary capacity (or ecological opportunity? Alhajeri et al. 2016) and this challenging notion can be representing a fresh avenue to research sigmodontine history.

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Figure legends

Figure 1. Generalized distributions of the two sigmodontine rodent groups containing semiaquatic forms superimposed on a map of Middle and South America highlighting current main fluvial systems.

Figure 2. Some of the fossil craniodental remains of sigmodontines conjectured to be semiaquatic extinguished taxa plus Pleistocene maximum range of the *Lundomys molitor* (colored area to the right) and Holocene extension of the distribution of *Holochilus* (colored area to the left). Based on several sources.

Data Accessibilty Statement

The datasets generated and analyzed during the current study are included (Appendix 1); fossils mentioned or discussed are available in the following public biological repositories: CNP: Colección de Mamíferos, Centro Nacional Patagónico, Puerto Madryn, Chubut,

Argentina; FMNH: Field Museum, Chicago, Illinois, United States; MLP: Museo de La Plata, La Plata, Argentina.

Competing Interests Statement

The authors declare no conflict of interest.

Author Contributions section

UFJP and ECC contribute equally to the conceptualization, design, and writing of this contribution.

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Appendix 1. A list of living genera and species of sigmodontine rodents indicating those considered semi-aquatic and "waders." Compilation based largely on Patton et al. (2015) and Pardiñas et al. (2017) with modifications; numbers updated to May 2023.

	Total	**Total**	**Semiaquatic**	**Semiaquatic**	**"Waders"**	**"Waders"**
	Genera	**Species**	**Genera**	**Species**	**Genera**	**Species**
ORYZOMYALIA INCERTAE SEDIS						
ABRAWAYAOMYS	1					
Abrawayaomys chebezi		1				
Abrawayaomys ruschii		1				
CHINCHILLULA	1					
Chinchillula sahamae		1				
DELOMYS	1					
Delomys altimontanus		1				
Delomys dorsalis		1				
Delomys sublineatus		1				
ABROTRICHINI						
ABROTHRIX	1					
Abrothrix andina		1				
Abrothrix hirta		1				

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	Total	Total	Semiaquatic	Semiaquatic	”Waders”	”Waders”
Abrothrix illutea		1				
Abrothrix jelskii		1				
Abrothrix lanosa		1				
Abrothrix longipilis		1				
Abrothrix manni		1				
Abrothrix olivacea		1				
Abrothrix sanborni		1				
Abrothrix xanthorhina		1				
CHELEMYS	1					
Chelemys megalonyx		1				
GEOXUS	1					
Geoxus annectens		1				
Geoxus lafkenche		1				
Geoxus michaelseni		1				
Geoxus valdivianus		1				
NOTIOMYS	1					
Notiomys edwardsii		1				
PAYNOMYS	1					
Paynomys macronyx		1				
AKODONTINI						
AKODON	1					
Akodon aerosus		1				
Akodon affinis		1				
Akodon albiventer		1				
Akodon azarae		1				
Akodon baliolus		1				
Akodon boliviensis		1				
Akodon budini		1				
Akodon caenosus		1				
Akodon cursor		1				
Akodon dayi		1				
Akodon diauarum		1				
Akodon dolores		1				
Akodon fumeus		1				
Akodon iniscatus		1				
Akodon josemariarguedasi		1				
Akodon juninensis		1				
Akodon kadiweu		1				
Akodon kofordi		1				
Akodon kotosh		1				
Akodon lindberghi		1				
Akodon lutescens		1				
Akodon mollis		1				
Akodon montensis		1				
Akodon mystax		1				
Akodon oenos		1				
Akodon orophilus		1				
Akodon paranaensis		1				
Akodon pervalens		1				
Akodon philipmyersi		1				

