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Undervalued habitat or impoverished guild? Explaining the scarcity of living semiaquatic sigmodontine rodents (Cricetidae)

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Sigmodontines (Rodentia: Cricetidae), the most diverse extant radiation of Neotropical rodents (91 genera, 507 species), include only a small fraction of taxa exhibiting morphological and ecological specializations associated with a semiaquatic mode of life. These specializations are unevenly distributed within the subfamily, being largely restricted to Ichthyomyini and to a limited number of mostly large-bodied species within Oryzomyini. Here, we examine the taxonomic, phylogenetic, and geographic distribution of semiaquatic sigmodontines within a historical framework. Phylogenetic analyses and ancestral-state reconstructions indicate that amphibious habits evolved convergently in these two lineages from a terrestrial ancestor. The resulting patterns reveal a marked phylogenetic clustering and a pronounced geographic asymmetry, with semiaquatic forms largely absent from extensive lowland and southern freshwater systems. These patterns are consistent with a scenario in which ecological constraints and historical processes jointly shaped the current distribution of semiaquatic taxa. In particular, predation pressure within continental freshwater environments may have limited successful colonization by small mammals, while occupation of predator-poor habitats may have facilitated localized diversification. In addition, paleontological and biogeographic evidence suggests that semiaquatic sigmodontines were more diverse and geographically widespread in the past, with subsequent reductions in diversity. In this context, the contemporary scarcity of semiaquatic sigmodontine rodents can be interpreted as consistent with a combination of ecological filtering associated with freshwater habitats and historical reductions in diversity through extinction. Comparison with murid rodents suggests that continental freshwater environments may represent a challenging ecological domain for small muroids more broadly.

Keywords: Ichthyomyini; Miocene; Oryzomyini; predation; South America.

Los sigmodontinos (Rodentia: Cricetidae), la radiación más diversa de roedores neotropicales contemporáneos (91 géneros, 507 especies), incluyen solo una pequeña fracción de taxones que exhiben especializaciones morfológicas y ecológicas asociadas a un modo de vida semiacuático. Estas especializaciones se distribuyen de manera desigual dentro de la subfamilia, estando restringidas principalmente a Ichthyomyini y a un número limitado de especies, en su mayoría de gran tamaño, dentro de Oryzomyini. En este estudio, examinamos la distribución taxonómica, filogenética y geográfica de los sigmodontinos semiacuáticos dentro de un marco histórico. Los análisis filogenéticos y las reconstrucciones de estados ancestrales indican que los hábitos anfibios evolucionaron convergentemente en estos dos linajes a partir de un ancestro terrestre. Los patrones resultantes revelan una marcada agrupación filogenética y una marcada asimetría geográfica, con formas semiacuáticas prácticamente ausentes en extensos sistemas de tierras bajas y de agua dulce del sur. Estos patrones son consistentes con un escenario en el que las limitaciones ecológicas y los procesos históricos moldearon conjuntamente la distribución actual de los taxones semiacuáticos. En particular, la presión de la depredación en los ambientes continentales de agua dulce pudo haber limitado la colonización exitosa por parte de pequeños mamíferos, mientras que la ocupación de hábitats con pocos depredadores pudo haber facilitado la diversificación localizada. Además, la evidencia paleontológica y biogeográfica sugiere que los sigmodontinos semiacuáticos fueron más diversos y geográficamente más extendidos en el pasado, con reducciones posteriores en la diversidad. En este contexto, la escasez actual de roedores sigmodontinos semiacuáticos puede interpretarse como consistente con una combinación de filtrado ecológico asociado a los hábitats de agua dulce y reducciones históricas en la diversidad por extinción. La comparación con los roedores múridos sugiere que los ambientes continentales de agua dulce pueden representar un dominio ecológico desafiante para los pequeños muroideos en general.

Palabras clave: América del Sur; depredación; Ichthyomyini; Mioceno; Oryzomyini.

Freshwater environments have repeatedly served as arenas for ecological innovation and lineage diversification among mammals, providing opportunities for dispersal, foraging, and niche expansion across evolutionary timescales (e.g., Hood 2020; He *et al.* 2021; Román-Palacios *et al.* 2022; Farina *et al.* 2023). In the Neotropics, this opportunity is particularly pronounced: the continent harbors some of the largest and most persistent river basins and wetland systems on Earth, forming an extensive freshwater network throughout much of the Cenozoic (e.g., Clapperton 1993). In principle, such conditions might be expected to promote repeated evolutionary responses to aquatic and semiaquatic habitats. However, the relationship between ecological opportunity and diversification is not necessarily direct, and the extent to which environmental availability translates into adaptive expansion varies among clades (e.g., Alhajeri *et al.* 2016; Maestri *et al.* 2017; 2022).

Within this context, sigmodontine rodents (Cricetidae:

Sigmodontinae), one of the most diverse mammalian radiations in South America, present an apparent paradox. Despite their extensive diversification across terrestrial environments, they exhibit a strikingly limited representation of semiaquatic forms (e.g., Hershkovitz 1969; Pine *et al.* 1981; Voss 1988; Pardiñas *et al.* 2017). This discrepancy between the widespread availability of freshwater habitats and the restricted occurrence of amphibious adaptations raises fundamental questions about the processes that structure ecological diversification in this group.

