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RESEARCH ARTICLE

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Incipient morphological specializations associated with fossorial life in the skull of ground squirrels (Sciuridae, Rodentia)

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Abstract

Anatomical and biological specializations have been studied extensively in fossorial rodents, especially in subterranean species, such as mole-rats or pocket-gophers. Sciurids (i.e., squirrels) are mostly known for their diverse locomotory behaviors, and encompass many arboreal species. They also include less specialized fossorial species, such as ground squirrels that are mainly scratch diggers. The skull of ground squirrels remains poorly investigated in a fossorial context, while it may reflect incipient morphological specializations associated with fossorial life, especially due to the putative use of incisors for digging in some taxa. Here, we present the results of a comparative analysis of the skull of five fossorial sciurid species, and compare those to four arboreal sciurids, one arboreal/fossorial sciurid and one specialized fossorial aplodontiid. The quantification of both cranial and mandibular shapes, using three dimensional geometric morphometrics, reveals that fossorial species clearly depart from arboreal species. Fossorial species from the Marmotini tribe, and also Xerini to a lesser extent, show widened zygomatic arches and occipital plate on the cranium, and a wide mandible with reduced condyles. These shared characteristics, which are present in the aplodontiid species, likely represent fossorial specializations rather than relaxed selection on traits related to the ancestral arboreal condition of sciurids. Such cranial and mandibular configurations combined with proodont incisors might also be related to the frequent use of incisors for digging (added to forelimbs), especially in Marmotini evolving in soft to hard soil conditions. This study provides some clues to understand the evolutionary mechanisms shaping the skull of fossorial rodents, in relation to the time spent underground and to the nature of the soil.

KEYWORDS

Aplodontiidae, chisel-tooth digging, convergent evolution, geometric morphometrics, Sciuromorpha, scratch digging, skull shape

1 | INTRODUCTION

Fossorial species are known for their digging abilities to construct burrows mainly to protect from external conditions (e.g., predators and climate), but also for dispersion and foraging, especially when they spend most of their lifetime underground (e.g., Ellerman, 1956; Hildebrand, 1985; Nevo, 1979). Among mammals, rodents show numerous morphological specializations for digging. These adaptations are notably related to the use of claws for digging (i.e, scratch-digging), but also to the use of ever-growing incisors (i.e., chisel-tooth digging), which is widespread in subterranean species, such as African and blind mole-rats, pocket-gophers, tuco-tucos or cururos (e.g., Stein, 2000; Gomes Rodrigues et al. in press). More than 10 families of extant rodents show convergent adaptations to fossorial life, impacting their long bones and girdles, as well as their skull to various extents (e.g., Stein, 2000; Gomes Rodrigues et al. in press). Subterranean rodents generally show the most extreme cranial specializations due to their more intense activity of chisel-tooth digging (e.g., procumbent incisors and massive masticatory muscles; Fournier et al., 2021; Gomes Rodrigues et al., 2016; Landry, 1957; Lessa & Patton, 1989; Marcy et al., 2016; McIntosh & Cox, 2016) and to the constraints related to life underground (e.g., reduced eyes and pinnae; Nevo, 1979; Scarpitti and Calede, 2022; Stein, 2000). The morphology of subterranean rodents has been studied, but a focus on less specialized fossorial taxa would have allowed a better comprehension of the evolutionary mechanisms underlying fossorial adaptations in rodents.

Ground squirrels of the family Sciuridae are not strongly specialized fossorial rodents. They notably encompass marmots, prairie dogs, or susliks, and most of them construct burrows, mainly as nest and protection, but do not spend all their lifetime underground (i.e., they are not defined as subterranean; Koprowski et al., 2016; Nowak, 1999). These rodents use mainly their claws for digging and far less their incisors (Agrawal, 1967). Focusing on susliks and relatives from the genus *Spermophilus*, Lagaria and Youlatos (2006) said that “given that scratch digging is an integral part of their biology that may increase fitness, it is very likely that (these) ground squirrels exhibit associated morphological correlates.” This statement can be generalized to all fossorial ground squirrels since it has been demonstrated that they do have muscular, anatomical and histological adaptations for scratch-digging revealed by investigations of both forelimbs and hindlimbs (Lagaria & Youlatos, 2006; Mielke et al., 2018; Scheidt et al., 2019; Thorington, Jr. et al., 1997; Wölfer & Nyakatura, 2019; Wölfer, Amson, et al., 2019). But, does the skull of ground squirrels similarly show fossorial specializations?

