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The role of ancestral monogamy and climate in the evolution of sociality in hystricognath rodents

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Per aspera ad astra

A mi y a quienes me apoyaron y estuvieron conmigo incluso en los momentos más difíciles ☺

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Tabla de contenido

Índice de Figuras

Índice de figuras suplementarias

Índice de Tablas

Índice de Tablas Suplementarias

RESUMEN

La evolución de la sociabilidad en animales ha sido un tema central en la sociobiología y la ecología evolutiva. La sociabilidad se define típicamente como la vida en grupo que incluye una amplia gama de formas de organización social, donde individuos animales, invertebrados y vertebrados, pasan parte o toda su vida en asociación con individuos coespecíficos, siendo la eusocialidad, el nivel más avanzado de organización social. En vertebrados, la eusocialidad es excepcionalmente rara y solo ha sido documentada en dos especies de la familia Bathyergidae (Rodentia). Diversas hipótesis han sido propuestas para explicar la transición hacia sistemas sociales. Entre ellas, la hipótesis de la monogamia de por vida postula que la monogamia aumenta la relación genética entre los miembros de un grupo, favoreciendo la cooperación y facilitando la evolución de la eusocialidad. Paralelamente, la hipótesis de las restricciones ecológicas sugiere que factores ambientales, como la aridez, pueden modular la sociabilidad al limitar la dispersión individual y promover la formación de grupos. Los roedores, debido a su diversidad social y amplia distribución, representan un modelo ideal para estudiar estos procesos.

En esta tesis, evaluamos estos dos mecanismos en roedores mediante análisis filogenéticos comparativos. En primer lugar, examinamos la evolución de la monogamia en Bathyergidae para evaluar su papel en la transición hacia la eusocialidad. Utilizando reconstrucciones de estados ancestrales y modelos de correlación evolutiva, nuestros resultados indican que la monogamia fue la condición ancestral en especies sociales y eusociales. Sin embargo, no encontramos evidencia de que la monogamia haya sido el factor causal en la evolución de la eusocialidad en este grupo. En segundo lugar, investigamos la relación entre la aridez y la sociabilidad en roedores del infraorden Hystricognathi. Estimamos el tiempo de divergencia de este grupo y caracterizamos las condiciones ambientales de su distribución. No encontramos una asociación significativa entre el índice de aridez y la sociabilidad, lo que sugiere que otros factores ecológicos, como la distribución de recursos y la presión de depredación, podrían ser más relevantes en la evolución de los sistemas sociales.

Estos hallazgos aportan nuevas perspectivas sobre los impulsores de la evolución de la sociabilidad en roedores y resaltan la importancia de un enfoque multifactorial que integre historia evolutiva, relaciones filogenéticas y condiciones ecológicas para comprender la diversificación de los sistemas sociales en mamíferos.

ABSTRACT

The evolution of sociality in animals has been a central topic in sociobiology and evolutionary ecology. Sociality is typically defined as group living, encompassing a wide range of social organization forms in which animal individuals, both invertebrates and vertebrates, spend part or all of their lives associating with conspecifics, with eusociality being the most advanced level of social organization. Among vertebrates, eusociality is exceptionally rare and has only been documented in two species of the Bathyergidae family (Rodentia). Various hypotheses have been proposed to explain the transition to social systems. Among them, the lifetime monogamy hypothesis posits that monogamy increases genetic relatedness among group members, promoting cooperation and facilitating the evolution of eusociality. In parallel, the ecological constraints hypothesis suggests that environmental factors, such as aridity, can shape sociality by limiting individual dispersal and promoting group formation. Due to their social diversity and broad distribution, rodents represent an ideal model for studying these processes.

In this thesis, we evaluate these two mechanisms in rodents through phylogenetic comparative analyses. First, we examine the evolution of monogamy in Bathyergidae to assess its role in the transition to eusociality. Using ancestral state reconstructions and evolutionary correlation models, our results indicate that monogamy was the ancestral condition in both social and eusocial species. However, we found no evidence that monogamy was the causal factor in the evolution of eusociality in this group. Second, we investigate the relationship between aridity and sociality in rodents of the infraorder Hystricognathi. We

estimate the divergence time of this group and characterize the environmental conditions of its distribution. We do not find a significant association between the aridity index and sociality, suggesting that other ecological factors, such as resource distribution and predation pressure, may be more relevant in the evolution of social systems.

These findings provide new insights into the drivers of social evolution in rodents and highlight the importance of a multifactorial approach integrating evolutionary history, phylogenetic relationships, and ecological conditions to understand the diversification of social systems in mammals.

INTRODUCCIÓN

Entender las causas de la formación y el mantenimiento de los grupos sociales ha sido el principal objetivo de la sociobiología y la ecología conductual (Alexander, 1974; Faulkes et al., 1997; Ebensperger & Cofré, 2001; Lacey & Solomon, 2003). Todos los animales son sociales en algún momento de su vida, mostrando comportamientos agonísticos y afiliativos (es decir, competencia reproductiva, búsqueda de alimento, defensa contra la depredación, cuidado de crías) con miembros de su propia especie (Rubenstein & Abbot, 2017). Además, muchas especies forman grupos, ya sean efímeros o permanentes, desde grupos de corta duración (como agregaciones temporales de individuos no relacionados) hasta grupos de larga duración (como la cría cooperativa y la eusociabilidad, donde los individuos cooperan ampliamente) (Wilson, 1975; Jarvis, 1981; Lott, 1991; Smith, Lacey & Hayes, 2017). La sociabilidad se define típicamente como la vida en grupo que incluye una amplia gama de formas de organización social, donde individuos animales, invertebrados y vertebrados, pasan parte o toda su vida en asociación con individuos coespecíficos (Alexander, 1974; Wilson, 1975; Lott, 1991; Rubenstein & Abbot, 2017). El nivel más avanzado de vida social es la eusociabilidad, donde una especie eusocial exhibe criterios clásicos específicos descritos por Wilson (1975); (i) una división reproductiva del trabajo (castas), (ii) cuidado cooperativo de los descendientes de una casta reproductiva por una casta de trabajadores no reproductivos o menos reproductivos, y (iii) superposición de dos o más generaciones. Sin embargo, la sociabilidad es poco frecuente en la naturaleza (Wilson, 1971; Cockburn, 2006; Lukas & Clutton-Brock, 2012; Smith, Lacey & Hayes, 2017).

En los mamíferos, la sociabilidad se da en todos los linajes principales, donde el 70% de las especies son solitarias (los adultos tienden a vivir solos) y el 30% restante son especies sociales que incluyen las formas más avanzadas de organización social conocidas entre los vertebrados (Sherman et al., 1995; Lacey & Sherman, 2008; Smith, Lacey & Hayes, 2017). Entre los mamíferos, Rodentia es el orden más numeroso con ~ 2000 especies (Wilson & Reeder, 2005). Este orden muestra una amplia gama de estructuras sociales, desde la estrictamente solitaria a la eusociabilidad, ofreciendo oportunidades para explorar las causas y la variación en la estructura social (Lacey & Sherman, 2008; Smith, Lacey & Hayes, 2017).

Se ha propuesto que la sociabilidad se produce cuando los beneficios de permanecer en grupo, en términos de adecuación biológica, superan los costes de este comportamiento (Alexander, 1974). Especialmente los roedores que viven en grupo se benefician del cuidado cooperativo de las crías (Armitage, 1981), la detección y defensa de recursos (Slobodchikoff, 1984; Travis, Slobodchikoff & Keim, 1995), el bajo riesgo de depredación y los costes de termorregulación (Klump & Shalter, 1984; Blumstein & Armitage, 1998; Ebensperger & Cofré, 2001; Krause & Ruxton, 2002), y la construcción y mantenimiento comunal de madrigueras (Reichman & Smith, 1990; Kinlaw, 1999). Por otro lado, los costes son la competencia por la reproducción y la supresión reproductiva (Keller &

Reeve, 1994; Emlen, 1995), el riesgo de enfermedades y la transmisión de parásitos (Altizer et al., 2003).

Se han propuesto múltiples hipótesis para comprender los factores y las causas del origen de la vida en grupo. Por ejemplo, se espera que la historia evolutiva sea un determinante importante de la sociabilidad y el sistema de apareamiento dentro de los grupos (Boomsma, 2009; Lukas & Clutton-Brock, 2012, 2013; Smith, Lacey & Hayes, 2017). Además, también se ha sugerido que la ecología desempeña un papel fundamental en la evolución de la sociabilidad. La hipótesis de las restricciones ecológicas (Emlen, 1982) propone que el hábitat y el medio ambiente actúan sobre las decisiones individuales de dispersión, promoviendo o restringiendo los patrones de agrupación. Pero además, esta hipótesis también reconoce el papel de la incertidumbre ambiental en la configuración de la evolución de los comportamientos cooperativos (Rubenstein, 2011). Además, para entender mejor cómo la ecología y la historia evolutiva interactúan para dar forma a la sociabilidad, muchos estudios han utilizado análisis filogenéticos comparativos. Dado que los roedores exhiben un amplio rango de organización social, incluyendo el sistema social más avanzado (eusociabilidad), y debido a que están distribuidos por todo el mundo en una gran variedad de ambientes, los roedores son un buen modelo para testear hipótesis sobre aproximaciones al mecanismo e impulsores de la sociabilidad. Por ello, en esta tesis pusimos a prueba dos de las hipótesis sobre la evolución de los sistemas sociales, una asociada al origen de los sistemas eusociales y otra relacionada con el papel de las condiciones climáticas en la promoción de la formación de grupos sociales.

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Chapter One: “Monogamy and the Evolution of Eusociality: Insights from African Mole-Rats (Rodentia: Bathyergidae)”

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ABSTRACT

Eusociality, the highest level of social organization, is rare among vertebrates and is best exemplified by two African mole-rat species (Rodentia: Bathyergidae). Among the hypotheses proposed to explain the emergence of eusociality, the lifetime monogamy hypothesis suggests that monogamy enhances genetic relatedness within colonies, favoring the evolution of cooperative behaviors. While empirical evidence supports this hypothesis in eusocial insects, its role in vertebrates, particularly in Bathyergidae, remains unclear. We evaluated the lifetime monogamy hypothesis in the Bathyergidae family to determine the role of monogamy in the evolution of eusociality in African mole-rats. A direct prediction of this hypothesis is that the ancestors of the eusocial species of Bathyergidae present a monogamous mating system, allowing a high ancestral genetic relatedness between the progeny that favors the transition to eusociality. We inferred phylogenetic relationships within the Bathyergidae, and then investigated mating system evolution, and the sociality of African mole-rats by estimating ancestral character states. We also evaluated the evolutionary correlation between mating system and sociality. Our results showed an ancestral monogamous state for social and eusocial African mole-rats. The evolutionary correlation analysis showed that one of the transitions with the highest rate of change goes from monogamy + solitary to monogamy + social. Although monogamy is associated with the evolution of sociality within the group, we found no evidence that the transition to monogamy promoted the transition to eusociality in African mole-rats. We conclude that monogamy plays an important role in the evolution of sociality in the Bathyergidae family.

Keywords: sociality, mating system, social evolution, ancestral state estimation, evolutionary correlation

INTRODUCTION

Understanding the formation and maintenance of social groups is a major focus of sociobiology and behavioral ecology (Alexander, 1974; Faulkes et al., 1997; Ebensperger and Cofré, 2001; Lacey and Solomon, 2003). All animals are social at some point in their lives, displaying agonistic and affiliative behaviors with members of their species (i.e., reproductive competition, foraging, predator defense, and parental care) (Rubenstein and Abbot, 2017). Sociality is typically defined as group living, and includes a wide range of forms of social organization, where individual animals spend part or all of their lives in association with conspecific individuals (Alexander, 1974; Wilson, 1975; Lott, 1991; Rubenstein and Abbot, 2017). The most advanced level of social organization is eusociality. Eusocial species exhibit criteria described by Wilson (1975): (i) a reproductive division of labor (castes), (ii) cooperative care of the descendants of a reproductive caste by a caste of non-reproductive or less reproductive workers, and (iii) overlapping of two or more generations. In eusocial bees and ants, for example, there is one reproductive female, the queen, and the other females are sterile workers who help the queen to raise her offspring.

Early work suggested that the evolution of eusociality relies on kinship selection, where selection can favor individuals who transmit their genes to the future generation through self reproduction (reproductive caste), obtaining direct fitness benefits, and individuals who transmit their genes to the future generation by helping their relatives to reproduce (working caste), obtaining indirect fitness benefits (Hamilton, 1964). Based on this kinship selection theory, others proposed the lifetime monogamy hypothesis, suggesting monogamy as the key factor for the evolution of eusociality since it increases the genetic relationship between siblings, increasing the benefits of inclusive fitness (Boomsma, 2007, 2009). Empirical studies supporting this hypothesis have revealed that in hymenopteran insects, the ancestral monogamous state is more likely in eusocial species (Hughes et al., 2008; Davies and Gardner, 2016, 2018; Quiñones and Pen, 2017). Furthermore, in birds and mammals, the evolution of cooperative breeding is strongly associated with monogamy (Cornwallis et al., 2010; Lukas and Clutton-Brock, 2012a). This hypothesis was primarily proposed for eusocial insects, which exhibit advanced eusociality. However, it could also be applied to other taxa if they are considered a eusocial lineage or advanced breeders on the brink of making the transition to eusociality (Boomsma, 2007, 2009). Here we test the lifetime monogamy hypothesis in the only known eusocial mammals, the naked mole-rat (*Heterocephalus glaber*) (Jarvis, 1981) and Damara mole-rat (*Fukomys damarensis*) (Bennett and Jarvis, 1988; Jarvis and Bennett, 1993).