The Neotropics encompass four of the largest river basins on Earth—the Amazon, Orinoco, La Plata, and São Francisco—which together cover nearly two-thirds of the South American continent (Ayres and Clutton-Brock 1992). Among these, the Amazon River alone drains approximately 7,050,000 km^2—almost 40% of the continent—and includes more than 1,000 tributaries (Ramos *et al.* 2026). When extensive wetland systems such as the Pantanal and the Iberá–Ñeembucú complex are also considered (Junk 2013; Urcola *et al.* 2025), South America emerges as a region exceptionally rich in surface freshwater habitats (Hurlbert *et al.* 1981). These environments have persisted through major climatic and tectonic events, providing long-term ecological continuity and repeated opportunities for aquatic and amphibious life histories to evolve (Clapperton 1993).

Despite this environmental context, sigmodontine rodents, the most species-rich and geographically widespread mammalian radiation in the Neotropics, exhibit only a modest degree of specialization toward semiaquatic environments. Of the more than 500 living species currently recognized (Brito and Pardiñas 2025), only a small proportion display morphological and behavioral traits associated with amphibious habits (e.g., Massoia 1976; Voss 1988; Bianchini and Delupi 1993; Patton *et al.* 2015; Pardiñas *et al.* 2017). Moreover, these adaptations are phylogenetically clustered, being largely restricted to Ichthyomyini and to a limited subset of Oryzomyini, whereas the majority of sigmodontine lineages remain terrestrial, scansorial, or semifossorial (and more rarely, arboreal; see Brito *et al.* 2021). This pattern indicates that transitions into freshwater environments have been rare and unevenly distributed across the phylogeny.

Several non-exclusive explanations may account for this pattern. One possibility is that freshwater habitats have been effectively underutilized by sigmodontines, either due to intrinsic biological constraints or to persistent ecological pressures limiting successful colonization. Predation risk, particularly from aquatic and semiaquatic vertebrates, has been proposed as a potential factor reducing the fitness of small mammals in freshwater systems (Wolff and Guthrie 1985). Alternatively, the present-day scarcity of semiaquatic sigmodontines may reflect a process of guild impoverishment, in which amphibious forms were more diverse in the past but experienced differential extinction during the Neogene or Quaternary. Under this scenario, extant diversity would represent a residual subset of a historically broader ecological spectrum (Voss 1988).

Distinguishing among these alternatives requires a historical perspective that integrates phylogenetic, ecological, and paleontological evidence. In this study, we compile information on mode of life across sigmodontine rodents and analyze its distribution within a molecular phylogenetic framework. Using ecomorphological classification and ancestral-state reconstruction, we document the phylogenetic placement and evolutionary distribution of semiaquatic habits. These analyses are not designed to directly test causal mechanisms, but rather to characterize patterns of ecological diversification and to provide a basis for evaluating alternative explanatory scenarios.

Based on these patterns, we explore the extent to which the limited representation of semiaquatic sigmodontines is consistent with (1) ecological constraints associated with freshwater environments or (2) historical reductions in diversity through extinction. More broadly, this case provides an opportunity to examine how ecological opportunity, constraint, and historical contingency interact to shape functional diversity within a major continental mammal radiation.

Materials and methods

Taxonomic and ecological data. Three recent and comprehensive syntheses of sigmodontine diversity (Patton *et al.* 2005; Pardiñas *et al.* 2017; Brito and Pardiñas 2025) were used as the primary taxonomic sources (Supplementary Data SD1). The dataset includes 507 species distributed in 91 genera, representing all the recognized sigmodontine contemporary richness.

Each species was classified as semiaquatic or non-semiaquatic based on a combination of external morphological traits and published natural history information. This classification follows an integrative approach commonly used in comparative ecomorphological studies (e.g., Maestri *et al.* 2017; 2022), in which ecological categories are inferred from concordant morphological and behavioral evidence.

Semiaquatic forms were defined as species exhibiting at least two of the following morphological features: (1) bi-layered pelage composed of a dense woolly underfur and a superficial overfur; (2) a continuous comb of stiff hairs along the metatarsal margins and between the digits, fringing the sole of the pes; (3) midventral tail hairs conspicuously longer than those on the dorsal and lateral surfaces; (4) moderately developed webbing between digits II–IV of the manus; (5) highly developed and numerous mystacial vibrissae; (6) nostrils positioned high on the snout, anterolaterally placed and posteriorly expanded by a small diverticulum flanked by a developed *ala nasi ventralis*; (7) small but distinct interdigital and metacarpal pedal pads; (8) a prismatic basal cross-section of the tail; and (9) well-developed interdigital webbing between pedal digits II–IV. These characters have been repeatedly identified as indicative of adaptation to aquatic environments in sigmodontines and other muroid rodents, reflecting behaviors such as swimming, diving, foraging, dispersal, nesting, and reproduction in freshwater systems (e.g., Sierra de Soriano 1965; 1969; Hershkovitz 1966; 1969; Starrett and Fisler 1970; Massoia 1976; Miller and Anderson 1977; Esher *et al.* 1978; Pine *et al.* 1981; Voss 1988; 2015a; 2015b; Kerbis Peterhans and Patterson 1995; Weksler 2006; Santori *et al.* 2008; Rowe *et al.* 2014).