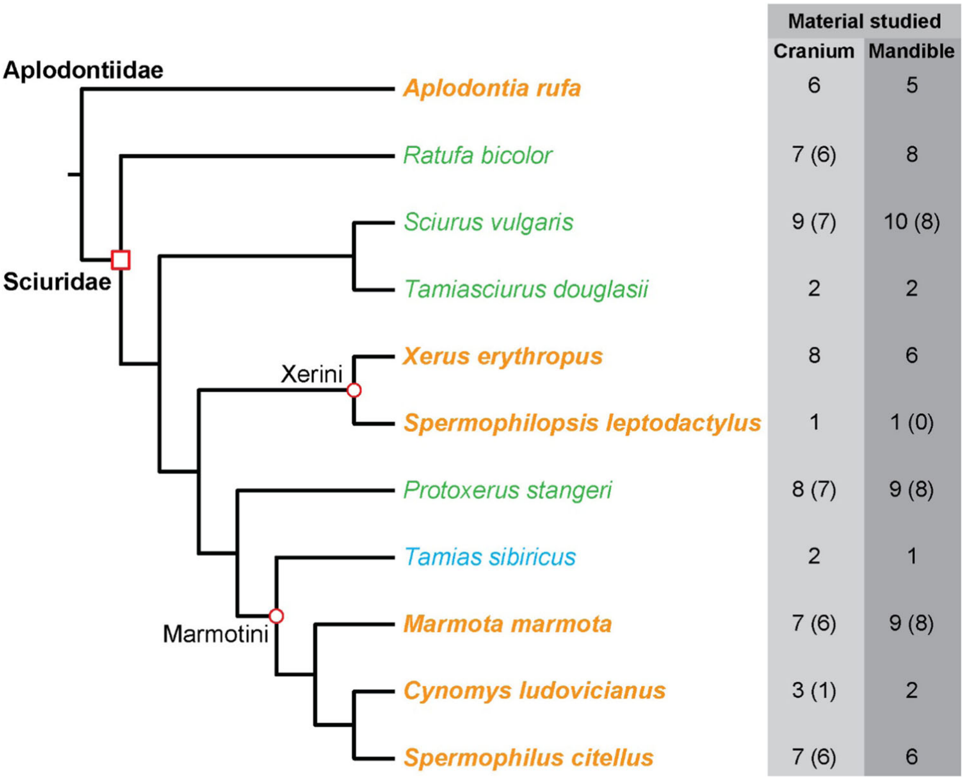
In a study on extinct burrowing beavers including a comparison with many fossorial rodents, Samuels and Valkenburgh (2009) did not detect any cranial specialization for fossorial life in ground squirrels. Most studies on sciurid skull shape have highlighted the strong phylogenetic signal, the lesser influence of size and dietary habits on the mandible and thus pointed out the near lack of ecomorphological convergence (e.g., Cardini, 2003; Casanovas-Vilar & Van Dam, 2013; Michaux et al., 2008; Zelditch et al., 2015, 2017). Nonetheless, some of them tend to show that ground squirrels set apart from tree squirrels (e.g., Lu et al., 2014; Michaux et al., 2008; Velhagen & Roth, 1997; Zelditch et al., 2015), in having morphologies clearly diverging from the ancestral arboreal condition of sciurids (Rocha et al., 2016; Steppan et al., 2004). One of these studies (Lu et al., 2014) also stressed putative fossorial traits on the skull of a few sciurids, but none of them mentioned morphological convergence in that respect. However, convergent evolution based on qualitative morphological similarities of the skull (i.e., flat and wide cranium, wide mandible) have been assumed between some ground squirrels and extinct and extant Aplodontiidae, a sister group of Sciuridae within Sciuromorpha, which has a stronger fossorial evolutionary history (Druzinsky, 2010; Hopkins, 2019).