The two eusocial African mole-rat species are part of the family Bathyergidae (30 or more species). The social structure in Bathyergidae comprises strict solitary genera (*Heliphobius, Bathyergus*, and *Georychus*) and social genera (*Heterocephalus, Cryptomys,* and *Fukomys*). The family is endemic to the Afrotropics and species occur in physically and climatically divergent habitats. Individuals from solitary genera are larger than those from social genera, and they are typically found in humid regions. Social genera live in colonies and are found in both humid and xeric regions, displaying varying degrees of social behavior (Bennett and Faulkes, 2000; Faulkes and Bennett, 2001). Eusocial species live in colonies of up to 300 individuals for *H. glaber* (Sherman, Jarvis and Braude, 1992) and up to 42 individuals for *F. damarensis* (Bennett and Jarvis, 1988). Both species inhabit regions with low and unpredictable precipitation and low food density (Jarvis et al., 1994; Faulkes et al., 1997). *H.glaber* and *F. damarensis* also have the highest reproductive skew among vertebrates, with only one reproductive female and one to three reproductive males (Jarvis, 1981; Jarvis and Bennett, 1993). They form long-term monogamy bonds (although in some colonies, the queen may have two or three male consorts) and exhibit a socially-induced suppression of reproductive physiology for subordinate members. Unlike eusocial insects, these reproductive blocks are reversible and are brought about by the presence of the queen (Faulkes and Bennett, 2021). In addition, *H. glaber* and *F. damarensis* show morphological differentiation between the castes (Sherman and Jarvis, 2002). The worker caste are philopatric, i.e. they do not disperse, and participate in various potentially cooperative activities as tunnel-digging, foraging, and colony defense (Bennett and Faulkes, 2000).

The Bathyergidae family provides one of the most extreme examples of sociality evolution in vertebrates (Jarvis, 1981; Jarvis and Bennett, 1993; Burda et al., 2000). However, monogamy's role in the evolution of these complex societies has yet to be tested. In this study, we evaluated the hypothesis of lifetime monogamy in the Bathyergidae family to determine the role of monogamy in the evolution of eusociality in African mole-rats. A direct prediction of this hypothesis is that the ancestors of the eusocial species of Bathyergidae present a monogamous mating system, allowing high ancestral genetic relatedness between the progeny that favors the transition from eusociality. To achieve this, we estimated the phylogenetic relationships of the Bathyergidae family, traced the evolution of their mating system and social structure by inferring ancestral character states, and assessed the evolutionary correlation between these two traits.

METHODS

Phylogeny inference and divergence time estimates

To reconstruct the phylogenetic relationships of Bathyergidae, we used the most comprehensive molecular database available on GenBank (http://www.ncbi.nlm.nih.gov/, Table S1): cytochrome b (cytb) and rRNA 12S genes for 23 Bathyergidae species. We selected two species as the outgroup, *Petromus typicus* (Petromuridae) and *Thryonomys swinderianus* (Thryonomyidae). We aligned the sequences using MUSCLE (Edgar, 2004) on MEGA X software (Kumar et al., 2018). To concatenate the sequences, we used Mesquite v 3.81 (Maddison and Maddison, 2001). To check for potential substitution saturation of the molecular dataset (Xia and Lemey, 2009) we performed the Xia test (Xia et al., 2003) using DAMBE V5.1.5 (Xia, 2013). The phylogeny was inferred using a general likelihood-based mixture model (MM) based on the general time-reversible (GTR) model (Rodriguez et al., 1990) of sequence evolution in a Bayesian framework. This model accommodates cases in which different sites in the alignment evolved in qualitatively distinct ways but does not require prior knowledge of these patterns or partitioning of the data. These analyses were conducted using the software BayesPhylogenies v1.1 (https://www.evolution.reading.ac.uk/BayesPhy.html, Pagel and Meade, 2004). To find the best mixture model of gene-sequence evolution, we allowed the "*rjpa*" parameter to freely converge to the number of GTR matrices that best describe the molecular data set. The convergence of an independent Markov Chain Monte Carlo run (141,100,000 generations, 10,000 sampling frequency, with 10% as burn-in) was assessed with the software Tracer v1.7.2 (Rambaut et al., 2018). The consensus tree was computed using BayesTrees v1.3 software (https://www.evolution.reading.ac.uk/BayesTrees.html).

Next, we collated age data for 13 fossils to date the tree. We used the fossils from Bryja et al. (2018) and the minimum and maximum ages from the Paleobiology Database (https://paleobiodb.org) and the literature (Table S2). We then used the Fossilized birth-death model (FBD, Heath, Huelsenbeck and Stadler, 2014) to estimate the divergence time of African Mole-rats. Under the FBD model, each fossil is treated along with extant species as part of the same unified macroevolutionary process, avoiding the use of arbitrary and sometimes problematic calibration densities ("node calibrations", Heath, Huelsenbeck and Stadler, 2014). Fossil taxa can be treated as direct ancestors or extinct tips, where their topological placement is estimated using a Markov chain Monte Carlo (MCMC) algorithm (Heath, Huelsenbeck and Stadler, 2014), allowing the inclusion of all reliable fossil taxa available for the group of interest, regardless of their precise location in the phylogeny. We use the FBD model implemented in the Sampled Ancestor package (Gavryushkina et al., 2014; Heath, Huelsenbeck and Stadler, 2014) in BEAST v2.7.3 (Bouckaert et al., 2019). We used an optimized relaxed clock (ORC), using ORC v1.1.1 a BEAST 2 package that includes optimizations that improve the performance of the phylogenetic relaxed clock model (Douglas, Zhang and Bouckaert, 2021). For all partitions, we used bModelTest (bModelTest v1.3.3 package for BEAST 2), which allows one to infer the site evolution model during the MCMC analysis (Bouckaert and

Drummond, 2017). Under this configuration, we ran two MCMC analyses for 400 million iterations, sampling every 10,000 iterations. We examined both runs in Tracer v1.7.2 (Rambaut et al., 2018) to check for convergence, and combined tree files from the two runs in LogCombiner implemented in BEAST v2.7.3 (Bouckaert et al., 2019), removing a burn-in of 10%. We extracted the maximum clade credibility tree using TreeAnnotator implemented in BEAST v2.7.3 (Bouckaert et al., 2019).

Mating and social systems: Database and Ancestral state estimation

We compiled a dataset (Table S3) of mating systems (monogamy, polyandry, polygyny) and social systems (solitary, social, and eusocial) for all 23 bathyergid species in our phylogeny. We classify the mating system according to Clutton-Brock (2021): monogamy, a mating system in which the same female-male pair typically reproduces together across multiple breeding attempts; polygyny, a mating system in which a single male typically mates with multiple females during the same breeding season; and polyandry, a mating system in which a single female typically mates with multiple males during a single breeding season. We classify the social system as solitary for species in which adults spend most of their lives alone. Social for those species that live in groups and are not eusocial. In the case of Bathyergidae, social species exhibit singular cooperative breeding where one reproductive pair is responsible for all breeding within a social group, wherein the rest of the members assist with the rearing of nonoffspring (Clutton-Brock, 2021). And for eusocial species we follow the description above.

To estimate the state transitions of both traits through time, we estimated the ancestral trait state using three different transition rate models: i) ER, all transition rates are equal; ii) SYM, the transition rate from going from an “x” state to a “y” state is the same as going from a “y” state to an “x” state, but it is different from “x” to “z”; and iii) ARD, all transition rates are different, we used the *fitdiscrete* function of the R package GEIGER (Pennell et al., 2014) in R (R Core Team, 2024). The best transition rate model was selected using small sample size corrected Akaike Information Criterion (AICc). To reconstruct the ancestral states under the best model, we used the make.simmap function of the phytools R package v 0.6.50 (Revell, 2012), which performs stochastic character maps on a phylogenetic tree under a Bayesian framework.

Evolutionary correlation between mating system and sociality in Bathyergidae

To estimate if monogamy and eusociality evolved in a correlated way, we evaluated whether the evolution between these traits coincided with an independent or dependent evolution model using BayesTraits v4.1.1 (available from http://www.evolution.rdg.ac.uk/). The test compares the marginal likelihood of a model where the transition rates of each state of one trait are independent of the state of the other trait (independent model) versus a model where the rates of change of the state of one trait depend on the state of another trait (dependent model). To perform this analysis, the states of the traits must be binary, so we categorized (i) mating system: monogamy (1) or polygamy (polyandry and polygyny, 0), and social system: eusocial (1) and non-eusocial (0). Also, for a second test, we categorized mating systems as polygamy (polyandry and polygyny, 1) or non-polygamy (monogamy, 0), and social systems as solitary (1) and non-solitary (social, 0). Both categorizations assessed coevolution between mating and social systems, considering the lowest (solitary) and the highest (eusocial) social levels. To choose the best model, we used Bayes Factor.

RESULTS

Phylogeny inference and divergence time estimation

The consensus tree topology (Fig. S1) showed that Bathyergidae is a fully supported monophyletic family (posterior probability [PP] = 100). Each genus is also well supported as monophyletic with high posterior probability (PP = 100 for *Heterocephalus*, *Heliophobius*, *Bathyergus*, *Georychus*, *Cryptomys* and *Fukomys*). *Heterocephalus* is the sister group of the other genera (PP = 100). *Heliophobius* is the sister group of a clade containing *Georychus*, *Bathyergus*, *Cryptomys* and *Fukomys* (PP = 100). *Georychus* and *Bathyergus* genera form a clade that is sister to the clade of *Cryptomys* and *Fukomys* (PP = 99).

The divergence of Bathyergidae (Fig. 1) was estimated as 23.39 (20.44 – 29.62) Mya (million years ago) in the late Oligoncene. *Heterocephalus* diverged around 15.97 Mya in the middle Miocene. *Heliophobius* diverged 15 Mya, also in the Miocene. The *Georychus* / *Bathyergus* clade diverged from their common ancestor with *Cryptomys* / *Fukomys* 11.27 (9.26 – 15.67) Mya. The divergence between *Georychus* and *Bathyergus* dated from 8.5 Mya, and the divergence between *Cryptomys* and *Fukomys* was estimated to occur at 8.93 (6.92 – 12.83) Mya.

Ancestral state estimation

The best fitting transition models were ER for social system (AICc = 28.958, Table S4) and ER for mating system (AICc = 28.553, Table S4). The ancestral character state estimation (Fig. 2) indicated that the most recent common ancestor (MRCA) of the

Bathyergidae was not well recovered with high certainty for the social system and exhibited a trend toward a monogamous mating system (PP = 0.458). The estimation for the MRCA of *Heliophobious* was similar, exhibiting a trend to be solitary (PP = 0.507) with a monogamous mating system (PP = 0.445). We estimated that the MRCA of *Cryptomys* / *Fukomys* and *Bathyergus* / *Georychus* was likely social (PP = 0.454) with a monogamous mating system (PP = 0.506) and that the MRCA of (eu)social *Cryptomys* and *Fukomys* species was most likely social (PP = 0.782) with a monogamous mating system (PP = 0.798). Similar for the MRCA of the eusocial species *F. damarensis*, it was most likely social (PP = 0.990) with a monogamous mating system (PP = 0.999). Only for the MRCA of the clade containing the solitary genera *Bathyergus* and *Georychus*, we estimated that it was most likely to be solitary (PP = 0.731) and have a non-monogamous mating system (polygynous; PP = 0.599).

Evolutionary correlation

We estimated, with weak evidence (Bayes Factor, BF = -1.169, Table S5), that eusociality and monogamy did not evolve in a correlated way, i.e. each state of one trait is independent of the state of the other trait (Table S5). The highest transition rates were from a eusocial state to a non-eusocial (61.345) and from a polygamous state to a monogamous state (60.921). We estimated, under moderate evidence (BF = 9.930, Table S6), that sociality and mating system evolved in a correlated way, where the highest transition rates (Fig. 3) were from monogamous + solitary to monogamous + social (60.275), from polygamous + social to monogamous + social (60.128), from monogamous + solitary to polygamous + solitary (56.923), and from polygamous + social to polygamous + solitary (52.814).

DISCUSSION

The rodent family Bathyergidae is a unique group to study the evolution of eusociality in vertebrates. Here, for the first time, we evaluated the lifetime monogamy hypothesis (Boomsma, 2007) to determine the role of monogamy in the evolution of eusociality in African mole-rat species. Our results showed that Bathyergidae is a monophyletic group with high posterior probability with well-resolved relationships among genera, concordant with previous studies (Faulkes et al., 2004; Kock et al., 2006; Daele et al., 2007a,b; Visser, Bennett and Vuuren, 2019). We estimated the origin of African mole-rats during the late Oligocene, with *Heterocephalus* the first extant genus to diverge. This is earlier than in some other studies (*e. g.* Faulkes et al., 2004; Visser, Bennett and Vuuren, 2019) but similar to Bryja et al. (2018). The formation of the Eastern Rift (Kenya) at 23 - 11 Mya began to shape the East African landscape (Van Couvering and Van Couvering, 1976), leading to climatic, physical, and environmental changes that could be important in determining species' divergence and distribution, driving to a radiation of Bathyergidae from eastern Africa to central and southern Africa. In addition, climatic changes associated with open and arid environments (ca. 2.7 – 2.5 Mya., 1.9 – 1.7 Mya., and 0.95 – 0.7 Mya) with alternate climatic changes leading to wet conditions and habitat fragmentation, may have played an important role in the diversification of *Fukomys*, the most species rich genus in the group. Interestingly, several cladogenetic events during the Plio–Pleistocene coincide with climate–mediated speciation bursts in other mammals living in the savanna (Bobe and Behrensmeyer, 2004; Trauth et al., 2005).