Molecular data and phylogenetic analyses. To infer phylogenetic relationships, nucleotide sequences were retrieved from GenBank for four unlinked loci widely used in rodent systematics: the mitochondrial cytochrome *b* gene (cytb) and the nuclear genes interphotoreceptor retinoid-binding protein (IRBP), growth hormone receptor (GHR), and recombination activating gene 1 (RAG1). The dataset includes representatives of all sigmodontine genera for which molecular data are available, excluding *Casiomys* and *Gyldenstolpia*, and incorporates 19 outgroup taxa representing other cricetid subfamilies and more distantly related muroids (Supplementary Data SD2). To maximize phylogenetic coverage while minimizing redundancy, a single representative species per genus was included in the main analysis.

Sequences were aligned separately for each gene using MAFFT v7 under default parameters, implemented in ClustalX, and subsequently inspected and edited in AliView. Alignments were trimmed to preserve reading frame integrity, resulting in final lengths of 1,140 bp (cytb), 1,184 bp (IRBP), 796 bp (GHR), and 2,022 bp (RAG1). The concatenated dataset comprised 5,142 bp.

Phylogenetic inference was conducted under the Maximum Likelihood (ML; Stamatakis 2014) criterion using IQ-TREE v2.2. Each gene was treated as an independent partition to allow locus-specific substitution models, which were selected using ModelFinder. Node support was assessed using ultrafast bootstrap (UFBoot) and SH-aLRT tests, each with 10,000 replicates. The resulting ML topology was visualized and annotated in FigTree v1.4 and used as the framework for subsequent analyses.

Mode of life classification and ancestral-state reconstruction. A discrete matrix of seven ecomorphological categories—arboreal, cursorial, saltatorial, scansorial, semiaquatic, semifossorial, and wader—was compiled from published ecological and behavioral sources. When species-level information was unavailable, genera were coded based on the predominant morphology exhibited by their constituent species. Each taxon was assigned a single dominant ecomorphological state using a categorical coding scheme appropriate for discrete-state evolutionary models.

Ancestral-state reconstructions were performed in Mesquite v3.7 (Maddison and Maddison 2019) using Maximum Likelihood under the Mk1 model, which assumes equal transition rates among states. Although this model does not accommodate potential asymmetries in transition probabilities among ecological states, it provides a conservative framework for reconstructing general patterns of trait evolution across the phylogeny.

The ML phylogeny obtained in IQ-TREE was imported into Mesquite and linked to the ecomorphological dataset. Likelihoods of alternative character states were estimated for all internal nodes and visualized using proportional-symbol reconstructions.

Analyses were conducted using default optimization settings (20 million iterations, sampling every 1,000 steps). Reconstructions were inspected for consistency with tree topology. Final trees and character-state graphics were exported as vector files and edited in Inkscape for figure preparation.

Results

Diversity of semiaquatic sigmodontines. Analysis of extant sigmodontine diversity indicates that only a small fraction of species can be classified as semiaquatic (Supplementary Data SD1). These include (1) all currently recognized members of Ichthyomyini (22 species in seven genera) and (2) a limited subset of Oryzomyini, comprising 15 species distributed among *Amphinectomys* (1 species), *Holochilus* (7), *Lundomys* (1), and *Nectomys* (6). Together, these taxa represent approximately 7% of living sigmodontine species and 12% of genera (n = 507 species; n = 91 genera; Supplementary Data SD1).

Several additional genera—three oryzomyines (*Oryzomys*, *Pseudoryzomys*, *Sigmodontomys*) and two akodontines (*Gyldenstolpia*, *Scapteromys*)—have historically been associated with aquatic environments (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 morphological and natural history evidence does not support their inclusion among semiaquatic taxa. In *Scapteromys*, individuals inhabit terrestrial and river-margin habitats, construct burrows, nest on dry ground, and engage in climbing activities (Massoia and Fornes 1964; Hershkovitz 1966; Barlow 1969). *Oryzomys* tolerates flooded environments but lacks the morphological traits observed in semiaquatic sigmodontines (Esher *et al.* 1978; Weksler 2006). Following Kerbis Peterhans and Patterson (1995), these genera are here classified as waders. Under this classification, wader taxa represent approximately 3% of sigmodontine species and 5% of genera (Supplementary Data SD1).

Other genera occasionally proposed as semiaquatic, such as *Mindomys* and *Neotomys*, were excluded from both semiaquatic and wader categories based on currently available evidence (Pardiñas *et al.* 2015; Brito *et al.* 2021).