	Total	Total	Semiaquatic	Semiaquatic	"Waders"	"Waders"
Akodon polopi		1				
Akodon reigi		1				
Akodon sanctipaulensis		1				
Akodon siberiae		1				
Akodon simulator		1				
Akodon spegazzinii		1				
Akodon subfuscus		1				
Akodon surdus		1				
Akodon sylvanus		1				
Akodon toba		1				
Akodon torques		1				
Akodon varius		1				
BIBIMYS	1					
Bibimys chacoensis		1				
Bibimys labiosus		1				
Bibimys torresi		1				
BLARINOMYS	1					
Blarinomys breviceps		1				
BRUCEPATTERSONIUS	1					
Brucepattersonius griserufescens		1				
Brucepattersonius iheringi		1				
Brucepattersonius nebulosus		1				
Brucepattersonius soricinus		1				
CASTORIA	1					
Castoria angustidens		1				
DELTAMYS	1					
Deltamys araucaria		1				
Deltamys kempi		1				
GYLDENSTOLPIA	1				1	
Gyldenstolpia fronto		1				1
Gyldenstolpia planaltensis		1				1
JUSCELINOMYS	1					
Juscelinomys candango		1				
Juscelinomys huanchacae		1				
KUNSIA	1					
Kunsia tomentosus		1				
LENOXUS	1					
Lenoxus apicalis		1				
MICROXUS	1					
Microxus mimus		1				
NECROMYS	1					
Necromys amoenus		1				
Necromys lactens		1				
Necromys lasiurus		1				
Necromys lilloi		1				
Necromys obscurus		1				
Necromys punctulatus		1				
Necromys urichi		1				
OXYMYCTERUS	1					
Oxymycterus amazonicus		1				

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	Total	Total	Semiaquatic	Semiaquatic	”Waders”	”Waders”
Oxymycterus caparoae		1				
Oxymycterus dasytrichus		1				
Oxymycterus delator		1				
Oxymycterus hiska		1				
Oxymycterus hucucha		1				
Oxymycterus inca		1				
Oxymycterus itapeby		1				
Oxymycterus josei		1				
Oxymycterus juliacae		1				
Oxymycterus nasutus		1				
Oxymycterus nigrifrons		1				
Oxymycterus paramensis		1				
Oxymycterus quaestor		1				
Oxymycterus rufus		1				
Oxymycterus wayku		1				
Oxymycterus willkaurco		1				
PODOXYMYS	1					
Podoxymys roraimae		1				
SCAPTEROMYS	1				1	
Scapteromys aquaticus		1				1
Scapteromys meridionalis		1				1
Scapteromys tumidus		1				1
THALPOMYS	1					
Thalpomys cerradensis		1				
Thalpomys lasiotis		1				
THAPTOMYS	1					
Thaptomys nigrita		1				
ANDINOMYINI						
ANDINOMYS	1					
Andinomys edax		1				
PUNOMYS	1					
Punomys kofordi		1				
Punomys lemminus		1				
EUNEOMYINI						
EUNEOMYS	1					
Euneomys chinchilloides		1				
Euneomys fossor		1				
Euneomys mordax		1				
Euneomys petersoni		1				
IRENOMYS	1					
Irenomys tarsalis		1				
NEOTOMYS	1					
Neotomys ebriosus		1				
NEOMICROXINI						
NEOMICROXUS	1					
Neomicroxus bogotensis		1				
Neomicroxus latebricola		1				
ORYZOMYINI						
”HANDLEYOMYS”	1					
“Handleyomys” alfaroi		1				