Ancestral monogamy is associated with the evolution of sociality in African mole-rats

Our results suggest that the eusocial state in African mole-rats evolved independently in each lineage of eusocial species. We estimated an ancestral monogamous state for social (cooperative breeding) and eusocial African mole-rats. The MRCAs of eusocial species (*H. glaber* and *F. damarensis*) were estimated to be social. We found that monogamy is associated with the evolution of sociality within the Bathyergidae. However, we found no evidence that the transition to monogamy generated the transition to eusociality in African mole-rats. Monogamy as the ancestral state in complex societies has been reported in different taxa, invertebrates, and vertebrates, suggesting that singular cooperative breeders evolve from monogamous ancestors (Hughes et al., 2008; Cornwallis et al., 2010; Lukas and Clutton-Brock, 2012a,b; Quiñones and Pen, 2017; Davies and Gardner, 2018; Clutton-Brock, 2021), where high levels of average kinship among group members have played an important role (Abbot et al., 2011; Boomsma et al., 2011). Monogamy leads to a high reproductive skew; in naked mole-rat (*H. glaber*), it has been found that the skew in lifetime reproductive success was at 99.9%, and in Damaraland mole-rat (*F. damarensis*), at 92% of non-breeding females never could breed (Sherman, Jarvis and Braude, 1992; Jarvis and Bennett, 1993; Jarvis et al., 1994). Therefore, monogamy is a prerequisite for complex social evolution such as cooperative breeding and eusociality; a monogamous condition could increase the genetic relationship inside a colony of cooperative breeding and eusocial African mole-rats, promoting altruist behavior and complex societies. Cooperative breeding exhibits some traits similar to eusociality, but there is no evidence of distinct castes in cooperative breeders (Clutton-Brock, 2021). It remains questioning on what factors drove the evolution of eusociality in vertebrates? What underlying mechanism led to the emergence of caste division in these eusocial species? How did non-reproductive castes evolve?

One recurrent explanation for the evolution of eusociality in African mole-rats is the aridity food distribution hypothesis (AFDH), which correlates eusociality to arid habitats, predicting that eusociality is necessary to cope with patchy distribution of resources in arid and semi–arid environments (Jarvis et al., 1994). Evidence supporting this hypothesis has been found in inter – and intraspecific studies in Bathyergidae (Jarvis, Bennett and Spinks, 1998; Spinks, Jarvis and Bennett, 2000; Comber et al., 2002; Sichilima et al., 2008; Lövy et al., 2012). However, the criticism to the AFDH is the lack of a causal mechanism at the evolutionary scale to consider the association among aridity, patchy distribution of food resources, and the evolution of eusociality in African mole-rats (Burda, 1999). Also, the distribution of cooperative breeding in mammals is associated with arid environments (Lukas and Clutton-Brock, 2017), so what made the difference between cooperative breeding and eusociality? On the other hand, another study has related other factors to the evolution of complex sociality in the Bathyergidae family. It has been shown that groups with a larger workforce present substantially higher recruitment rates for offspring, while maintaining high rates of youth survival, correlations that may have favored the evolution of philopatry, cooperation, morphological specialization and the unusual longevity patterns that characterize African mole rat species (Young et al., 2015). However, like AFDH, there is a lack of causal evolutionary mechanism. Consequently, it is necessary a historical biogeography study to estimate the environmental conditions that could lead to a eusocial state in African mole-rats to complement our results. Thus, to understand the evolution of eusociality in

African mole-rats it is necessary to know the preconditions for the development of their complex societies. Therefore, our present study is a significant contribution since we estimated an evolutionary association between an ancestral monogamy state and sociality in Bathyergidae. Furthermore, we concluded that monogamy plays an important role in the evolution of sociality in the Bathyergidae family and that eusociality was acquired independently throughout the life history of each eusocial lineage. Consequently, it is essential to conduct new studies to expand our understanding of the development of these unique complex societies in vertebrates.

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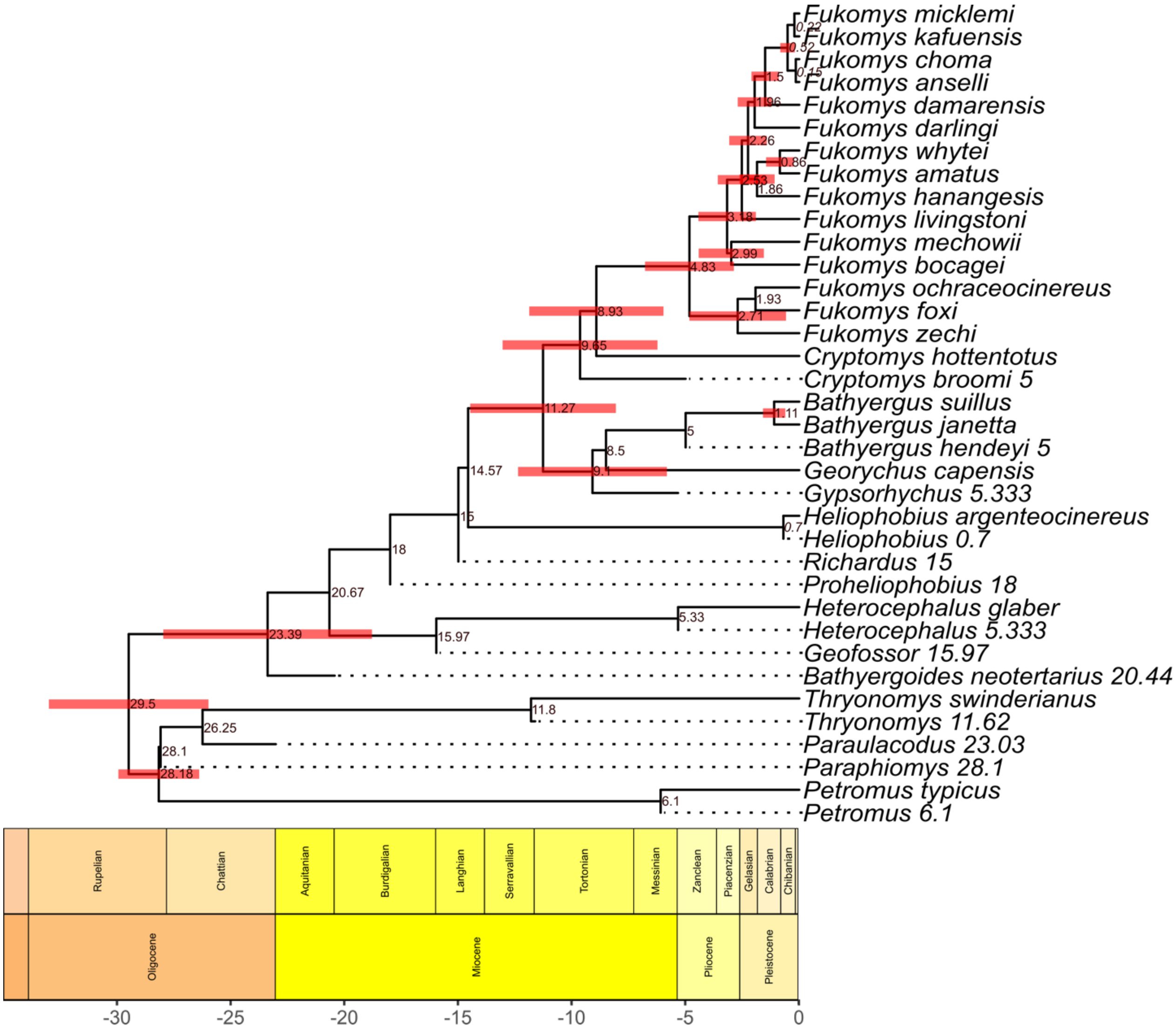

Figure 1. Calibrated phylogenetic tree of African Mole-rats (Bathyergidae) based on the sequence substitution rates of two genes (Cytb and 12S rRNA). The mean divergence time is shown to the right of each node with a 95% higher posterior density (HPD, red bars).

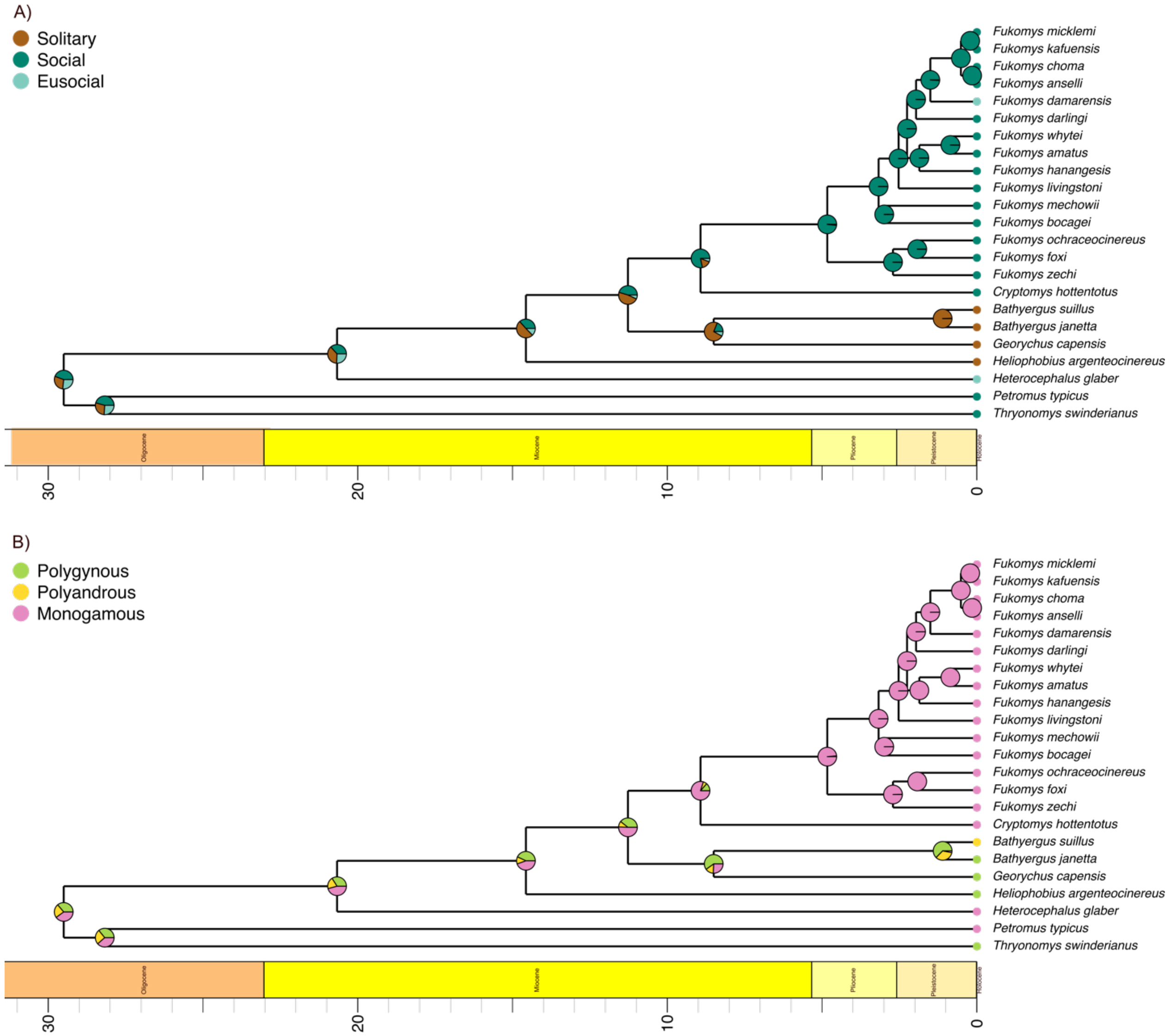

Figure 2. Estimation of ancestral states of Bathyergidae sociality (A) and mating system (B) using a Bayesian framework. The pie charts at each node represent the probability of each inferred mating system state for that node.

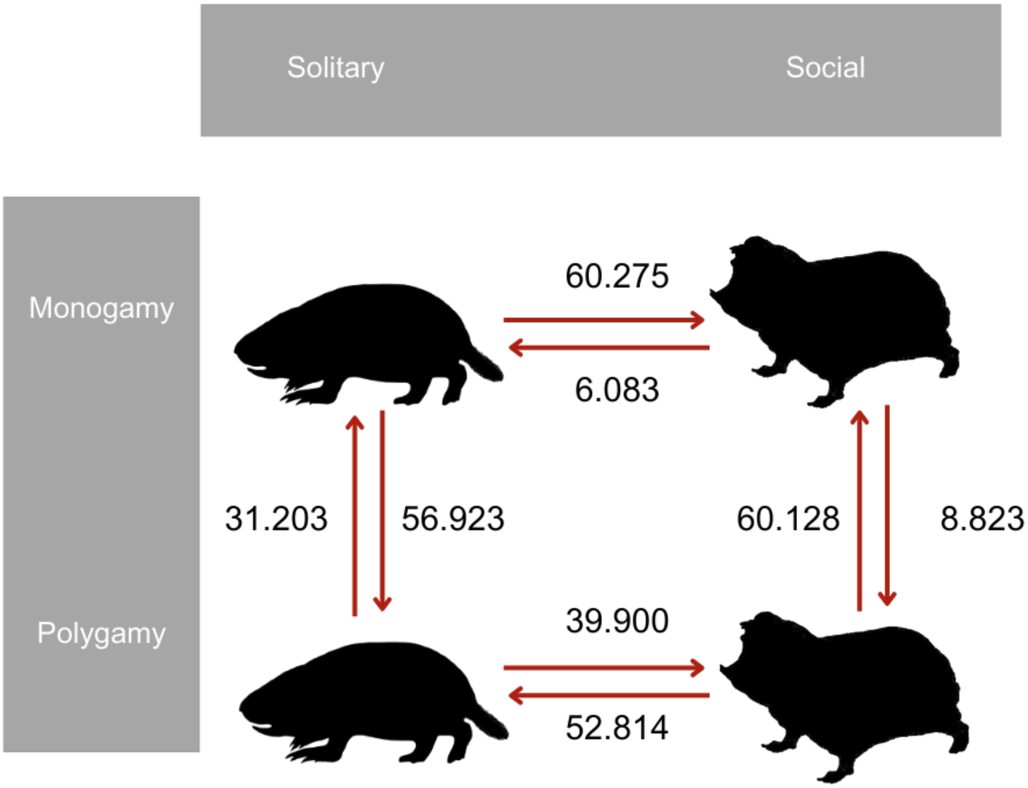

Figure 3. Evolutionary transitions between sociality and monogamy. Arrows indicate transition rates estimated in BayesTraits.