Phylogenetic analyses. The maximum-likelihood analysis of the concatenated dataset recovered a well-resolved phylogeny (Figure 1). Major sigmodontine tribes were recovered with strong statistical support and with relationships congruent with previous multilocus reconstructions (e.g., Leite *et al.* 2014; Gonçalves *et al.* 2020; Parada *et al.* 2021; Pardiñas *et al.* 2022; 2024; Bangs *et al.* 2025).

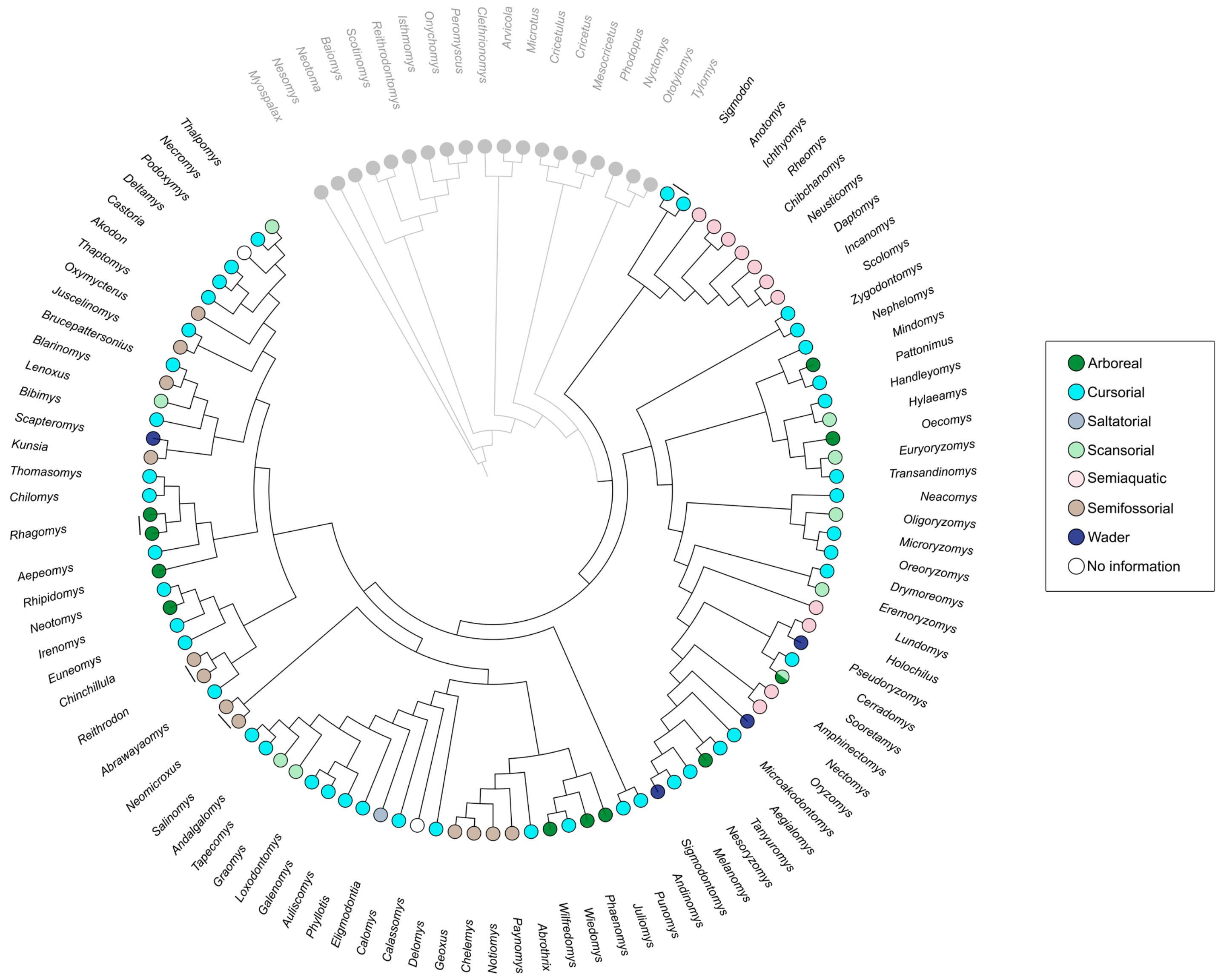

Figure 1. Phylogeny of Sigmodontinae showing the assignment of analyzed genera to ecomorphological categories.

Within Sigmodontinae, Oryzomyini, Phyllotini, Akodontini, Thomasomyini, and Abrotrichini were recovered as monophyletic (UFBoot > 95; SH-aLRT > 0.90). Oryzomyini constituted the earliest-diverging lineage within the sampled sigmodontines, followed by successive divergences involving the akodontine–phyllotine complex and the thomasomyine–abrotrichine assemblage. Outgroup taxa provided a stable root for the ingroup topology and recovered Sigmodontinae within Cricetidae.

The ancestral reconstruction of ecomorphological categories estimated a log-likelihood value of −132.83 and an overall transition rate of 1.18. The proportional-likelihood reconstruction recovered the ancestral sigmodontine condition as cursorial, with a markedly higher likelihood than alternative states (Figure 2).