Here, our aim is to quantify and compare the skull shape of phylogenetically distant species of fossorial ground squirrels, involving Marmotini (e.g., marmots, prairie dogs, susliks, and chipmunks) and Xerini (e.g., unstriped ground squirrel, and long-clawed ground squirrels; Figure 1). All these species are scratch diggers, but some works mentioned the occasional use of incisors for digging in Marmotini (e.g., Agrawal, 1967; Burns et al., 1989; Ramos-Lara et al., 2014). Comparisons of fossorial species with some arboreal species are also drawn to quantify their morphological differences. Comparisons with the mountain beaver, which is a highly specialized fossorial species and the sole extant representative of Aplodontiidae, allow to evaluate the morphological similarities with fossorial sciurid species. Numerous studies on the mandible of sciurids have been published. Fewer studies have focused on the cranium (e.g., Cardini & O'Higgins, 2004; Roth, 1996), while the cranial shape of sciurids is assumed to be more importantly influenced by lifestyle than the mandible (Lu et al., 2014). Therefore, both parts of the skull are quantified here using three dimensional geometric morphometrics. We will consider to what extent the fossorial activities of sciurids impact their cranial and mandibular shapes compared with Aplodontiidae and arboreal species. We will also discuss these results in light of the fossorial adaptations observed in more specialized fossorial rodents (i.e., subterranean and chisel-tooth digging species).

2 | MATERIAL AND METHODS

2.1 | Sample composition

Specimens of Sciuromorpha are all from the collections of the Muséum National d'Histoire Naturelle in Paris (MNHN). We analyzed 59 mandibles and 60 crania representing one aplodontiid genus/species and 10 sciurid genera/species (Supporting Information: Table 1 in Supporting Information Online Material). Among them, one aplodontiid (*Aplodontia*) and five sciurids (*Marmota*, *Cynomys*, *Spermophilus*, *Xerus*, and *Spermophilopsis*) were here defined as fossorial because of their significant digging activity and the time they spent in burrows (Koprowski et al., 2016; Thorington, Jr. et al., 1997). Four other sciurids were defined as arboreal



	Material studied	
	Cranium	Mandible
Aplodontia rufa	6	5
Ratufa bicolor	7 (6)	8
Sciurus vulgaris	9 (7)	10 (8)
Tamiasciurus douglasii	2	2
Xerus erythropus	8	6
Spermophilopsis leptodactylus	1	1 (0)
Protoxerus stangeri	8 (7)	9 (8)
Tamias sibiricus	2	1
Marmota marmota	7 (6)	9 (8)
Cynomys ludovicianus	3 (1)	2
Spermophilus citellus	7 (6)	6

FIGURE 1 Phylogenetic relationships between the investigated Sciuromorpha (from Fabre et al., 2012; and Menéndez et al., 2021) and associated number of specimens. Specimens studied with their incisors intact are indicated in brackets. In bold and orange: fossorial taxa, in blue: arboreal/fossorial taxa, in green: arboreal taxa.

(*Ratufa*, *Protoxerus*, *Sciurus Tamiasciurus*), and one sciurid (*Tamias*) is defined as arboreal/fossorial because of its intermediate lifestyle (see Rocha et al., 2016; Steppan et al., 2004; and Mielke et al., 2018). These different categories of locomotor behavior also follow the nomenclature used in recent ecomorphological studies on Sciuromorpha (Mielke et al., 2018; Scheidt et al., 2019; Wölfer & Nyakatura, 2019; Figure 1). Numerous studies that focused on sciurid skull shape, especially on mandibles, have been performed on large comparative databases, which also permitted to reliably test for phylogenetic signal, dietary imprint on shape, as well as the allometric component (e.g., Calede et al., 2019; Casanovas-Vilar & Van Dam, 2013; Lu et al., 2014; Michaux et al., 2008; Velhagen & Roth, 1997; Zelditch et al., 2015, 2017). We consider that the present sample, although smaller, is appropriate to evaluate the main morphological traits shared by the fossorial aplodontiid and the two targeted sciurid tribes encompassing iconic fossorial species (i.e., Marmotini and Xerini), and to assess the main potential differences between fossorial and arboreal sciurid species.