SUPPLEMENTARY MATERIALS

Table S1. GenBank Accession numbers of used sequences to infer the phylogenetic tree and the divergence time of Bathyergidae.

ID	12S rRNA	CYTB
Bathyergus suillus	AY427020	AY425913.1
Bathyergus janetta	M63565.1	AY425916.1
Georychus capensis	M63566.1	AF012243.1
Heliophobius argenteocinereus	AY427070	AY425943.1
Heterocephalus glaber	AY012120	AF155870.1
Cryptomys hottentotus	AY425841.1	AY425886.1
Fukomys amatus	AY427021.1	EF043468.1
Fukomys anselli	AY427025.1	
Fukomys bocagei	AF012213.1	
Fukomys damarensis	AY427032.1	KT321364.1
Fukomys darlingi	AY427034.1	AF012232.1
Fukomys foxi	AY427036.1	
Fukomys kafuensis	AY427037.1	
Fukomys mechowii	AY427042.1	EF043452.1
Fukomys micklemi	AY427044.1	EF043494.1
Fukomys ochraceocinereus	AY427045.1	
Fukomys whytei	AY427047.1	EF043477.1
Fukomys zechi		KX905198.1

Fukomys livingstoni		KX905196
Fukomys hanangesis		KX905185
Fukomys choma		AF012234
Thryonomys swinderianus	M63570	KJ742647.1
Petromus typicus	M63571	MH186591.1

Table S2. The list of used fossils, with their maximum and minimum age (in millions of years).

Fossil	**Max Age**	**Min Age**	**References**
Paraphiomys	28.1	5.333	https://paleobiodb.org/
Paraulacodus	23.03	5.333	https://paleobiodb.org/
Thryonomys	11.62	0	https://paleobiodb.org/
Petromus	6.1	0	Mein & Pickford, 2006
Bathyergoides neotertarius	20.44	15.97	https://paleobiodb.org/
Geofossor	15.97	11.608	https://paleobiodb.org/
Proheliophobius	18	16	Denys 2022
Richardus	15	14	Denys 2022
Gypsorhychus	5.333	2.588	https://paleobiodb.org/
Bathyergus hendeyi	5	4.5	Denys 1998
Cryptomys broomi	5	4.5	Denys 1998
Heterocephalus	5.333	0	https://paleobiodb.org/
Heliophobius	0.7	0.3	Brugal & Denys 1989

Table S3. Sociality and mating system of the rodents studied in this study.

	Sociality	Mating system	References
Bathyergidae			
Heterocephalus glaber	Eusocial	Monogamous	Jarvis, 1981; Faulkes & Bennett, 2021
Heliophobius argenteocinereus	Solitary	Polygynous	Patzenhauerová, Bryja & Šumbera, 2010; Faulkes & Bennett, 2021
Bathyergus janetta	Solitary	Polygynous	Herbst, Jarvis & Bennett, 2004; Happold, 2013; Faulkes & Bennett, 2021
Bathyergus suillus	Solitary	Polyandrous	Bray et al., 2012; Faulkes & Bennett, 2021; Happold
Georychus capensis	Solitary	Polygynous	Happold, 2013; Visser, Bennett & Jansen Van Vuuren, 2017; Faulkes & Bennett, 2021
Cryptomys hottentotus	Social	Monogamous	Bishop et al., 2004; Faulkes & Bennett, 2021
Fukomys foxi	Social	Monogamous	Faulkes & Bennett, 2021
Fukomys ochraceocinereus	Social	Monogamous	Faulkes & Bennett, 2021
Fukomys bocagei	Social	Monogamous	Faulkes & Bennett, 2021
Fukomys mechowii	Social	Monogamous	Sichilima et al., 2008; Faulkes & Bennett, 2021
Fukomys darlingi	Social	Monogamous	Bennett, Jarvis & Cotterill, 1994; Faulkes & Bennett, 2021
Fukomys damarensis	Eusocial	Monogamous	Bennett & Jarvis, 1988; Jarvis & Bennett, 1993; Faulkes & Bennett, 2021
Fukomys kafuensis	Social	Monogamous	Faulkes & Bennett, 2021
Fukomys anselli	Social	Monogamous	Sichilima, Bennett & Faulkes, 2011; Faulkes & Bennett, 2021
Fukomys whytei	Social	Monogamous	Faulkes & Bennett, 2021
Fukomys amatus	Social	Monogamous	Faulkes & Bennett, 2021
Fukomys micklemi	Social	Monogamous	Faulkes & Bennett, 2021
Fukomys zechi	Social	Monogamous	Faulkes & Bennett, 2021
Fukomys livingstoni	Social	Monogamous	Faulkes & Bennett, 2021
Fukomys hanangesis	Social	Monogamous	Faulkes & Bennett, 2021
Fukomys choma	Social	Monogamous	Faulkes & Bennett, 2021

Petromuridae			
Petromus typicus	Social	Monogamous	Rathbun & Rathbun, 2006
Thryonomyidae			
Thryonomys swinderianus	Social	Monogamous	Happold, 2013

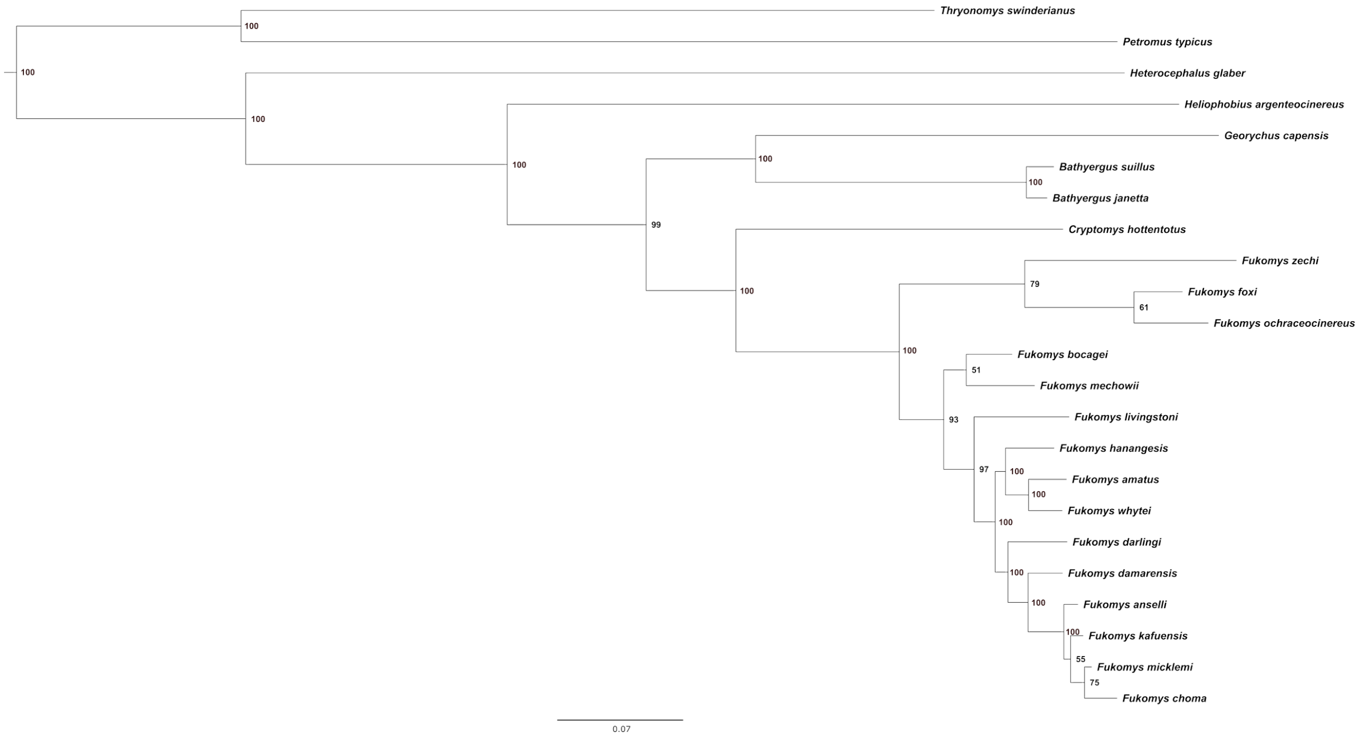

Figure S1. Phylogenetic tree of African mole-rats (Bathyergidae) estimated by Bayesian inference, based on a two-gene sequence matrix (Cytb and 12S rRNA). The numbers on the nodes indicate the posterior probability (PP) of the Bayesian inference.

Table S4. AICc values for estimating ancestral state under ER, SYM, and ARD models for social and mating systems. In bold is the model that best fits the data.

	ER	SYM	ARD
Social system	**28.958**	33.878	40.235
Mating system	**28.553**	28.696	34.629

Table S5. Evolutionary correlation. Values of the marginal loglikelihood for both models, independent and dependent. Value of Bayes Factor to find the best model that fits data. Transition rate values under the best model (Independent model).

	Independent model	Dependent model
Marginal logLikelihood	-21.291	-22.460
Bayes Factor	-1.169	
Transition rates		
Polygamy to Monogamy	60.921	
Monogamy to Polygamy	22.263	
Non-eusocial to Eusocial	9.642	
Eusocial to Non-eusocial	61.345	

Table S6. Evolutionary correlation. Values of the marginal loglikelihood for both models, independent and dependent. Value of Bayes Factor to find the best model that fits data. Transition rate values under the best model (Dependent model).

	Independent model		Dependent model	
Marginal logLikelihood	-24.684		-19.718	
Bayes Factor	9.930			
Transition rates				
	Social + Monogamy	Social + Polygamy	Solitary + Monogamy	Solitary + Polygamy
Social + Monogamy	-	8.823	6.083	0
Social + Polygamy	60.128	-	0	52.814
Solitary + Monogamy	60.275	0	-	56.923
Solitary + Polygamy	0	39.900	31.203	-

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Capter Two: Environmental Aridity does not explain the evolution of sociality in Hystricognath rodents

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ABSTRACT

Sociality encompasses a range of forms of social organization. Forces that drive the transition from a solitary to a cooperative social life are the generation of a kinship structure. Ecological factors could play an important role in developing social systems. Harsh environments could impose a high cost related to breeding, where cooperation and social strategies may lower this cost. Therefore, the emergence of sociality facilitates cooperative behaviors that offset the physiological demands of living in a harsh environment, such as arid habitats. Hystricognathi infraorder displays a wide social range distributed in a wide variety of habitats. This study evaluates the role of aridity in the evolution of sociality in hystricognath rodents. We estimated the divergence time of hystricognath rodents and characterized the environmental conditions of their distribution range. Finally, we determined whether environmental condition of aridity drives the sociality in hystricognath rodents. We estimated the origin of hystricognath rodents during the middle Eocene. We did not find an effect of aridity on sociality in Hystricognathi rodents.

Our study determined the extent to which aridity may contribute to the general pattern of social structure at a broader taxonomic scale, for Hystricognathi we did not find a relationship between the aridity index and sociality. Therefore, other ecological factors could play a key role in the evolution of sociality in hystricognath rodents, such as habitat type and avoidance of predators. Thus, subsequent phylogenetic comparative research should study the link between sociality and ecological traits, such as resource distribution and predator avoidance in a multifactorial approach in order to understand the evolution of sociality in hystricognath rodents.

Keywords: Hystricognathi, Harsh environment, aridity index, phylogenetic comparative methods

INTRODUCTION

Sociality encompasses a range of forms of social organization in which various cooperative behaviors are typically expressed (Rubenstein & Abbot, 2017). One of the main forces driving the transition from a solitary to a cooperative social life is the generation of a kinship structure or a high level of kinship coefficient within the group (Boomsma, 2009; Rubenstein, 2011; Lukas & Clutton-Brock, 2012b; Davies & Gardner, 2018). In addition, ecological factors have been proposed to play an important role in the origin and development of social systems.

One proposed idea is the ecological constraints hypothesis (Emlen, 1982). Based primarily on a cooperative breeding system, this concept highlights that non-breeding individuals care for the offspring of dominant members. It suggests that offspring stay home as non-breeders when key factors limit breeding opportunities: (i) the lack of openings in stable environments or (ii) the high cost of raising young in unpredictable environmental harshness. The latter is based on the assumption that individuals should help others with whom they share genes in inhospitable environments, either because individual reproduction is likely to fail or because helpers provide greater benefits when environmental conditions are harsh (Covas, Plessis & Doutrelant, 2008; Rubenstein, 2011). Therefore, the emergence of sociality facilitates cooperative behaviors that offset the physiological demands of living in a harsh environment (e.g., communal nesting, constructing burrows, and resource defense). Recent studies have explored the role of environmental variation in driving cooperative behavior and the evolution of cooperative group living in different animal clades: fish (cichlids), birds, and mammals (Rubenstein & Lovette, 2007; Jetz & Rubenstein, 2011; Lukas & Clutton-Brock, 2017; Dey et al., 2017; Firman et al., 2020). For instance, cooperative breeding in birds and mammals is related to temporally fluctuating environments, where rainfall is low and unpredictable on both ecological and evolutionary scales (Jetz & Rubenstein, 2011; Lukas & Clutton-Brock, 2017). However, Cornwallis et al. (2017) found that, although cooperatively breeding birds are found in inhospitable environments, cooperative breeding is more likely to evolve from ancestors that occupied relatively cool environmental niches with predictable precipitation. Then, cooperation would be the key factor facilitating the colonization of inhospitable environments rather than vice versa. Nevertheless, this could depend on the dispersal rate of the species group. On the other hand, it has been proposed that life-history traits limit the opportunities for independent parenting (Russell, 1989; Cockburn, 1996; Arnold & Owens, 1998). However, life-history traits (e.g., time to sexual maturation, longevity) would not be associated with the evolution of cooperative breeding in mammals (Lukas & Clutton-Brock, 2012a).