Independent transitions toward arboreal and scansorial conditions were reconstructed in multiple oryzomyine and thomasomyine lineages. Semiaquatic ecomorphologies were reconstructed independently within Ichthyomyini and Oryzomyini. Semifossorial conditions were recovered primarily within the akodontine complex. Saltatorial morphologies occurred only in a limited number of terminal branches.

Semiaquatic sigmodontines exhibit a geographically heterogeneous distribution (Figure 3). Ichthyomyines are associated primarily with streams and rivers of Andean and montane regions in northwestern South America and Central America (Voss 1988, 2015a). In contrast, lowland wetlands and river systems of eastern tropical, subtropical, and temperate South America are occupied mainly by a small number of oryzomyine taxa, principally *Holochilus* and *Nectomys* (e.g., Hershkovitz 1955; Bonvicino and Weksler 2015; Chiquito 2015; Prado *et al.* 2021).

No semiaquatic sigmodontines were recorded from southern South America. The southernmost extant representatives correspond to *Holochilus brasiliensis* and *Holochilus lagigliai*, which reach the northern limit of Patagonia (Formoso *et al.* 2010; Pardiñas *et al.* 2013; Figure

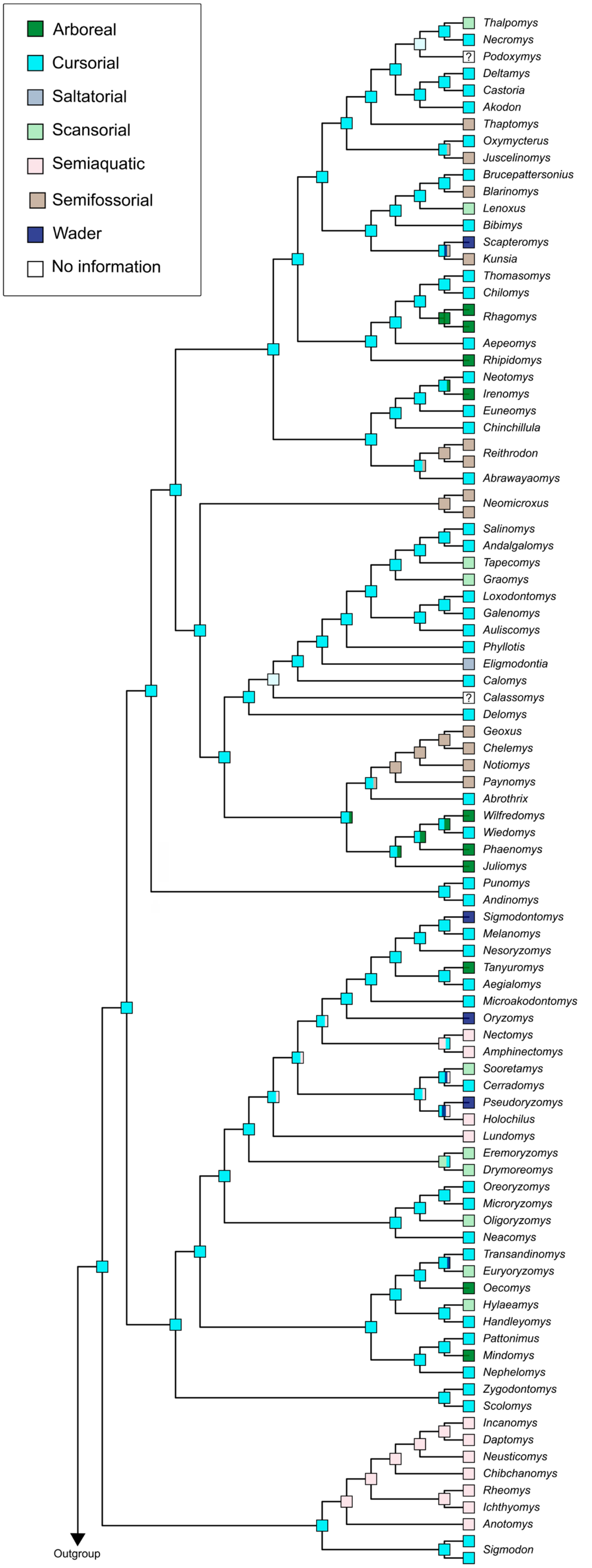

Figure 2. Ancestral-state reconstruction of ecomorphological categories within Sigmodontinae.

3). Fossil records indicate broader past distributions for some semiaquatic taxa (Figure 4).

Discussion

Evolutionary rarity of freshwater specialization. Our phylogenetic and ancestral-state reconstructions indicate that semiaquaticity evolved independently within Sigmodontinae but remained restricted to a limited number of lineages. This combination of repeated origin and limited diversification raises the question of why freshwater specialization remained uncommon despite its apparent evolutionary accessibility.

Our results indicate that semiaquatic sigmodontines constitute only a small fraction of the extant diversity of the subfamily, both taxonomically and phylogenetically. Only two major lineages—Ichthyomyini and a restricted subset of Oryzomyini—include species exhibiting the suite of traits associated with freshwater specialization. Most sigmodontine genera associated with humid or seasonally flooded habitats instead correspond to wader forms lacking the morphological specializations characteristic of sustained swimming and diving.