2.2 | Geometric morphometric methods

Mandibular and cranial forms were quantified using 11 and 62 anatomical landmarks, respectively (Figure 2; Supporting Information Online Material 2). This landmark data set was based on previous studies (Fournier et al., 2021; Gomes Rodrigues et al., 2016; Hautier et al., 2012) and was adapted to our sample. Landmarks #37 and #55 were not used in the analyses, because pterygoid processes are broken in some specimens, as was the tip of incisors. We nonetheless included additional landmarks (#70, #71, and #72) at the tip of upper incisors to obtain complementary information on a sub sample of crania for which eight specimens were removed due to damaged or extremely worn incisors (see Figure 1 and Supporting Information Online Material 1). Only the right hemi-mandible was investigated here. Similar to the cranium, we also included an additional landmark (#73) at the tip of the right lower incisor on a sub sample of hemi-mandibles for which five specimens were removed (see Figure 1 and Supporting Information Online Material 1). Digital data for most specimens were acquired using a Microscribe 3-D digitizer (G2X, Immersion Corporation, measurement error: 0.0001 mm). The cranium and mandible of *Cynomys ludovicianus* (MNHN.ZM.MO1960-3673) were scanned with a v|tome|x 240 L, Baker Hughes Digital Solutions, at the AST-RX platform (MNHN, Paris) using a cubic voxel of 34.4 μm, to visualize virtual deformations within the data set. Landmarks were then digitized on this reconstructed mesh using the "LANDMARK editor" (http://graphics.idav.ucdavis.edu/research/EvoMorph). This protocol, involving digitization of both osteological and scanned specimens, was already tested in previous analyses in which measurement biases were negligible (e.g., Fournier et al., 2021; Gomes Rodrigues et al., 2016; Hautier et al., 2012).

For the cranium, landmarks are mostly of type 1 (juxtaposition of tissues). Because the hemimandible of rodents is composed of a unique dentary bone of relatively simple shape, most of the landmarks taken on the dentary were of type 2 (e.g., maxima of curvature—Figure 2; Bookstein, 1991). All configurations (sets of landmarks) were superimposed using the Procrustes method of generalized least squares superimposition (GLS scaled, translated, and rotated configurations so that the intralandmark distances were minimized) following the method used by Rohlf and Slice (1990), Bookstein (1991), and Rohlf (1999). Shape variation of the cranium and mandible was analyzed using principal components analyses (PCA; Figures 3 and 4, Supporting Information Online Material 3, 4, 5, and 6). Analysis and visualization of patterns of shape variation were performed with the interactive software package MORPHOTOOLS (Lebrun et al., 2010). We computed phylomorphospaces based on the mean coordinates of each genus from the first PC axes and on a simplified phylogeny of Sciuromorpha (Figure 1), and using the *phylomorphospace* function from the phytools R package (Revell, 2012; Figures 3 and 4). We calculated neighbor joining (NJ) trees to propose an overall representation of the morphological distance between each specimen and to evaluate the phenetic affinities of species (i.e., morphological similarity; Figure 5). We used the *nj* function from the APE R package (Paradis & Schliep, 2019) computed on a matrix of Euclidean distances, previously calculated on the first PCs representing more than 90% of the total variation. Multivariate analyses of variation (MANOVA) were also realized on these data (i.e., first PCs > 90%) to test for similarities between fossorial and arboreal categories. To do so, data were previously rank transformed data because they did not meet the assumptions required for such parametric tests (i.e., normality, homoscedasticity of variances; Conover et al., 1981). In parallel, these tests were performed on sciurids only, after removal of *Aplodontia* to test for morphological differences between fossorial and arboreal sciurids only. The arboreal/fossorial *Tamias* was not included in these tests, because of its small sample.

3 | RESULTS

Both PCAs on crania and mandibles show a clear differentiation between most fossorial and arboreal genera on the first axis, especially concerning the mandibular analysis (Figures 3 and 4; Supporting Information Online Material 3 and 4). PC1, PC2, and PC3 account for 29.55%, 14.22%, and 8.01% of the total variation respectively for the cranium, and PC1, PC2, and PC3 account for 34.81%, 22.98%, and 9.49% of the total variation, respectively, for the mandible. Contributions on each axis as well as distributions of specimens are quite similar when coordinates for upper and lower incisors are included in the analyses (for crania—PC1: 30.56%, PC2: 14.49%, PC3: 8.89% of the total variation; for mandibles—PC1: 32.81%, PC2: 23.22, and PC3: 10.00% of the total variation; Supporting Information Online Material 5 and 6).