Among mammals, rodents display a wide social range (Gromov, 2017). The infraorder Hystricognathi is the group with the broadest social range, from solitary species to eusocial species (with caste division and one breeding pair), and these rodents are distributed in a wide variety of habitats (Jarvis, 1981; Bennett & Jarvis, 1988; Bennett & Faulkes, 2000; Patton, Pardiñas & D'Elía, 2015). Thus, hystricognath rodents are the ideal clade to test the influence of ecological factors on the evolution of sociality. The infraorder Hystricognathi is subdivided into two groups: (i) Phiomorpha (*sensu lato*), with four living families distributed in Africa and Asia (Bathyergidae, Petromuridae, Thryonomyidae, and Hystricidae) and (ii) Caviomorpha with four superfamilies (Erethizontoidea, Chichilloidea, Cavioidea and Octodontoidea) distributed in all South American and with a remarkable social diversity (Bennett & Faulkes, 2000; Patton, Pardiñas & D'Elía, 2015; Ebensperger & Hayes, 2016; Gromov, 2017). In Bathyergidae, sociality is associated with arid environments and low, unpredictable rainfall (Faulkes et al., 1997). However, this relationship between inhospitable climatic conditions and the development and maintenance of sociality has not been tested in the rest of the group (Ebensperger & Hayes, 2016). Therefore, and considering the availability of high-resolution climatic and genetic data that allow us to estimate well-resolved phylogenies, the present study aims to test whether inhospitable (harsh) environmental conditions of aridity favor the evolution of sociality in hystricognath rodents. The study's main aim is to evaluate the role of climate in the evolution of sociality in hystricognath rodents. For this purpose, we estimated the divergence time of hystricognath rodents. We also characterized the environmental conditions of their distribution range, and finally, we determined whether the environmental condition of aridity drives the sociality in hystricognath rodents.

METHODS

Phylogeny and divergence time

We estimated the Hystricognathi calibrated phylogeny to have a well-resolved historical substrate on which to evaluate the role of climate in the evolution of sociality in Hystricognath rodents. We used the most comprehensive molecular database available at GenBank (http://www.ncbi.nlm.nih.gov/): the mitochondrial Cytochrome b (Cytb), Cytochrome Oxidase I (COI), and rRNAs (12S and 16S); the nuclear growth Hormone receptor (GHR), von Willebrand factor (vWF), recombination activating 1 (RAG1), and the interphotoreceptor retinoid-binding protein (IBRP) for 178 caviomorph species (reaching the highest percentage of coverage of the extant diversity: 72%) and 25 phiomorph species (Table S1). We aligned the sequences using MUSCLE (Edgar, 2004) on MEGA X software (Kumar et al., 2018). To concatenate the sequences, we used Mesquite (Maddison & Maddison, 2001). To check the potential substitution saturation of the molecular data set (Xia & Lemey, 2009), we performed the Xia test (Xia et al., 2003), using DAMBE V5.1.5 (Xia, 2013).

The fossil databases of Caviomorpha and Phiomorpha were downloaded from the Paleobiology Database (https://paleobiodb.org). We discarded fossil records of extant species. Following the proposals in the literature, fossil species were classified at the superfamily, family, and subfamily levels. We leave out the fossil species that we could not assign to any clade except the oldest fossil species of both taxa.

Then, based on the topologies of the molecular phylogenies (Superfamily and family level; Caviomorpha from Upham and Patterson 2015; Phiomorpha from Chapter One of this thesis) and the refined fossil data (Table S2), we used the

Fossilized birth-death (FBD) model to estimate time divergence of Hystricognathi (Heath, Huelsenbeck & Stadler, 2014). Under the FBD model, the fossil is treated along with extant species as part of the same unified macroevolutionary processes, avoiding the use of arbitrary and sometimes problematic calibration densities (“node calibrations”, Heath et al. 2014). Moreover, fossil taxa can be treated as direct ancestors or extinct tips, where their topological placement is integrated out using an MCMC algorithm (Heath, Huelsenbeck & Stadler, 2014), allowing the inclusion of all reliable fossil taxa available for the group of interest, regardless of their precise location in the phylogeny. We used the FBD model implemented in the Sample Ancestor package (Gavryushkina et al., 2014; Heath, Huelsenbeck & Stadler, 2014) for the BEAST v2.7.6 program (Bouckaert et al., 2019). We used an optimized relaxed clock (ORC), using ORC v1.1.1 a BEAST 2 package that includes optimizations that improve the performance of the phylogenetic relaxed clock model (Douglas, Zhang and Bouckaert 2021). For all partitions, we used bModelTest (bModelTest v1.3.3 package for BEAST 2), which allows one to infer the site evolution model during the MCMC analysis (Bouckaert and Drummond 2017). The origin was fixed to 48 Mya. Under this configuration, we run two MCMC analyses with 400,000,000 iterations, sampling every 40,000. Finally, we examined both runs in Tracer v1.7.2 (Rambaut et al., 2018) to check for convergence, and combined tree files from the two runs in LogCombiner implemented in BEAST v2.7.6 (Bouckaert et al., 2019), removing a burn-in of 10%. We extracted the maximum clade credibility tree using TreeAnnotator implemented in BEAST v2.7.6 (Bouckaert et al., 2019). The resultant calibrated tree was used to evaluate if harsh environments facilitated sociality in hystricomorph rodents.

Data collection

Social system

We collected the social systems from the literature to evaluate whether climatic variation facilitates sociality in hystricomorph rodents. For those species included in the phylogeny with available data on the social system, we categorized each species as either social or non-social. For this purpose, a species was defined as social when there is evidence that individuals live with conspecifics in groups and express cooperative behaviors (Rubenstein & Abbot, 2017). Alternatively, non-social species will be when they show evidence of solitary existence. We excluded those species for which no information is available.

Environment

We used the area of habitat (AOH) available for 111 hystricognath species (Lumbierres et al., 2022). AOH is defined by Brooks et al. (2019) as “the habitat available to a species, that is, habitat within its range”. AOH maps are generated by removing areas that are unsuitable for species within their range, utilizing data on each species’ habitat and elevation associations. The resolution of each map is about 100m at the equator (1º/1008, Lumbierres et al., 2022)

We used the global aridity index raster to measure harsh environments (arid environments) (Zomer, Xu & Trabucco, 2022). As a ratio of precipitation to potential evapotranspiration, the aridity index provides a measure of moisture availability for the potential growth of any specific vegetation type. The global aridity index has a 30-second spatial resolution.

To estimate the aridity index for each species, we used the raster R package (Hijmans, 2015), for each species; using the crop function, we cut the extension of the aridity index layer based on the AOH map layer. Then we used the resample function to match the pixel size between the two layers; it resamples the aridity index layer (larger pixel) to the AOH layer so that both rasters have the same resolution, and finally, we used the overlay function that intersects the aridity index resampled raster with the map AOH raster creating a new layer based on the AOH map that in each pixel contains the information from the aridity index raster. Therefore, we obtain an aridity index map for each species within its AOH with the mean, standard deviation, minimum, and maximum aridity index information.

Statistical analyses

We calculate the degree of phylogenetic signal between our categorical trait (sociality) and our phylogeny (Borges et al., 2019). Then, given that we found evidence of phylogenetic signal, we perform a logistic regression using the function phyloglm of the phylolm R package (Ho et al., 2024) to identify if our climatic variable (aridity index) predicts the occurrence of sociality in hystricognath rodents. This function fits the phylogenetic logistic regression described in Ives & Garland (2010).

RESULTS

The divergence time analysis using the FBD model with 68 fossils presents a calibrated chronology of Histrycognathi (Fig. 4 and Fig. 5). We estimated that the origin of Hystricognathi occurred during the middle Eocene (46.89 Ma.). The split between Phiomorpha and Caviomorpha is dated at 46 Ma. The diversification of Caviomorpha was estimated to occur during the middle Eocene (45.83 Ma.), while the diversification of Phiomorpha was estimated to occur during the late Eocene (37.5 Ma.). Within Caviomorpha, the divergences of Chinchilloidea + Octodontoidea and Cavioidea + Erethizontoidea are dated at 43.12 Ma. and 39.28 Ma. correspondingly, during the middle Eocene. Octodontoidea diverged during the middle Eocene (38.43 Ma.), Chinchilloidea and Cavioidea diverged during the late Eocene (34.19 Ma. and 33.96 Ma., respectively), and Erethizontoidea diverged during the early Oligocene (29.68 Ma.). At the family level, most of the caviomorph families diverged between the Oligocene and Miocene. Within Phiomorpha, the diversification of Bathyergidae was estimated during the late Eocene (35.9 Ma.), and Petromuridae + Thryonomyidae diverged during the middle Oligocene (25.5 Ma.).

The results of the phylogenetic regression based on 10000 fitted replicates did not show a significant logistic relationship between sociality and aridity index (p-value = 0.057, Table 1).

DISCUSSION

We estimated the divergence time of Hystricognathi using the most complete phylogeny of the infraorden (69% of extant species). We estimated the origin of hystricognath rodents during the middle Eocene, similar to previous studies (Huchon et al., 2007; Rowe et al., 2010; Upham & Patterson, 2012, 2015; Boivin, Marivaux & Antoine, 2019). The split of Phiomorpha and Caviomorpha is about 46 Ma. occurred earlier than reported by molecular studies (see Upham and Patterson 2015). The divergence of Caviomorpha was estimated to have occurred during the middle Eocene concordant to some studies (Rowe et al., 2010; Vucetich et al., 2015; Boivin, Marivaux & Antoine, 2019; Marivaux et al., 2020) but earlier than other previous studies (Huchon et al., 2007; Sallam et al., 2009; Upham & Patterson, 2015). Caviomorpha ancestors arrived in South America during the middle Eocene through transatlantic dispersal by rafting from Africa, and the first steps of their evolution occurred in intertropical areas (Vucetich et al., 2015). The middle Eocene was a period of higher global temperatures, known as the mid-Eocene Climatic Optimum (MECO). Warm and humid conditions would have favored the expansion of tropical and subtropical habitats in both Africa and South America, providing a suitable environment for caviomorphs to adapt and diversify rapidly once they arrived in South America. Also, the transatlantic dispersal is supported by evidence from the fossil record, geographic proximity, possible rafting islands, climatic and oceanographic changes that occurred in the Eocene, and the similarity of habitat between Africa and South America during the Late Cretaceous and Eocene (Flynn & Wyss, 1998; MacFadden, 2006; Poux et al., 2006; Rowe et al., 2010). A single colonization event has been suggested in South America after the arrival of the ancestral lineage during the Eocene (Rowe & Honeycutt, 2002; Poux et al., 2006). This event was followed by the splits of Cavioidea/Erethizonotoidea and Octodontoidea/Chinchilloidea during the middle Eocene. Our results show that Chinchilloidea and Cavioidea diverged during the late Eocene, and Erethizontoidea diverged during the early Oligocene. These were earlier than previous molecular studies where they used points of calibrations instead of the FBD model, where we used fossils as part of the phylogeny (see Upham and Patterson 2015). Therefore, using a larger number of fossils and the FBD model generates significant differences in the divergence time estimation that should be considered in future studies. On the other hand, we estimated the divergence of Phiomorpha during the late Eocene concordant to some previous studies (Huchon et al., 2007; Upham & Patterson, 2012, 2015) but earlier than we previously estimated in Chapter One.

Evolution of sociality

We did not find an effect of aridity on sociality in Hystricognathi rodents. Our results differ from those found in social Australian rodents (Firman et al., 2020) and from Lukas & Clutton-Brock (2017) where they found that cooperative breeding mammal species inhabits arid environments. Our results are contrary to what is expected by the aridity and food distribution hypothesis, which states that sociality in bathyergid (subterranean) rodents is a response to arid environments and the resulting patchy distribution of resources (Jarvis et al., 1994; Faulkes & Bennett, 2013). Then, this relationship cannot be extended to all hystricognath rodents. Moreover, in caviomorphs, aridity does not seem to explain the interspecific differences in the sociality of subterranean rodents (Ctenomyidae), where sociality has been related to patchy but not arid habitats (Lacey & Wieczorek, 2003; Ebensperger & Hayes, 2016). Thus, the patchy distribution of resources, rather than the arid environment, may limit dispersion and drive sociality in this group.

Another plausible alternative is that the type of habitat drives the sociality in hystricognath rodents. Some social caviomorph rodents inhabit mesic areas, such as grasslands (i.e., *Hydrochoerus hydrochaeris*), so rather than aridity per se, it is perhaps the type of habitat (open) that drives sociality in hystricognath rodents. Social species of caviomorph rodents are distributed throughout South America, with a higher concentration in areas with less vegetation cover (Lazo-Cancino in preparation). The vegetation cover has been examined previously by Sobrero et al.

(2014), where they found an association between evolutionary changes in group living, changes in habitat use, and the phylogenetic relationships across hystricognath rodents. Ecological traits such as larger body sizes, diurnal habits, and open habitats would be associated with larger social group sizes in caviomorph rodents (Lazo-Cancino in preparation). This could favor the predation risk hypothesis since individuals of a species in an open environment would be easier for predators to see, so group living would be a survival strategy, increasing the likelihood that threats will be detected and creating opportunities for cooperative defense against predators (Ebensperger, 2001).

Our study determined the extent to which aridity, an important ecological factor for the sociality of Bathyergidae, may contribute to the general pattern of social structure at a broader taxonomic scale, Hystricognathi, where we did not find a relationship between the aridity index and sociality. Therefore, other ecological factors could play a key role in the evolution of sociality in hystricognath rodents, such as habitat type and avoidance of predators.

Despite the large number of hystricognath species (+250), we found sociality data for only 111. Future studies should study and quantify the sociality of this group of species. In addition, subsequent phylogenetic comparative studies should study the link between sociality and ecological traits, such as resource distribution and predator avoidance, where multifactorial causal studies have great potential to contribute to understanding the evolution of sociality in hystricognath rodents.