The ancestral-state reconstruction further suggests that the earliest sigmodontines were primarily cursorial (see also Rodríguez-Serrano *et al.* 2008). From this ancestral condition, multiple locomotor strategies evolved independently across the subfamily, including arboreal, scansorial, semifossorial, and semiaquatic forms (e.g., Hershkovitz 1969). The repeated emergence of semiaquaticity demonstrates that freshwater adaptation evolved convergently within Sigmodontinae and was therefore evolutionarily accessible. At the same time, its restricted representation indicates that relatively few lineages followed this trajectory.

This combination of evolutionary accessibility and low diversification is notable. In many mammalian radiations, ecological opportunities associated with freshwater systems have promoted repeated colonization and diversification (Fish 1992; Fish *et al.* 2002). In sigmodontines, however, semiaquaticity remained both geographically restricted and taxonomically limited despite the broad ecological diversification achieved by the subfamily throughout South America (Patton *et al.* 2015; Pardiñas *et al.* 2017).

Convergent evolution of semiaquatic adaptations. Adaptation to freshwater environments imposes multiple functional challenges for small mammals, including locomotion, thermoregulation, feeding, and predator avoidance (e.g., Voss 1988; Fish 1992; Fish *et al.* 2002). Several morphological specializations observed in semiaquatic sigmodontines appear associated with these challenges. Dense insulating fur likely reduces heat loss during immersion (Santori *et al.* 2008), whereas enlarged hindfeet, interdigital webbing, and laterally compressed tails probably enhance swimming efficiency (e.g., Starrett and Fisler 1970; Voss 1988).

Figure 3. Schematic geographic distributions of the two sigmodontine rodent groups that include semiaquatic forms, superimposed on a map of Middle and South America highlighting the main contemporary fluvial systems.

Ichthyomyines represent the most specialized expression of these adaptations within Sigmodontinae. Members of this tribe exhibit traits facilitating swimming, diving, and prey capture in shallow, fast-flowing streams (e.g., Starrett and Fisler 1970; Voss 1988; Salazar-Bravo *et al.* 2023). Nevertheless, semiaquatic specialization is not restricted to ichthyomyines. Oryzomyine taxa occupying freshwater environments independently evolved several comparable traits, including expanded interdigital webbing, enlarged pes, dorsoventrally flattened heads, reduced pinnae, nostril-closing folds, and dense underfur (Hershkovitz 1955; Sierra de Soriano 1965; 1969; Massoia 1976; Voss and Carleton 1993).

Thermal constraints may also contribute to the distribution of semiaquatic forms. Small mammals experience rapid heat loss in aquatic environments, generating energetic demands that frequently favor larger body sizes in semiaquatic taxa (Wolff and Guthrie 1985). Consistent with this expectation, *Holochilus* and *Lundomys* rank among the largest sigmodontines (Hershkovitz 1955; Weksler 2006).

Taken together, these patterns indicate that both major sigmodontine clades—Oryzomyalia and Sigmodontalia—independently evolved comparable functional solutions to freshwater challenges. The critical question, therefore, is not whether sigmodontines were capable of freshwater adaptation, but why so few lineages underwent this transition.

Geographic asymmetry and environmental constraints. The distribution of semiaquatic sigmodontines exhibits a pronounced geographic asymmetry. Ichthyomyines are concentrated primarily in Andean and montane systems of northwestern South America and Central America (Voss 1988; 2015a; Salazar-Bravo *et al.* 2023), whereas lowland wetlands and floodplains of eastern South America are occupied mainly by a few oryzomyine genera, especially

Figure 4. Selected fossil craniodental remains of sigmodontines hypothesized to represent extinct semiaquatic taxa, together with the maximum Pleistocene range of *Lundomys molitor* (colored area to the right) and the Holocene extension of the distribution of *Holochilus* (colored area to the left). Based on multiple sources.

Holochilus and *Nectomys* (e.g., Hershkovitz 1955; Bonvicino and Weksler 2015; Chiquito 2015; Prado *et al.* 2021). In contrast, southern South America lacks any extant semiaquatic sigmodontine fauna (Lessa *et al.* 2012; Chebez *et al.* 2014).

This pattern suggests that freshwater specialization was not only rare, but also spatially constrained. The absence of semiaquatic forms in southern regions may partially reflect present climatic conditions. Small-bodied aquatic and semiaquatic mammals experience substantial energetic constraints in cold environments because of their high surface-area-to-volume ratios and the high thermal conductivity of water, which greatly increase heat loss and thermoregulatory demands (Scholander *et al.* 1950; McNab 1978; Dawson and Fanning 1981). Additionally, paleoenvironmental evidence indicates substantial reduction and fragmentation of wetland systems during the Late Quaternary and Holocene, potentially reducing the availability of suitable freshwater habitats across southern South America (e.g., Roig 1991; Stoessel *et al.* 2008; Pardiñas and Teta 2011; Hadler *et al.* 2026).