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	Total	**Total**	**Semiaquatic**	**Semiaquatic**	**”Waders”**	**”Waders”**
“Handleyomys” chapmani		1				
“Handleyomys” guerrerensis		1				
“Handleyomys” melanotis		1				
“Handleyomys” rhabdops		1				
“Handleyomys” rostratus		1				
“Handleyomys” saturatior		1				
AEGIALOMYS	1					
Aegialomys baroni		1				
Aegialomys galapagoensis		1				
Aegialomys ica		1				
Aegialomys xanthaeolus		1				
AMPHINECTOMYS	1		1			
Amphinectomys savamis		1		1		
CERRADOMYS	1					
Cerradomys akroai		1				
Cerradomys goytaca		1				
Cerradomys langguthi		1				
Cerradomys maracajuensis		1				
Cerradomys marinhus		1				
Cerradomys scotti		1				
Cerradomys subflavus		1				
Cerradomys vivoi		1				
DRYMOREOMYS	1					
Drymoreomys albimaculatus		1				
EREMORYZOMYS	1					
Eremoryzomys mesocaudis		1				
Eremoryzomys polius		1				
EURYORYZOMYS	1					
Euryoryzomys emmonsae		1				
Euryoryzomys lamia		1				
Euryoryzomys legatus		1				
Euryoryzomys macconnelli		1				
Euryoryzomys nitidus		1				
Euryoryzomys russatus		1				
HANDLEYOMYS	1					
Handleyomys fuscatus		1				
Handleyomys intectus		1				
HOLOCHILUS	1		1			
Holochilus brasiliensis		1		1		
Holochilus chacarius		1		1		
Holochilus lagigliai		1		1		
Holochilus nanus		1		1		
Holochilus oxe		1		1		
Holochilus sciureus		1		1		
Holochilus venezuelae		1		1		
HYLAEAMYS	1					
Hylaeamys acritus		1				
Hylaeamys laticeps		1				
Hylaeamys megacephalus		1				
Hylaeamys oniscus		1				

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	Total	**Total**	**Semiaquatic**	**Semiaquatic**	**"Waders"**	**"Waders"**
Hylaeamys perenensis		1				
Hylaeamys tatei		1				
Hylaeamys yunganus		1				
LUNDOMYS	1		1			
Lundomys molitor		1		1		
MELANOMYS	1					
Melanomys caliginosus		1				
Melanomys chrysomelas		1				
Melanomys columbianus		1				
Melanomys idoneus		1				
Melanomys robustulus		1				
Melanomys zunigae		1				
MICROAKODONTOMYS	1					
Microakodontomys transitorius		1				
MICRORYZOMYS	1					
Microryzomys altissimus		1				
Microryzomys minutus		1				
MINDOMYS	1					
Mindomys hammondi		1				
Mindomys kutuku		1				
NEACOMYS	1					
Neacomys aletheia		1				
Neacomys amoenus		1				
Neacomys auriventer		1				
Neacomys carceleni		1				
Neacomys dubosti		1				
Neacomys elieceri		1				
Neacomys guianae		1				
Neacomys jau		1				
Neacomys leilae		1				
Neacomys macedoruizi		1				
Neacomys marajoara		1				
Neacomys minutus		1				
Neacomys musseri		1				
Neacomys oliveirai		1				
Neacomys paracou		1				
Neacomys pictus		1				
Neacomys rosalindae		1				
Neacomys serranensis		1				
Neacomys spinosus		1				
Neacomys tenuipes		1				
Neacomys vargasllosai		1				
Neacomys vossi		1				
Neacomys xingu		1				
NECTOMYS	1		1			
Nectomys apicalis		1		1		
Nectomys magdalenae		1		1		
Nectomys palmipes		1		1		
Nectomys rattus		1		1		
Nectomys saturatus		1		1		