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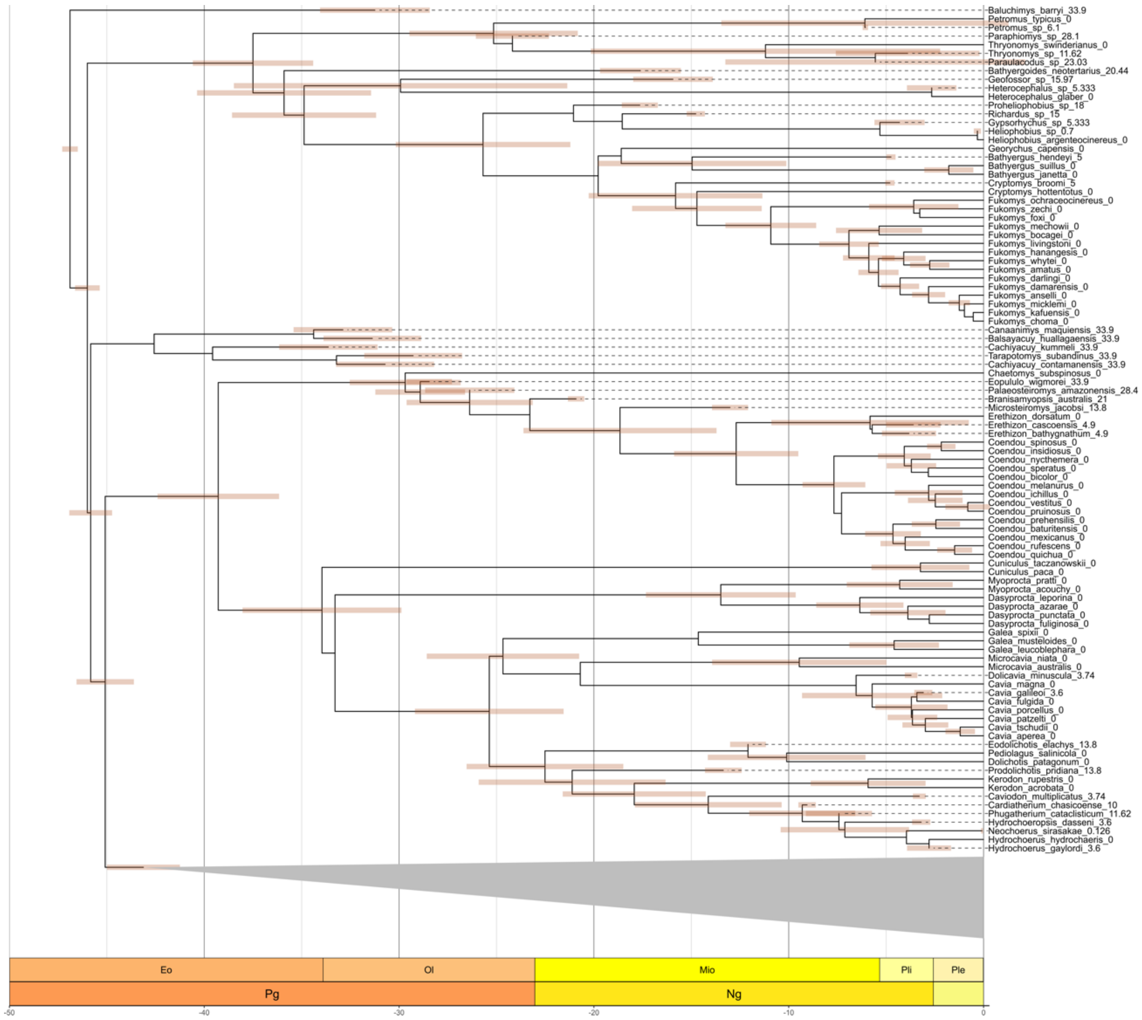

Figure 4. Calibrated phylogenetic tree of Hystricognathi based on the sequence substitution rates of eight genes (Cytb, COI, rRNA12S, rRNA16S, GHR, vWF, RAG1, and IBRP) with a 95% higher posterior density (HPD, light red bars). In grey, the clade that contains Chinchilloidea and Octodontoidea superfamilies.

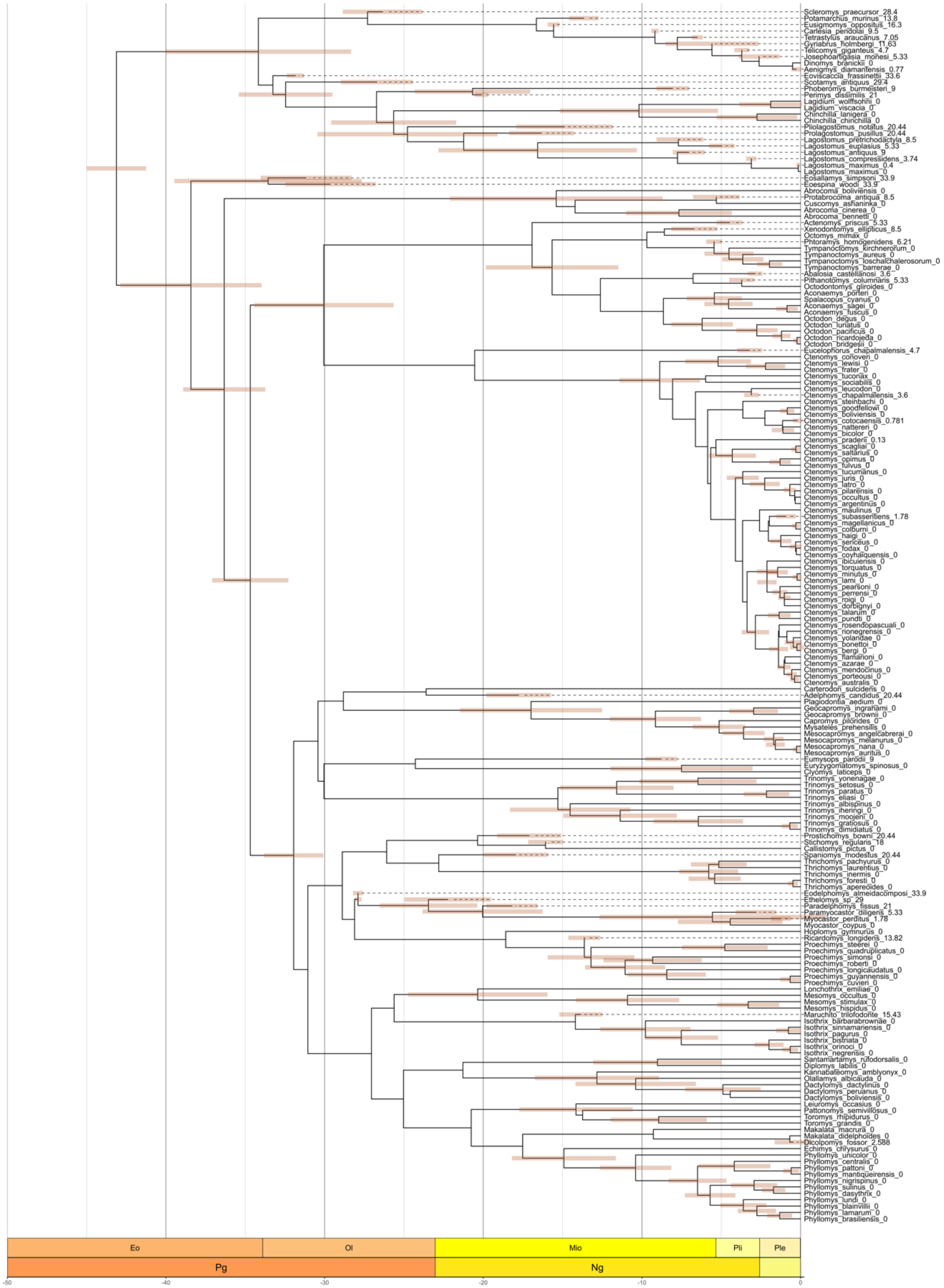

Figure 5. Continuation of Figure 4 with the clade that contains Chinchilloidea and Octodontoidea superfamilies.

Table 1. Phylogenetic logistic regression between sociality and aridity index.

	Estimate	StdErr	z.value	lowerbootCI	upperbootCI	p.value
(Intercept)	-0.095	0.628	-0.151	-1.214	1.113	0.880
Aridity index (normalized)	-0.364	0.191	-1.903	-0.841	-0.001	0.057

Suplementary materials

Table S7. GenBank Accession numbers of used sequences to estimate the divergence time of Hystricognathi.

Species	**Cytb**	**12s RNA**	**GHR**	**vWF**	**RAG1**	**16S RNA**	**COI**
Cavia aperea	NC 046949.1	NC 046949.1	AF433930			NC 046949.1	NC 046949.1
Cavia fulgida	gu136737						
Cavia magna	gu136734	AY765986.1					
Cavia patzelti	GU136760.1						
Cavia porcellus	NC 000884.1	NC 000884.1	AF238492	AJ224663		NC 000884.1	NC 000884.1
Cavia tschudii	gu067538	AY012121	FJ855206		AY011890	AY011153	
Galea leucoblephara	GU067535.1						
Galea musteloides	GU067527	AF433911	AF433933	KJ742608.1	KJ742673.1		
Galea spixii	GU067492	AF433913.1	AF433935				
Microcavia australis	AF491750	AF433915.1	AF433937				
Microcavia niata	gu136725						
Dolichotis patagonum	AY382787	AF433917.1	AF433939				
Dolichotis salinicola	GU136723	AF433919.1	AF433941				
Hydrochoerus hydrochaeris	GU136721	AF433924	AF433947	AJ251137	AY011891	AF069533	KF771219.1
Kerodon acrobata	GU477346.1						
Kerodon rupestris	GU136722	AF433916	AF433938				
Cuniculus paca	AY206570	AF520693	AF433928	AJ251136			JF459150.1
Cuniculus taczanowskii	KJ742656.1	AY012125	AF433929	JN415074.1	AY011894	AY011157.1	
Dasyprocta azarae	KJ936945.1						
Dasyprocta fuliginosa	AF437784.1						
Dasyprocta leporina	AF437783	AY093660	FJ855207	U31607			HQ919680.1

Dasyprocta punctata		AF433921.1	AF433942	JN415079.1			
Myoprocta acouchy	AF437781.1	AF433922	AF433945	KJ742609.1	KJ742695.1		
Myoprocta pratti		AF433923.1	AF433946.1			AF422880.1	JF444937.1
Chinchilla chinchilla	AF464758.1						
Chinchilla lanigera	AF122820	AF520696	AF332036	AJ238385	KF590658	AY062170.1	GU130595.1
Lagidium viscacia	AY254888.1		FJ855209				
Lagidium wolffsohni	AY227023.1						
Lagostomus maximus	AF245485.1		FJ855210				
Dinomys branickii	AY254884	AF520697	AF332038	AJ251145	AY011893.1	AY011156.1	
Chaetomys subspinosus	EU544660						KT236247.1
Coendou baturitensis	KY784125						
Coendou bicolor	KC463859	AF520695	AF520663				
Coendou ichillus	KC463861						
Coendou insidiosus	NC 021387.1	NC 021387.1				NC 021387.1	NC 021387.1
Coendou melanurus	AF411583	KX381511.1		AJ224664			
Coendou mexicanus	KC463863		FJ855212.1				JF445347.1
Coendou nycthemera	KC463864						
Coendou prehensilis	AF411584	KX381640.1					
Coendou pruinosus	KC463880						
Coendou quichua	KC463882						
Coendou rufescens	KC463884						
Coendou speratus	KC261596.1						
Coendou spinosus	KU253493.1						
Coendou vestitus	KC463888						
Erethizon dorsatum	FJ357428	U12450.1	FJ855211.1	AJ251135.1	AY011887.1	AY011150.1	JF456596.1
Abrocoma bennetti	AF244387.1		FJ855213	AJ251143	JN633625.1		
Abrocoma boliviensis	KJ742657.1						

Abrocoma cinerea	AF244388	AF520666	AF520643				
Cuscomys ashaninka	KJ742658.1	KJ742598.1	KJ742626.1	KJ742610.1	KJ742683.1		
Ctenomys argentinus	AF370680						
Ctenomys australis	AF370697						JQ341043.1
Ctenomys azarae	AF144289.1						JQ341046.1
Ctenomys bergi	AF144284.1						
Ctenomys bicolor	JX880049.1						
Ctenomys boliviensis	AF007038	U12446	FJ855214	JN415078.1			JQ341048.1
Ctenomys bonettoi	AF144287.1						
Ctenomys colburni	HM777474						
Ctenomys conoveri	AF007055						JX275552.1
Ctenomys coyhaiquensis	AF119112	KF590700	KF590678	KF590666	KF590659		
Ctenomys dorbignyi	KT818653.1						JX275542.1
Ctenomys flamarioni	AF119107						JQ341052.1
Ctenomys fodax	HM777475						
Ctenomys frater	AF007045						
Ctenomys fulvus	AF370688						
Ctenomys goodfellowi	AF007050						
Ctenomys haigi	AF422920	AF422853				AF422887.1	JQ341050.1
Ctenomys ibicuiensis	JQ389026.1						JQ389081.1
Ctenomys juris	AF144275.1						
Ctenomys lami	HM777477						JQ322907.1
Ctenomys leucodon	NC 020659.1	NC 020659.1				NC 020659.1	NC 020659.1
Ctenomys lewisi	AF007049						
Ctenomys magellanicus	HM777479						
Ctenomys maulinus	AF370703			AJ251138			MZ050257.1
Ctenomys mendocinus	HM777480						MZ050317.1