The cranial analysis shows that *Aplodontia* plot on the negative side of PC1 (Figure 3a, Supporting Information Online Material 3a). *Marmota* and *Cynomys* also have negative values. They are closer to other fossorial taxa, *Spermophilus*, *Xerus* and *Spermophilopsis*, which are however located at the positive side of PC1, in the vicinity of arboreal taxa and of the arboreal/fossorial *Tamias*. The negative side of PC1 is characterized by a flat cranium showing an enlarged rostrum including elongated dental rows, but also reduced frontal bone areas and cranial vault, widened and posteriorly oriented zygomatic arches, a widened and anteriorly-tilted occipital plate, and massive tympanic bullae. It can be mentioned that in the analysis involving incisors these specimens also present elongated and

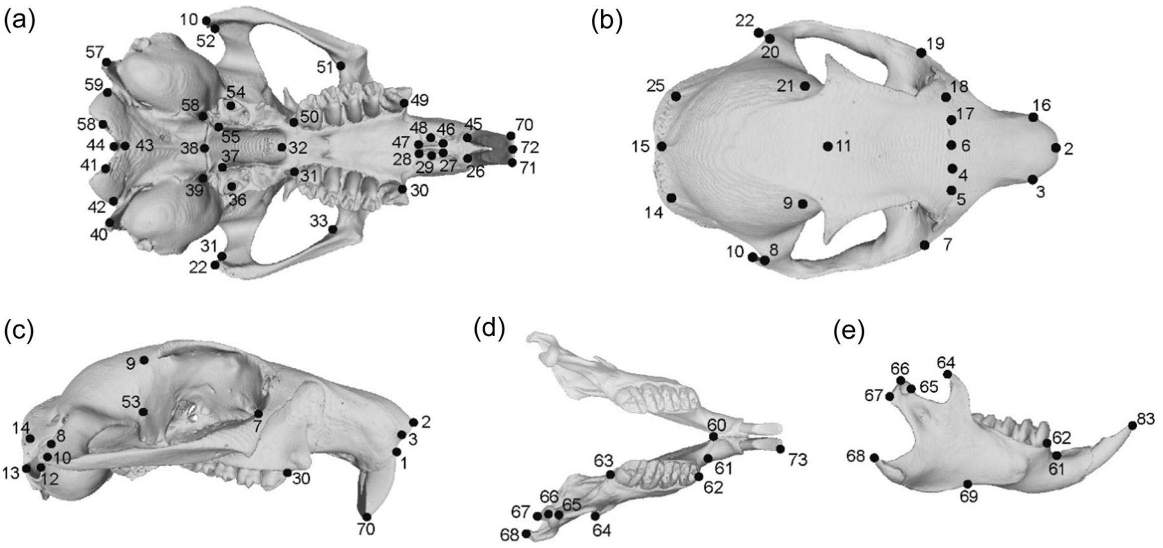


FIGURE 2 Landmarks digitized on the cranium (a, ventral view, b, dorsal view; c, lateral view) and the mandible (d, occlusal view; e, lateral view) of *Cynomys ludovicianus* (MNHN.ZM.MO1960-3673) imaged by using X-ray conventional microtomographic 3D rendering. 3D, three dimensional.