	Total	Total	Semiaquatic	Semiaquatic	"Waders"	"Waders"
Nectomys squamipes		1		1		
NEPHELOMYS	1					
Nephelomys albigularis		1				
Nephelomys auriventer		1				
Nephelomys caracolus		1				
Nephelomys childi		1				
Nephelomys devius		1				
Nephelomys keaysi		1				
Nephelomys levipes		1				
Nephelomys maculiventer		1				
Nephelomys meridensis		1				
Nephelomys moerex		1				
Nephelomys nimbosus		1				
Nephelomys pectoralis		1				
Nephelomys pirrensis		1				
Nephelomys ricardopalmai		1				
NESORYZOMYS	1					
Nesoryzomys fernandinae		1				
Nesoryzomys narboroughi		1				
Nesoryzomys swarthi		1				
OECOMYS	1					
Oecomys auyantepui		1				
Oecomys bicolor		1				
Oecomys catherinae		1				
Oecomys cleberi		1				
Oecomys concolor		1				
Oecomys flavicans		1				
Oecomys franciscorum		1				
Oecomys mamorae		1				
Oecomys matogrossensis		1				
Oecomys paricola		1				
Oecomys phaeotis		1				
Oecomys rex		1				
Oecomys roberti		1				
Oecomys rutilus		1				
Oecomys speciosus		1				
Oecomys superans		1				
Oecomys sydandersoni		1				
Oecomys tapajinus		1				
Oecomys trinitatis		1				
OLIGORYZOMYS	1					
Oligoryzomys andinus		1				
Oligoryzomys arenalis		1				
Oligoryzomys melanostoma		1				
Oligoryzomys brendae		1				
Oligoryzomys chacoensis		1				
Oligoryzomys costaricensis		1				
Oligoryzomys delicatus		1				
Oligoryzomys destructor		1				
Oligoryzomys flavescens		1				

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	Total	Total	Semiaquatic	Semiaquatic	”Waders”	”Waders”
Oligoryzomys fulvescens		1				
Oligoryzomys griseolus		1				
Oligoryzomys guille		1				
Oligoryzomys longicaudatus		1				
Oligoryzomys mattogrossae		1				
Oligoryzomys messorius		1				
Oligoryzomys microtis		1				
Oligoryzomys moojeni		1				
Oligoryzomys nigripes		1				
Oligoryzomys pachecoi		1				
Oligoryzomys rupestris		1				
Oligoryzomys stramineus		1				
Oligoryzomys utiaritensis		1				
Oligoryzomys vegetus		1				
Oligoryzomys yatesi		1				
OREORYZOMYS	1					
Oreoryzomys balneator		1				
ORYZOMYS	1				1	
Oryzomys albiventer		1				1
Oryzomys couesi		1				1
Oryzomys dimidiatus		1				1
Oryzomys gorgasi		1				1
Oryzomys palustris		1				1
Oryzomys texensis		1				1
PATTONIMUS	1					
Pattonimus ecominga		1				
Pattonimus musseri		1				
PSEUDORYZOMYS	1				1	
Pseudoryzomys simplex		1				1
SCOLOMYS	1					
Scolomys melanops		1				
Scolomys ucayalensis		1				
SIGMODONTOMYS	1				1	
Sigmodontomys alfari		1				1
SOORETAMYS	1					
Sooretamys angouya		1				
TANYUROMYS	1					
Tanyuromys aphrastus		1				
Tanyuromys thomasleei		1				
TRANSANDINOMYS	1					
Transandinomys bolivaris		1				
Transandinomys talamancae		1				
ZYGODONTOMYS	1					
Zygodontomys brevicauda		1				
Zygodontomys brunneus		1				
PHYLLOTINI						
ANDALGALOMYS	1					
Andalgalomys olrogi		1				
Andalgalomys pearsoni		1				
AULISCOMYS	1					