Ctenomys minutus	HM777481						HM237043.1
Ctenomys nattereri	HM777484						JQ389082.1
Ctenomys occultus	HM777485						
Ctenomys opimus	AF007042						
Ctenomys pearsoni	AF119108						KT900157.1
Ctenomys perrensi	HM777487						JX275509.1
Ctenomys pilarensis	AF144266.1						
Ctenomys rionegrensis	HM544130.1	HM544130.1				HM544130.1	HM544130.1
Ctenomys roigi	HM777492						
Ctenomys rosendopascuali	AF143220.1						
Ctenomys saltarius	HM777493						
Ctenomys scagliai	HM777494						
Ctenomys sericeus	HM777496						
Ctenomys sociabilis	HM544129.1	HM544129.1				HM544129.1	HM544129.1
Ctenomys steinbachi	AF007044	AF520667	AF520656				JQ341047.1
Ctenomys talarum	HM777497						JQ341049.1
Ctenomys torquatus	AF119111						JQ389073.1
Ctenomys tuconax	AF370684						MZ050315.1
Ctenomys tucumanus	AF370691						
Ctenomys pundti	HM777491.1						
Ctenomys yolandae	AF143221.1						
Ctenomys porteousi	AF370682.1						JQ341045.1
Ctenomys latro	HM777478.1						
Dactylomys boliviensis	L23339	AF422875	JX515334	AJ849307	EU313298	AF422909	
Dactylomys dactylinus	L23337	AF422874	KF590681	KF590667	EU313300	AF422908	
Dactylomys peruanus	EU313207						
Kannabateomys amblyonyx	AF422916	AF422849		AJ849310		AF422883	

Olallamys albicaudus	KU892774.1	KU892774.1	KF590690.1	KF590673.1		KU892774.1	KU892774.1
Callistomys pictus	KU892754.1	KU892754.1	KY303654.1	KY303659.1	KJ742677.1	KU892754.1	KU892754.1
Diplomys labilis	KU892776.1	KU892776.1	KJ742636.1	KJ742613.1		KU892776.1	KU892776.1
Echimys chrysurus	L23341	AF422877	JX515333	AJ251141	EU313302	AF422911	JF458603.1
Isothrix barbarabrownae	EU313214	KF590701	KF590682	KF590668	EU313304		
Isothrix bistriata	L23355	AF422873	JX515336	AJ849308	EU313305	AF422907	
Isothrix negrensis	EU313220						
Isothrix orinoci	EU313223	KF590702	KF590683	KF590669	KF590660		
Isothrix pagurus	EU313227	KF590703	KF590684	KF590670			
Isothrix sinnamariensis	KU892785.1	KU892785.1	KF590685	AJ849309	EU313312	KU892785.1	KU892785.1
Makalata didelphoides	EU302692	AF422878	JX515332	AJ849311	EU313314	AF422912	JF444311.1
Makalata macrura	NC 037779.1	NC 037779.1	KF590687	AJ849312.1	EU313328	NC 037779.1	NC 037779.1
Pattonomys semivillosus	NC 037781.1	NC 037781.1		KJ742616.1		NC 037781.1	NC 037781.1
Pattonomys occasius	KJ742661.1		KJ742637.1				
Phyllomys blainvilii	KU892756.1	KU892756.1	JX515331	AJ849314	JX515323	KU892756.1	KU892756.1
Phyllomys brasiliensis	EF608182.1	AY093666	KX852226.1	JF297729.1	KX852253.1		JF297680.1
Phyllomys dasythrix	KU892757.1	KU892757.1	KJ742641.1	JF297709.1	KJ742689.1	KU892757.1	KU892757.1
Phyllomys lamarum	EU313244.1		KX852240.1	JF297731.1	KX852267.1		JF297682.1
Phyllomys lundi	KU892758.1	KU892758.1	KX852249.1	JF297721.1	KX852276.1	KU892758.1	KU892758.1
Phyllomys mantiqueirensis	KU892759.1	KU892759.1	KX852250.1	JF297720.1	KX852277.1	KU892759.1	KU892759.1
Phyllomys nigrispinus	EF608184.1		KX852244.1	JF297719.1	KX852271.1		JF297670.1
Phyllomys pattoni	EF608187.1	KJ742606.1	KJ742642.1	JF297754.1	KJ742690.1		JF297705.1
Phyllomys sulinus	JF297834.1		KX852230.1	JF297713.1	KX852257.1		JF297664.1
Phyllomys unicolor	EF608188.1						
Phyllomys centralis	KX852222		KX852243	KX852279	KX852270		KX852224
Santamartamys rufodorsalis	KU892777.1	KU892777.1				KU892777.1	KU892777.1
Toromys grandis	KU892784.1	KU892784.1	KF590694	KF590676	EU313336	KU892784.1	KU892784.1

Toromys rhipidurus	NC 037783.1	NC 037783.1	KJ742638.1	KJ742617.1		NC 037783.1	NC 037783.1
Carterodon sulcidens	KU892752.1	KU892752.1	KY303655.1	KY303660.1	KJ742678.1	KU892752.1	KU892752.1
Clyomys laticeps	AF422918	AF422851	JX515326	AJ849306	KJ742679.1	AF422885	
Euryzygomatomys spinosus	EU544667	AF422854	JX515327	AJ849319	KJ742680.1	AF422888.1	GU938885.2
Hoplomys gymnurus	AF422922	AF520668	AF520661	JN415080.1		AF422896	
Lonchothrix emiliae	EU313229	AF422857				AF422891	
Mesomys hispidus	KU892787.1	KU892787.1	JX515335	AJ849305	EU313322	KU892787.1	KU892787.1
Mesomys occultus	L23388	AF422858	KF590689		EU313331	AF422893.1	
Mesomys stimulax	KU892788.1	KU892788.1	KJ742630.1	KJ742618.1	KJ742674.1	KU892788.1	KU892788.1
Proechimys quadriplicatus	KX768726.1	KX768726.1		AJ849313.1		KX768726.1	KX768726.1
Proechimys guayannensis	NC 039098.1	NC 039098.1				NC 039098.1	NC 039098.1
Proechimys roberti	KX755319.1	KX755319.1		AJ251139		KX755319.1	KX755319.1
Proechimys cuvieri	NC 039099.1	NC 039099.1	KF590693	KF590675	KF590665	NC 039099.1	NC 039099.1
Proechimys longicaudatus	KX688205.1	KX688205.1	FJ855217	AJ849313	KJ742681.1	KX688205.1	KX688205.1
Proechimys simonsi	NC 039444.1	NC 039444.1	JX515324	AJ849320	EU313332	NC 039444.1	NC 039444.1
Proechimys steerei	NC 039550.1	NC 039550.1				NC 039550.1	NC 039550.1
Thrichomys apereoides	KU892773.1	KU892773.1	JX515325	AJ849315	EU313334	KU892773.1	KU892773.1
Thrichomys inermis	JX459892.1						
Thrichomys laurentius	JX459885.1						
Thrichomys pachyurus	JX459897.1						
Thrichomys foresti	JX459894						
Trinomys dimidiatus	JX312694.1	JX312694.1		KJ742620.1	KJ742682.1	JX312694.1	JX312694.1
Trinomys eliasi	KJ707247.1	AF422869				AF422903.1	
Trinomys iheringi	KU892762.1	KU892762.1	KF590695	KF590677	EU313337	KU892762.1	KU892762.1
Trinomys moojeni	KF562097.1						
Trinomys paratus	KU892763.1	KU892763.1	JX515330	AJ849316		KU892763.1	KU892763.1

Trinomys setosus	KU892764.1	KU892764.1	JX515329	AJ849317		KU892764.1	KU892764.1
Trinomys yonenagae	KU892765.1	KU892765.1	JX515328	AJ849318		KU892765.1	KU892765.1
Trinomys gratiosus	KJ707248.1						
Trinomys albispinus	KU892761.1	KU892761.1	KM013987.1	KM014003.1	KM013992.1	KU892761.1	KU892761.1
Myocastor coypus	EU544663	AF422852	AF520662	AJ251140	AY011892	AF422886	
Capromys pilorides	AF422915	AF422848	AF433950	AJ251142	JX515322	AF422882	MF351907.1
Plagiodontia aedium	KM014007	KM013963	KM013986	KM014002	KM013991	KM013975	
Geocapromys ingrahami	KM014006	KM013961	KM013985	KM014000	KM013990	KM013973	
Geocapromys brownii	KJ742653.1	KJ742599.1	KJ742644.1	KJ742621.1	KM013989.1	KM013972.1	
Mysateles prehensilis	KU892770.1	KU892770.1	KJ742634.1	KM014001	KJ742696.1	KU892770.1	KU892770.1
Mesocapromys melanurus	KU892769.1	KU892769.1			KJ742691.1	KU892769.1	KU892769.1
Mesocapromys auritus	KJ742655.1	KJ742601.1	KJ742633.1	KJ742623.1	KJ742693.1		MF351911.1
Mesocapromys angelcabrerai	KJ742654.1	KJ742595.1	KJ742632.1	KJ742622.1	KJ742694.1		MF351910.1
Mesocapromys nana	MF346160	MF322768					MF351915
Aconaemys fuscus	KC731571.1	AF520674	AF520657				
Aconaemys porteri	MT461704.1	AF520671	AF520644.1	MT461904.1			
Aconaemys sagei	KJ742650.1	AF520672	AF520645.1		KJ742675.1		
Octodon degus	HM544134.1	HM544134.1	AM407928.1	MT461916.1	MT461887.1	HM544134.1	HM544134.1
Octodon lunatus	AF227514.1	AF520681	AF520651.1	AJ238386			
Octodon pacificus	KX298475.1	KX646496.1	MT461872.1	MT461931.1			
Octodon bridgesii	KJ742651.1	AF520677.1	MT461861.1	KJ742611.1	KJ742676.1		
Octodon ricardojeda			MT877238	MT461929			
Octodontomys gliroides	AF370706	AF520683	AF520664	KF590672	KF590663		GQ121079.1
Octomys mimax	GQ121098.1	AF520686	AF520652				GQ121048.1
Spalacopus cyanus	NC 020660.1	NC 020660.1	AF520653	MT461905.1		NC 020660.1	NC 020660.1
Tympanoctomys aureus		AY249753.1	AY249752.1				
Tympanoctomys barrerae	NC 020792.1	NC 020792.1	AF520655			NC 020792.1	NC 020792.1

Tympanoctomys kirchnerorum		KX646514.1	KX646539.1				MZ050345.1
Tympanoctomys loschalchalerosorum	KJ742652.1	KJ742607.1	MT461872.1	KJ742612.1	KJ742684.1		
Bathyergus suillus	KJ866685.1	AY427020.1	FM162080	AJ238384			
Bathyergus janetta	AY425916.1	M63565.1					
Georychus capensis	AF012243.1	M63566.1					
Heliophobius argenteocinereus	AY425943.1	AY427070					
Heterocephalus glaber	NC 015112.1	NC 015112.1	AF332034	AJ251134	AY011889	NC 015112.1	NC 015112.1
Cryptomys hottentotus		AY425841.1					
Fukomys amatus	EF043468.1	AY427021.1					
Fukomys anselli		AY427025.1					
Fukomys bocagei		AF012213.1					
Fukomys damarensis		AY427032.1					
Fukomys darlingi	AF012232.1	AY427034.1					
Fukomys foxi		AY427036.1					
Fukomys kafuensis		AY427037.1					
Fukomys mechowii	EF043452.1	AY427042.1					
Fukomys micklemi	EF043494.1	AY427044.1					
Fukomys ochraceocinereus		AY427045.1					
Fukomys whytei	EF043477.1	AY427047.1					
Fukomys zechi	KX905198.1						
Fukomys livingstoni	KX905196						
Fukomys hanangesis	KX905185						
Fukomys choma	AF012234						
Thryonomys swinderianus	U59181.1	KJ192687.1	AF332035	AJ224674	JN633637.1	KJ193249.1	KJ192953.1
Petromus typicus	DQ139935.1	M63571.1	FM162079	AJ251144			

Table S8. The list of used fossils, with their maximum and minimum age (in millions of years).

ID	Max. age	Min. age
Abalosia_castellanosi_3.6	3.6	2.588
Actenomys_priscus_5.33	5.33	3.6
Adelphomys_candidus_20.44	20.44	15.97
Aenigmys_diamantensis_0.77	0.77	0.13
Branisamyopsis_australis_21	21	20.1
Cardiatherium_chasicoense_10	10	9
Carlesia_pendolai_9.5	9.5	9
Cavia_galileoi_3.6	3.6	2.588
Caviodon_multiplicatus_3.74	3.74	3.04
Ctenomys_chapalmalensis_3.6	3.6	2.588
Ctenomys_cotocaensis_0.781	0.781	0.126
Ctenomys_praderii_0.13	0.13	0.01
Ctenomys_subassentiens_1.78	1.78	0.4
Dicolpomys_fossor_2.588	2.588	0.01117
Dolicavia_minuscula_3.74	3.74	3.04
Draconomys_verai_33.9	33.9	28.1
Eodelphomys_almeidacomposi_33.9	33.9	27.82
Eodolichotis_elachys_13.8	13.8	11.8
Eoespina_woodi_33.9	33.9	27.82
Eopululo_wigmorei_33.9	33.9	27.82
Eosallamys_simpsoni_33.9	33.9	27.82
Eoviscaccia_frassinettii_33.6	33.6	31.3
Erethizon_bathygnathum_4.9	4.9	1.8
Erethizon_cascoensis_4.9	4.9	1.8
Ethelomys_29	29	21
Eucelophorus_chapalmalensis_4.7	4.7	3.04
Eumysops_parodii_9	9	6.8
Eusigmomys_oppositus_16.3	16.3	15.5
Gyriabrus_holmbergi_11.608	11.608	5.333
Hydrochoeropsis_dasseni_3.6	3.6	2.588
Hydrochoerus_gaylordi_3.6	3.6	0.781
Josephoartigasia_monesi_5.33	5.33	2.58
Lagostomus_antiquus_9	9	6.8
Lagostomus_compressidens_3.74	3.74	3.04
Lagostomus_euplasius_5.33	5.33	3.6
Lagostomus_maximus_0.4	0.4	0.13