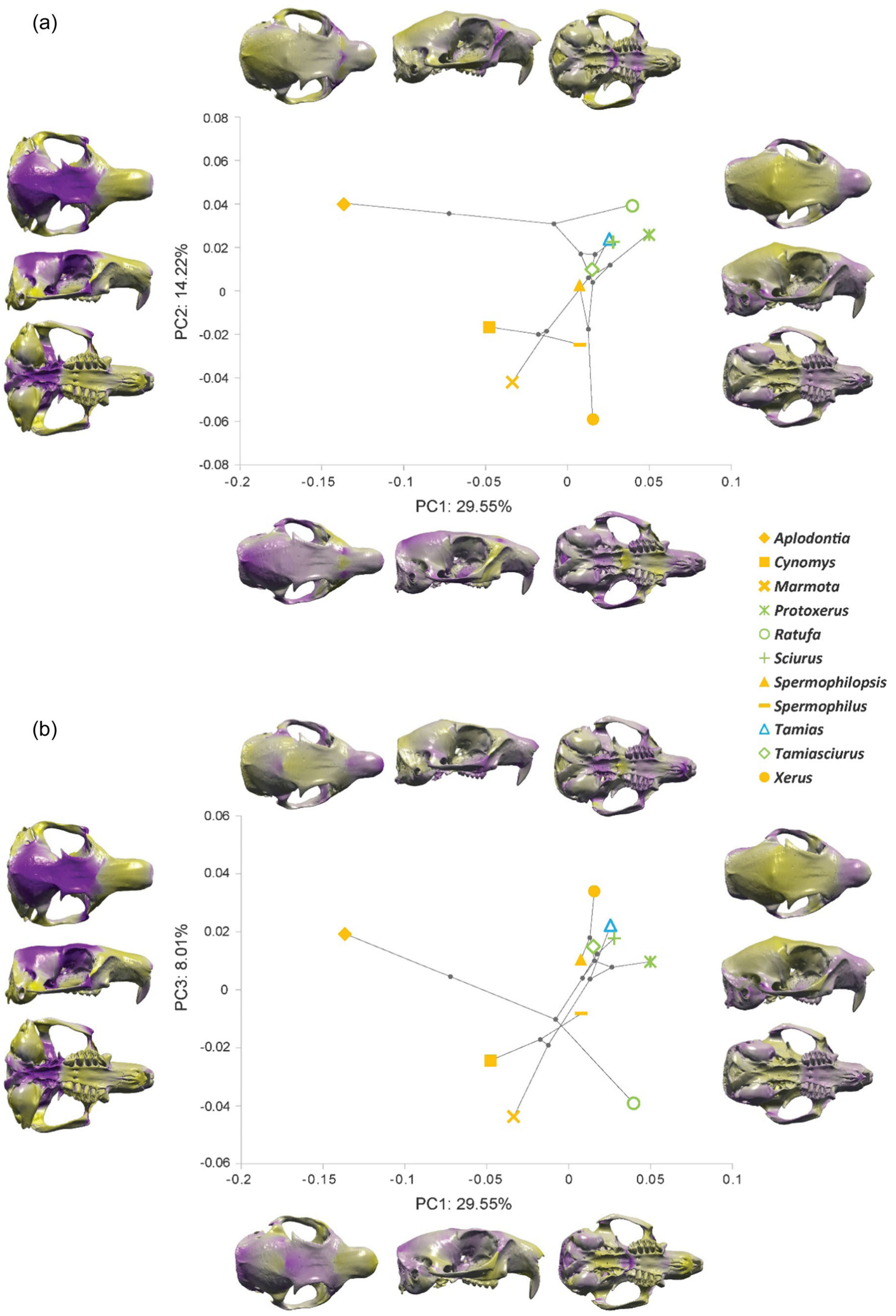


FIGURE 3 Principal component analyses performed on crania of Sciuromorpha (mean specimens for each genus) with phylogenetic relationships and associated virtual deformation on the extreme sides of each axis. Yellow and violet code for increases and decreases in surface area, respectively. In orange: fossorial taxa, in blue: arboreal/fossorial taxa, in green: arboreal taxa.

orthodont incisors (Supporting Information Online Material 5). At the positive side, the deformations are mostly represented by a higher, but slender cranium displaying enlarged cranial vault and frontal areas, a ventrally oriented foramen magnum, but a reduced rostrum combined with incisors reduced and curved backward. On PC2, most fossorial taxa plot on the negative side and are associated with a slender cranium including a reduced braincase, zygomatic plates posteriorly expanded and an elongated rostrum (Figure 3a, Supporting Information Online Material 3a). In contrast, *Aplodontia* and arboreal taxa are associated with a more massive, but shorter cranium on the positive side of PC2. On the negative side of PC3 (Figure 3b, Supporting Information Online Material 3b), *Marmota*, *Cynomys* and *Ratufa* present a virtual deformation with a widened rostrum, a reduced frontal area, combined with slightly proodont incisors (according to the additional analysis), conversely to *Xerus* plotting on the extreme part of the positive side of PC3.