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	Total	Total	Semiaquatic	Semiaquatic	"Waders"	"Waders"
Auliscomys boliviensis		1				
Auliscomys pictus		1				
Auliscomys sublimis		1				
CALASSOMYS	1					
Calassomys apicalis		1				
CALOMYS	1					
Calomys achaku		1				
Calomys boliviae		1				
Calomys callidus		1				
Calomys callosus		1				
Calomys cerqueirai		1				
Calomys chinchilico		1				
Calomys expulsus		1				
Calomys fecundus		1				
Calomys frida		1				
Calomys hummelincki		1				
Calomys laucha		1				
Calomys lepidus		1				
Calomys miurus		1				
Calomys musculinus		1				
Calomys sorella		1				
Calomys tener		1				
Calomys tocantinsi		1				
Calomys venustus		1				
ELIGMODONTIA	1					
Eligmodontia bolsonensis		1				
Eligmodontia dunaris		1				
Eligmodontia hirtipes		1				
Eligmodontia moreni		1				
Eligmodontia morgani		1				
Eligmodontia puerulus		1				
Eligmodontia typus		1				
GALENOMYS	1					
Galenomys garleppii		1				
GRAOMYS	1					
Graomys chacoensis		1				
Graomys domorum		1				
Graomys edithae		1				
Graomys griseoflavus		1				
LOXODONTOMYS	1					
Loxodontomys micropus		1				
Loxodontomys pikumche		1				
PHYLLOTIS	1					
Phyllotis alisosiensis		1				
Phyllotis amicus		1				
Phyllotis andium		1				
Phyllotis anitae		1				
Phyllotis bonariensis		1				
Phyllotis camiari		1				
Phyllotis caprinus		1				

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	Total	Total	Semiaquatic	Semiaquatic	"Waders"	"Waders"
Phyllotis darwinii		1				
Phyllotis definitus		1				
Phyllotis gerbillus		1				
Phyllotis haggardi		1				
Phyllotis limatus		1				
Phyllotis limatus		1				
Phyllotis magister		1				
Phyllotis nogalaris		1				
Phyllotis occidens		1				
Phyllotis osgoodi		1				
Phyllotis osilae		1				
Phyllotis pearsoni		1				
Phyllotis pehuenche		1				
Phyllotis rupestris		1				
Phyllotis stenops		1				
Phyllotis tucumanus		1				
Phyllotis vaccarum		1				
Phyllotis xanthopygus		1				
SALINOMYS	1					
Salinomys delicatus		1				
TAPECOMYS	1					
Tapecomys primus		1				
Tapecomys wolffsohni		1				
REITHRODONTINI						
REITHRODON	1					
Reithrodon auritus		1				
Reithrodon caurinus		1				
Reithrodon typicus		1				
RHAGOMYINI						
RHAGOMYS	1					
Rhagomys longilingua		1				
Rhagomys rufescens		1				
Rhagomys septentrionalis		1				
THOMASOMYINI						
AEPEOMYS	1					
Aepeomys lugens		1				
Aepeomys reigi		1				
CHILOMYS	1					
Chilomys carapazi		1				
Chilomys fumeus		1				
Chilomys instans		1				
Chilomys georgeledecii		1				
Chilomys neisi		1				
Chilomys percequilloi		1				
Chilomys weksleri		1				
RHIPIDOMYS	1					
Rhipidomys albujai		1				
Rhipidomys austrinus		1				
Rhipidomys baturiteensis		1				
Rhipidomys bezerrensis		1				

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Rhipidomys caracolensis		1				
Rhipidomys cariri		1				
Rhipidomys caucensis		1				
Rhipidomys couesi		1				
Rhipidomys emiliae		1				
Rhipidomys fulviventer		1				
Rhipidomys gardneri		1				
Rhipidomys ipukensis		1				
Rhipidomys itoan		1				
Rhipidomys latimanus		1				
Rhipidomys leucodactylus		1				
Rhipidomys macconnelli		1				
Rhipidomys macrurus		1				
Rhipidomys mastacalis		1				
Rhipidomys modicus		1				
Rhipidomys nitela		1				
Rhipidomys ochoagrateroli		1				
Rhipidomys ochrogaster		1				
Rhipidomys similis		1				
Rhipidomys tenuicauda		1				
Rhipidomys tribei		1				
Rhipidomys venezuelae		1				
Rhipidomys venustus		1				
Rhipidomys wetzeli		1				
THOMASOMYS	1					
Thomasomys andersoni		1				
Thomasomys antoniobracki		1				
Thomasomys apeco		1				
Thomasomys aureus		1				
Thomasomys auricularis		1				
Thomasomys australis		1				
Thomasomys baeops		1				
Thomasomys bombycinus		1				
Thomasomys burneoi		1				
Thomasomys caudivarius		1				
Thomasomys cinereiventer		1				
Thomasomys cinereus		1				
Thomasomys cinnameus		1				
Thomasomys contradictus		1				
Thomasomys daphne		1				
Thomasomys dispar		1				
Thomasomys eleusis		1				
Thomasomys emeritus		1				
Thomasomys erro		1				
Thomasomys fumeus		1				
Thomasomys gracilis		1				
Thomasomys hudsoni		1				
Thomasomys hylophilus		1				
Thomasomys incanus		1				
Thomasomys ischyrus		1				