Lagostomus_pretrichodactyla_8.5	8.5	5.28
Maruchito_trilofodonte_15.43	15.43	12.5
Microsteiromys_jacobsi_13.8	13.8	11.8
Myocastor_perditus_1.78	1.78	0.4
Neochoerus_sirasakae_0.126	0.126	0.0117
Palaeosteiromys_amazonensis_28.4	28.4	23.03
Paradelphomys_fissus_21	21	17.5
Paramyocastor_diligens_5.33	5.33	2.59
Perimys_dissimilis_21	21	20.1
Phoberomys_burmeisteri_9	9	6.8
Phtoramys_homogenidens_6.21	6.21	5.12
Phugatherium_cataclisticum_11.62	11.62	7.246
Pithanotomys_columnaris_5.33	5.33	3.6
Pliolagostomus_notatus_20.44	20.44	13.82
Potamarchus_murinus_13.8	13.8	11.8
Prodolichotis_pridiana_13.8	13.8	11.8
Prolagostomus_pusillus_20.44	20.44	15.98
Prostichomys_bowni_20.44	20.44	15.97
Protabrocoma_antiqua_8.5	8.5	5.28
Pseudoplataeomys_formosus_4.7	4.7	3.7
Ricardomys_longidens_13.82	13.82	11.63
Scleromys_praecursor_28.4	28.4	23.03
Scotamys_antiquus_29.4	29.4	24.2
Spaniomys_modestus_20.44	20.44	15.97
Stichomys_regularis_18	18	15.6
Telicomys_giganteus_4.7	4.7	3.7
Tetrastylus_araucanus_7.05	7.05	6.32
Xenodontomys_ellipticus_8.5	8.5	5.28
Cachiyacuy_kummeli_33.9	33.9	28.4
Cachiyacuy_contamanensis_33.9	33.9	28.4
Caanimys_maquiensis_33.9	33.9	28.4
Balsayacuy_huallagaensis_33.9	33.9	28.4
Tarapotomys_subandinus_33.9	33.9	28.4
Baluchimys_barryi_33.9	33.9	28.4
Paraphiomys_28.1	28.1	5.333
Paraulacodus_23.03	23.03	5.333
Thryonomys_11.62	11.62	0
Petromus_6.1	6.1	0
Bathyergoides_neotertarius_20.44	20.44	15.97
Geofossor_15.97	15.97	11.608

Proheliophobius_18	18	16
Richardus_15	15	14
Gypsorhychus_5.333	5.333	2.588
Bathyergus hendeyi_5	5	4.5
Cryptomys broomi_5	5	4.5
Heterocephalus_5.333	5.333	0
Heliophobius_0.7	0.7	0.3

Table S9. Social organization of Hystricognath rodents.

Species	**Sociality**	**References**
Cavia aperea	Social	(Patton, Pardiñas & D'Elía, 2015; Ebensperger & Hayes, 2016)
Cavia magna	Solitary	(Patton, Pardiñas & D'Elía, 2015; Ebensperger & Hayes, 2016)
Cavia porcellus	Social	(Patton, Pardiñas & D'Elía, 2015; Ebensperger & Hayes, 2016)
Cavia tschudii	Social	(Patton, Pardiñas & D'Elía, 2015; Ebensperger & Hayes, 2016)
Galea leucoblephara	Social	(Ebensperger & Hayes, 2016)
Galea musteloides	Social	(Patton, Pardiñas & D'Elía, 2015; Ebensperger & Hayes, 2016)
Galea spixii	Solitary	(Ebensperger & Hayes, 2016)
Microcavia australis	Social	(Patton, Pardiñas & D'Elía, 2015; Ebensperger & Hayes, 2016)
Microcavia niata	Social	(Marquet et al., 1993; Patton, Pardiñas & D'Elía, 2015; Ebensperger & Hayes, 2016)
Dolichotis patagonum	Social	(Dubost & Genest, 1974; Patton, Pardiñas & D'Elía, 2015; Ebensperger & Hayes, 2016)
Dolichotis salinicola	Social	(Patton, Pardiñas & D'Elía, 2015; Ebensperger & Hayes, 2016)
Hydrochoerus hydrochaeris	Social	(Macdonald, 1981; Herrera et al., 2011; Patton, Pardiñas & D'Elía, 2015; Ebensperger & Hayes, 2016)
Kerodon acrobata	Social	(Ebensperger & Hayes, 2016)
Kerodon rupestris	Social	(Patton, Pardiñas & D'Elía, 2015; Ebensperger & Hayes, 2016)
Cuniculus paca	Social	(Pérez, 1992; Patton, Pardiñas & D'Elía, 2015; Ebensperger & Hayes, 2016)
Dasyprocta azarae	Social	(Ebensperger & Hayes, 2016)
Dasyprocta fuliginosa	Social	(Patton, Pardiñas & D'Elía, 2015; Ebensperger & Hayes, 2016)
Dasyprocta leporina	Social	(Patton, Pardiñas & D'Elía, 2015; Ebensperger & Hayes, 2016)
Dasyprocta punctata	Social	(Patton, Pardiñas & D'Elía, 2015; Ebensperger & Hayes, 2016)
Myoprocta acouchy	Solitary	(Patton, Pardiñas & D'Elía, 2015; Ebensperger & Hayes, 2016)
Myoprocta pratti	Social	(Patton, Pardiñas & D'Elía, 2015; Ebensperger & Hayes, 2016)
Chinchilla chinchilla	Social	(Patton, Pardiñas & D'Elía, 2015; Ebensperger & Hayes, 2016)
Chinchilla lanigera	Social	(Patton, Pardiñas & D'Elía, 2015; Ebensperger & Hayes, 2016)
Lagidium viscacia	Social	(Patton, Pardiñas & D'Elía, 2015; Ebensperger & Hayes, 2016)

Lagidium wolffsohni	Social	(Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Lagostomus maximus	Social	(Branch, 1993; Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Dinomys branickii	Social	(White & Alberico, 1992; Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Chaetomys subspinosus	Solitary	(Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Coendou bicolor	Social	(Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Coendou mexicanus	Social	(Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Coendou prehensilis	Solitary	(Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Coendou speratus	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Erethizon dorsatum	Social	(Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Abrocoma bennetti	Social	(Ebensperger & Hayes, 2016)
Abrocoma cinerea	Social	(Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Ctenomys argentinus	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys australis	Solitary	(Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Ctenomys azarae	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys bergi	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys bicolor	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys boliviensis	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys bonettoi	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys colburni	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys conoveri	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys coyhaiquensis	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys dorbignyi	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys flamarioni	Solitary	(Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Ctenomys fodax	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys frater	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys fulvus	Social	(Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Ctenomys goodfellowi	Solitary	(Patton, Pardiñas & D’Elía, 2015)

Ctenomys haigi	Solitary	(Lacey, Braude & Wieczorek, 1998; Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Ctenomys ibicuiensis	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys juris	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys lami	Solitary	(Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Ctenomys leucodon	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys lewisi	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys magellanicus	Solitary	(Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016), Lacey per. Comm.)
Ctenomys maulinus	Solitary	(Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Ctenomys mendocinus	Solitary	(Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Ctenomys minutus	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys nattereri	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys occultus	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys opimus	Social	(Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Ctenomys pearsoni	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys perrensi	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys pilarensis	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys rionegrensis	Solitary	(Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Ctenomys roigi	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys rosendopascuali	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys saltarius	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys scagliai	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys sericeus	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys sociabilis	Social	(Lacey, Braude & Wieczorek, 1997; Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Ctenomys steinbachi	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys talarum	Solitary	(Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Ctenomys torquatus	Solitary	(Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Ctenomys tuconax	Solitary	(Patton, Pardiñas & D’Elía, 2015)

Ctenomys tucumanus	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys pundti	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys yolandae	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys porteousi	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Ctenomys latro	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Dactylomys dactylinus	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Kannabateomys amblyonyx	Social	(Silva, Vieira & Izar, 2008; Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Diplomys labilis	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Echimys chrysurus	Solitary	(Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Isothrix bistriata	Social	(Ebensperger & Hayes, 2016)
Makalata didelphoides	Solitary	(Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Phyllomys blainvilii	Social	(Ebensperger & Hayes, 2016)
Clyomys laticeps	Social	(Ebensperger & Hayes, 2016)
Mesomys hispidus	Solitary	(Ebensperger & Hayes, 2016)
Proechimys quadriplicatus	Solitary	(Ebensperger & Hayes, 2016)
Proechimys cuvieri	Solitary	(Ebensperger & Hayes, 2016)
Thrichomys apereoides	Solitary	(Ebensperger & Hayes, 2016)
Trinomys iheringi	Solitary	(Ebensperger & Hayes, 2016)
Trinomys yonenagae	Social	Santos and Lacey 2011, Patton et al. 2015, Ebensperger and Hayes 2016
Trinomys albispinus	Solitary	(Ebensperger & Hayes, 2016)
Myocastor coypus	Social	(Guichón et al., 2003; Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Capromys pilorides	Social	(Ebensperger & Hayes, 2016)
Plagiodontia aedium	Social	(Ebensperger & Hayes, 2016)
Geocapromys ingrahami	Social	(Clough, 1972; Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Geocapromys brownii	Social	(Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Mysateles prehensilis	Social	(Ebensperger & Hayes, 2016)
Aconaemys fuscus	Social	(Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)

Aconaemys porteri	Social	(Patton, Pardiñas & D’Elía, 2015)
Octodon degus	Social	(Fulk, 1976; Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Octodon lunatus	Social	(Sobrero, Prieto & Ebensperger, 2014; Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Octodontomys gliroides	Social	(Rivera et al., 2014; Ebensperger & Hayes, 2016)
Octomys mimax	Solitary	(Ebensperger et al., 2008; Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Spalacopus cyanus	Social	(Reig, 1970; Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Tympanoctomys aureus	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Tympanoctomys barrerae	Solitary	(Patton, Pardiñas & D’Elía, 2015; Ebensperger & Hayes, 2016)
Tympanoctomys kirchnerorum	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Tympanoctomys loschalchalerosorum	Solitary	(Patton, Pardiñas & D’Elía, 2015)
Heterocephalus glaber	Social	(Jarvis, 1981; Faulkes & Bennett, 2021)
Heliophobius argenteocinereus	Solitary	(Patzenhauerová, Bryja & Šumbera, 2010; Faulkes & Bennett, 2021)
Bathyergus janetta	Solitary	(Happold, 2013; Faulkes & Bennett, 2021)
Bathyergus suillus	Solitary	(Happold, 2013; Faulkes & Bennett, 2021)
Georychus capensis	Solitary	(Happold, 2013; Faulkes & Bennett, 2021)
Cryptomys hottentotus	Social	(Bishop et al., 2004; Faulkes & Bennett, 2021)
Fukomys foxi	Social	(Faulkes & Bennett, 2021)
Fukomys ochraceocinereus	Social	(Faulkes & Bennett, 2021)
Fukomys bocagei	Social	(Faulkes & Bennett, 2021)
Fukomys mechowii	Social	(Sichilima et al., 2008; Faulkes & Bennett, 2021)
Fukomys darlingi	Social	(Bennett, Jarvis & Cotterill, 1994; Faulkes & Bennett, 2021)
Fukomys damarensis	Social	(Bennett & Jarvis, 1988; Jarvis & Bennett, 1993; Faulkes & Bennett, 2021)
Fukomys kafuensis	Social	(Faulkes & Bennett, 2021)
Fukomys anselli	Social	(Sichilima, Bennett & Faulkes, 2011; Faulkes & Bennett, 2021)
Fukomys whytei	Social	(Faulkes & Bennett, 2021)
Fukomys amatus	Social	(Faulkes & Bennett, 2021)
Fukomys micklemi	Social	(Faulkes & Bennett, 2021)

Fukomys zechi	Social	(Faulkes & Bennett, 2021)
Fukomys livingstoni	Social	(Faulkes & Bennett, 2021)
Fukomys hanangesis	Social	(Faulkes & Bennett, 2021)
Fukomys choma	Social	(Faulkes & Bennett, 2021)
Petromus typicus	Social	(Rathbun & Rathbun, 2006)
Thryonomys swinderianus	Social	(Happold, 2013)

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CONCLUSIONES

Esta tesis evaluó los factores evolutivos y ecológicos que influyen en la evolución de la sociabilidad en roedores, evaluando dos hipótesis principales: el papel de la monogamia en la transición hacia la eusociabilidad en la familia Bathyergidae y la influencia de la aridez en la evolución de la sociabilidad en el infraorden Hystricognathi. A través de análisis filogenéticos comparativos, reconstrucción de estados ancestrales y modelos de correlación evolutiva, se obtuvieron hallazgos clave que contribuyen a la comprensión de la diversidad de sistemas sociales en este grupo de mamíferos.

En relación con la primera hipótesis, la estimación de estados ancestrales sugiere que la monogamia fue la condición ancestral en los roedores sociales y eusociales de la familia Bathyergidae. Sin embargo, no se encontró evidencia de que la monogamia haya sido el factor determinante en la transición hacia la eusociabilidad. La adquisición de la eusociabilidad ocurrió de manera independiente en cada linaje. Además, se observó que una de las transiciones evolutivas con mayor tasa de cambio fue de un estado monógamo+solitario a un estado monógamo+social, lo que indica que la monogamia puede facilitar la formación de grupos sociales, pero no necesariamente la aparición de la eusociabilidad.

Respecto a la segunda hipótesis, los análisis no encontraron una relación significativa entre la aridez y la evolución de la sociabilidad en los roedores del infraorden Hystricognathi. Esto sugiere que la aridez, como factor ambiental, no explica por sí sola la transición hacia sistemas sociales más complejos en este grupo. En cambio, otros factores ecológicos, como la distribución de recursos y la presión de depredación, podrían tener un papel más relevante en la evolución de la sociabilidad.

Los resultados de esta tesis resaltan la importancia de considerar múltiples factores en la evolución de los sistemas sociales, incluyendo la historia filogenética y las condiciones ecológicas específicas de cada linaje. Se requiere un enfoque multifactorial para comprender la evolución de la sociabilidad en vertebrados, integrando estudios sobre disponibilidad de recursos, presiones selectivas y biogeografía histórica.

En conjunto, esta investigación aporta nuevas perspectivas sobre los impulsores de la sociabilidad en roedores y destaca la necesidad de estudios que combinen aproximaciones evolutivas y ecológicas para comprender la diversificación de los sistemas sociales en los mamíferos.