The paleontological record supports this interpretation. Fossil occurrences of *Holochilus* and *Lundomys* indicate broader past distributions (e.g., Pardiñas and Lezcano 1995; Pardiñas 1999; Teta *et al.* 2005; Teta and Pardiñas 2006), including regions that currently lack extensive freshwater systems, such as Bolivian Chaco (e.g., Hoffstetter 1968; Pardiñas and Galliari 1998; Coltorti *et al.* 2012) and northern Patagonia (e.g., Fernández and Crivelli-Montero 2004; Fernández *et al.* 2011; Pardiñas and Teta 2011). These records suggest that semiaquatic taxa formerly occupied habitats that later disappeared or became substantially reduced.

Historical timing, ecological opportunity, and niche saturation. Sigmodontine diversification likely began in northern South America following colonization from Central and North America during the late Miocene (Prevosti *et al.* 2021; Ronez *et al.* 2021b; 2023; Candela *et al.* 2023; Romano *et al.* 2023). One possible explanation for the low representation of semiaquatic forms is that freshwater niches were already occupied by other mammalian groups at the onset of sigmodontine radiation. This hypothesis of niche saturation (Northfield *et al.* 2010; Cassini 2020) directs attention to marsupials and caviomorph rodents.

Among marsupials, freshwater specialization is rare, with *Chironectes* representing the only extant semiaquatic form (Pine *et al.* 1981; Stein and Patton 2008). Caviomorph rodents include amphibious taxa such as *Hydrochoerus* and *Myocastor*, as well as species capable of diving, such as *Cuniculus* (Patton *et al.* 2015). In addition, the fossil record documents a Miocene–Pleistocene diversity of true or potentially semiaquatic caviomorphs (e.g., Vucetich *et al.* 2015; Kerber *et al.* 2016; Rasia 2026). However, given the marked body-size differences separating these rodents from sigmodontines, direct ecological competition may have been limited.

An alternative explanation involves evolutionary timing. Molecular estimates place the initial sigmodontine diversification at approximately 10-8 Ma (e.g., Parada *et al.* 2021; Bangs *et al.* 2025), whereas the earliest confident fossil records appear around 5.7 Ma (Prevosti *et al.* 2021; Candela *et al.* 2023; Romano *et al.* 2023). Although the fossil record remains incomplete, the existence of a specialized ichthyomyine radiation suggests that time alone is unlikely to explain the limited diversification of semiaquatic forms. Semiaquatic oryzomyines appear later within the tribe (Percequillo *et al.* 2021), potentially accounting for their more limited degree of specialization. Differences in evolutionary rates among ecological guilds may instead have contributed to the observed asymmetry (Maestri *et al.* 2017).

Predation as a macroecological filter. Predation risk may represent an additional factor constraining freshwater colonization by sigmodontines. Although direct observations remain scarce, predation by fishes on sigmodontine rodents has been documented in multiple regions (e.g., Mann 1978; Pardiñas *et al.* 2004; Vitule *et al.* 2015; Borges *et al.* 2025).

Neotropical freshwater ecosystems harbor exceptionally diverse predator assemblages. The Amazon basin alone contains more than 3,000 fish species (Junk 2007), including numerous large predators (Reis *et al.* 2016). Freshwater predation pressure further includes reptiles, birds, and mammals. Fossil assemblages from Late Miocene and Pliocene deposits indicate that this predator diversity has deep temporal roots (e.g., Sánchez-Villagra *et al.* 2010; Carrillo-Briceño *et al.* 2019; Cadena *et al.* 2020; Viñola López *et al.* 2025).

Under these conditions, freshwater systems may function as strong biotic filters (*sensu* Vermeij 1991), limiting the establishment and diversification of small mammalian lineages. Although this hypothesis remains difficult to test directly, the structure and diversity of Neotropical predator assemblages are broadly consistent with such an interpretation.

A synthetic scenario: habitat undervaluation and extinction. Integrating these observations, we propose a working hypothesis in which predation risk and extinction jointly shaped the current scarcity of semiaquatic sigmodontines. During the late Miocene, northern South America comprised a mosaic of freshwater and brackish systems (e.g., Lundberg *et al.* 1998; de Souza *et al.* 2021; McDermott 2021), partly representing the remnants of the Pebas system encountered by early sigmodontines during their colonization of the continent (Ronez *et al.* 2021b, 2023). Lowland lineages may have been constrained by intense predation pressure from aquatic vertebrates, whereas an early lineage colonizing Andean environments encountered clearer, shallower streams with fewer large predators, facilitating the radiation of Ichthyomyini. Concurrently, a small number of lowland oryzomyines colonized marshes and ponds with comparatively reduced predation pressure, evolving larger body sizes (e.g., *Holochilus* and *Nectomys*, with the largest species reaching approximately 250–300 g, and *Lundomys*, exceeding 300 g; Massoia 1976; Voss and Carleton 1993) and herbivorous tendencies as additional defensive strategies.