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	Total	**Total**	**Semiaquatic**	**Semiaquatic**	**"Waders"**	**"Waders"**
Thomasomys kalinowskii		1				
Thomasomys ladewi		1				
Thomasomys laniger		1				
Thomasomys macrotis		1				
Thomasomys monochromos		1				
Thomasomys nicefori		1				
Thomasomys niveipes		1				
Thomasomys notatus		1				
Thomasomys onkiro		1				
Thomasomys oreas		1				
Thomasomys paramorum		1				
Thomasomys pardignasi		1				
Thomasomys popayanus		1				
Thomasomys praetor		1				
Thomasomys princeps		1				
Thomasomys pyrrhonotus		1				
Thomasomys rosalinda		1				
Thomasomys salazari		1				
Thomasomys silvestris		1				
Thomasomys taczanowskii		1				
Thomasomys ucucha		1				
Thomasomys vestitus		1				
Thomasomys vulcani		1				
WIEDOMYINI						
JULIOMYS	1					
Juliomys ossitenuis		1				
Juliomys pictipes		1				
Juliomys rimofrons		1				
Juliomys ximenezi		1				
PHAENOMYS	1					
Phaenomys ferrugineus		1				
WIEDOMYS	1					
Wiedomys cerradensis		1				
Wiedomys pyrrhorinos		1				
WILFREDOMYS	1					
Wilfredomys oenax		1				
"SIGMODONTALIA"						
ICHTHYOMYINI						
ANOTOMYS	1		1			
Anotomys leander		1		1		
CHIBCHANOMYS	1		1			
Chibchanomys trichotis		1		1		
DAPTOMYS	1		1			
Daptomys ferreirai		1		1		
Daptomys mussoi		1		1		
Daptomys oyapocki		1		1		
Daptomys peruviensis		1		1		
Daptomys venezuelae		1		1		
ICHTHYOMYS	1		1			
Ichthyomys hydrobates		1		1		

	Total	Total	Semiaquatic	Semiaquatic	"Waders"	"Waders"
Ichthyomys orientalis		1		1		
Ichthyomys pinei		1		1		
Ichthyomys pittieri		1		1		
Ichthyomys stolzmanni		1		1		
Ichthyomys tweedii		1		1		
NEUSTICOMYS	1		1			
Neusticomys monticolus		1		1		
Neusticomys orcesi		1		1		
Neusticomys vossi		1		1		
RHEOMYS	1		1			
Rheomys mexicanus		1		1		
Rheomys raptor		1		1		
Rheomys thomasi		1		1		
Rheomys underwoodi		1		1		
SIGMODONTINI						
SIGMODON	1					
Sigmodon alleni		1				
Sigmodon alstoni		1				
Sigmodon arizonae		1				
Sigmodon fulviventer		1				
Sigmodon hirsutus		1				
Sigmodon hispidus		1				
Sigmodon inopinatus		1				
Sigmodon leucotis		1				
Sigmodon mascotensis		1				
Sigmodon ochrognathus		1				
Sigmodon peruanus		1				
Sigmodon planifrons		1				
Sigmodon toltecus		1				
Sigmodon zanjonensis		1				
TOTALS	**90**	**489**	**10**	**35**	**5**	**13**
%			**11**	**7**	**6**	**3**

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