The present scarcity of semiaquatic sigmodontines may also partly reflect extinction. Several extinct taxa plausibly associated with freshwater environments are known from Pleistocene deposits, including †*Carletonomys*, †*Ichthyurodon*, †*Noronhomys*, and †*Reigomys* (Steppan 1996; Carleton and Olson 1999; Pardiñas 2008; Machado *et al.* 2014; Pardiñas and Barbière 2018; Barbière 2019). If these rodents occupied semiaquatic niches, their disappearance would substantially alter the apparent historical diversity of this ecological guild.

A similar pattern is suggested by the fossil distribution of extant semiaquatic genera. Fossil records indicate that *Holochilus* and *Lundomys* formerly occupied broader geographic areas than at present, including regions currently lacking extensive wetlands or permanent freshwater systems. These contractions are consistent with major paleoenvironmental changes during the Late Quaternary, particularly wetland reduction and increasing aridity in parts of southern South America (e.g., López and Chiavazza 2021).

Integrating these observations, the current distribution of semiaquatic sigmodontines may reflect the combined effects of ecological filtering and extinction. Freshwater colonization likely occurred repeatedly but remained limited by predation pressure and environmental constraints, whereas subsequent climatic and habitat changes may have further reduced the diversity and distribution of these lineages.

Freshwater specialization in a broader muroid context. Comparison with Murinae—the only muroid subfamily comparable to Sigmodontinae in diversity and geographic extent (e.g., Denys *et al.* 2017)—reinforces the broader significance of these patterns. Despite a longer evolutionary history and wider distribution (e.g., Aghová *et al.* 2018; López-Antoñanzas *et al.* 2024), murines also include relatively few semiaquatic taxa (e.g., Musser and Heaney 1992; Helgen 2005; Rowe *et al.* 2014; Denys *et al.* 2017).

This convergence suggests that freshwater environments may represent a broadly challenging ecological domain for small muroid rodents rather than a constraint unique to sigmodontines. In this context, sigmodontines appear relatively successful rather than exceptionally limited, having independently evolved semiaquatic forms in at least two major lineages.

Notably, within Oryzomyalia, only Oryzomyini evolved fully semiaquatic representatives, paralleling the remarkable ecological flexibility already documented for this tribe (Ronez *et al.* 2021a; Bover *et al.* 2025). More generally, the uneven distribution of semiaquaticity across Sigmodontinae suggests that ecological opportunity and evolutionary potential were not uniformly distributed within the subfamily (e.g., Alhajeri *et al.* 2016; Missagia *et al.* 2023). These patterns provide a useful framework for future investigations into the ecological and macroevolutionary processes shaping functional diversification in continental mammal radiations.

Conclusions

The limited representation of semiaquatic sigmodontine rodents is unlikely to reflect an absence of evolutionary potential, nor solely a consequence of restricted time or ecological opportunity. Instead, the available phylogenetic and ecomorphological evidence indicates that semiaquatic adaptations evolved convergently within the subfamily—primarily in Ichthyomyini and in a small subset of Oryzomyini—demonstrating that freshwater colonization was feasible, but comparatively rare.

The patterns documented here are consistent with a scenario in which persistent ecological constraints and historical processes jointly shaped this outcome. In particular, predation risk within continental freshwater systems may have acted as an important selective filter, limiting the number of lineages able to exploit aquatic habitats and favoring either occupation of predator-poor montane environments or shifts toward traits such as larger body size in lowland systems. These constraints may have been further amplified by extinction, as suggested by the fossil record and by evidence of range contraction in semiaquatic taxa during the Quaternary.

Viewed in a broader muroid context, the sigmodontine case appears illustrative rather than exceptional. Freshwater environments may represent a challenging ecological domain for small mammals, despite their spatial extent and long-term persistence. In this framework, the present-day scarcity of semiaquatic sigmodontines can be interpreted as consistent with a combination of ecological filtering associated with freshwater habitats and historical reductions in diversity through extinction. More generally, this case highlights how ecological constraints and historical contingency interact to shape the distribution of functional traits within continental mammal radiations.

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Declaration of Artificial Intelligence use

Artificial intelligence was used exclusively to assist with language editing and stylistic refinement of the manuscript. Specifically, the authors used ChatGPT (OpenAI; model version GPT-5.2) to improve clarity, grammar, coherence, and consistency of academic

English. ChatGPT is accessible via: https://openai.com/chatgpt. AI tools were not used for data generation, data analysis, figure preparation, image manipulation, statistical analyses, or interpretation of results. All scientific content, analyses, conclusions, and final editorial decisions are entirely the responsibility of the authors.

Author contributions

The authors accepted responsibility for the entire content of this manuscript and approved its submission. Erika Cuéllar Soto and Ulyses F. J. Pardiñas: conceptualization, investigation, supervision, writing–original draft. Carola Cañón: laboratory analysis. All the authors: Writing–review and editing.

Data availability

The datasets generated and analyzed during the current study are included (Supplementary Data); the concatenated matrix, alignment partitions, and Mesquite project files are available upon request; 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.

Supplementary data

SD1. A list of living genera and species of sigmodontine rodents indicating those considered semiaquatic and waders. Numbers updated to December 2025.
SD2. List of sequences downloaded from GenBank that were used to construct the phylogeny.

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