Concerning the PCA on mandibles, most fossorial taxa plot on the negative side of PC1, whereas arboreal taxa, the arboreal/fossorial *Tamias* and the fossorial *Spermophilopsis* plot on the positive side (Figure 4a, Supporting Information Online Material 4a). On the negative side, the virtual deformation is characterized by a short ramus including an enlarged and laterally projected angular process, and an enlarged body with an elongated dental row. The additional analysis including incisor also displays a mandibular shape with an elongated and anteriorly projected incisor (Supporting Information Online Material 6). Conversely, the virtual deformation on the positive side of PC1 shows a shorter mandible, but enlarged articular condyle and coronoid process. PC2 are mainly characterized by *Xerus* plotting on the negative side and *Aplodontia* on the positive side, while other taxa are located in between. If the negative side is characterized by a slender hemi-mandible with a more developed condyle, on the positive side, the hemi-mandible is more robust with an elongated coronoid process and a laterally projected angular process. The main information on PC3 relies on the plotting of *Cynomys* on the negative side with a virtual deformation showing a short but massive condyle close to the coronoid process, and an enlarged angular process (Figure 4b, Supporting Information Online Material 4b). On the additional analysis including the incisor, we observe slight differences on the plot with *Marmota*, *Ratufa*, and some *Protoxerus* plotting close to *Cynomys* on the negative side of PC3, and the associated virtual deformation also shows an elongated incisor.

Both NJ analyses show a clear clustering of fossorial genera on one side and of arboreal genera and *Tamias* on the other side (Figure 5). Intrageneric clustering is higher for the cranium than for the mandible for which *Spermophilus* and arboreal taxa are not strongly clustered. Among fossorial taxa, the cranial and mandibular shapes of *Cynomys* and *Marmota* are close to *Aplodontia*, which however shows more elongated branches. *Spermophilopsis* is the fossorial taxa showing the smallest cranial and mandibular morphological distances from arboreal taxa, in agreement with PCA analyses. These results are confirmed by the MANOVA showing that significant differences exist between fossorial and arboreal taxa for both the cranium ($F = 48.7$, $p < .001$) and the mandible ($F = 57.73$, $p < .001$), and even after removal of *Aplodontia* from the tests (for the cranium: $F = 71.8$, $p < .001$; for the mandible: $F = 43$, $p < .001$).

4 | DISCUSSION

4.1 | Shared cranial and mandibular traits associated with fossorial life

Both analyses of cranial and mandible shapes show that the fossorial and arboreal Sciuromorpha species investigated here are clearly distinct. Aplodontiidae, Marmotini (except *Tamias*), and Xerini share cranial and mandibular traits (detailed below), even if they are less marked in this latter tribe. These results support previous analogous observations on the skull of aplodontiids and some ground squirrels (Druzinsky, 2010; Hopkins, 2019). They also concur with different analyses on mandible shape showing a similarity between some Marmotini and Xerini (Casanovas-Vilar & Van Dam, 2013; Michaux et al., 2008; Zelditch et al., 2015). *Tamias*, the arboreal/fossorial species, which is an excellent climber and also digs burrows for nesting (Koprowski et al., 2016; Nowak, 1999), has a skull shape closer to arboreal species. This pattern probably highlights both inherited characters from the putative arboreal condition of the sciurid ancestor (Rocha et al., 2016; Steppan et al., 2004) and the fact that its fossorial activity does not have a significant imprint on its cranial morphology. In previous studies (Michaux et al., 2008; Zelditch et al., 2015), the definition of the skull shape of *Tamias* tends to be variable, but generally in-between ground and arboreal squirrels.

It could have been assumed that the clustering of phylogenetically distant fossorial sciurid species is simply related to relaxed selection on the skull because of a less constrained locomotion on the ground contrary to life on trees. These ground squirrels notably show: more posterior zygomatic arches and plates implying more posterior orbits limiting arboreal life; elongated rostrum and mandible, which preclude the consumption of hard tree seeds; and a less ventral foramen magnum similar to non-fossorial ground squirrels not investigated here (e.g., *Rhinosciurus*, *Menetes*; Casanovas-Vilar & Van Dam, 2013; Zelditch et al., 2015). However, the ground squirrels investigated here do show morphological characters associated with fossorial life. These characters are missing in nonfossorial ground squirrels, but are shared with *Aplodontia*, as suggested (yet not discussed) in Michaux et al. (2008) regarding clustering of mandible shapes. These taxa, especially Marmotini, notably present posteriorly oriented and widened zygomatic arches allowing insertion of massive masticatory muscles—as noticed by Lu et al. (2014)—coupled to more proodont incisors. These characters are observed in chisel-tooth diggers, but in a markedly more pronounced way (e.g., Echeverría et al., 2017; Fournier et al., 2021; Gomes Rodrigues et al., 2016, in press; Marcy et al., 2016). They show a relatively wide and anteriorly tilted occipital plate for insertion of massive neck muscles necessary for removing earth out of the burrows (Stein, 2000), a distinctive

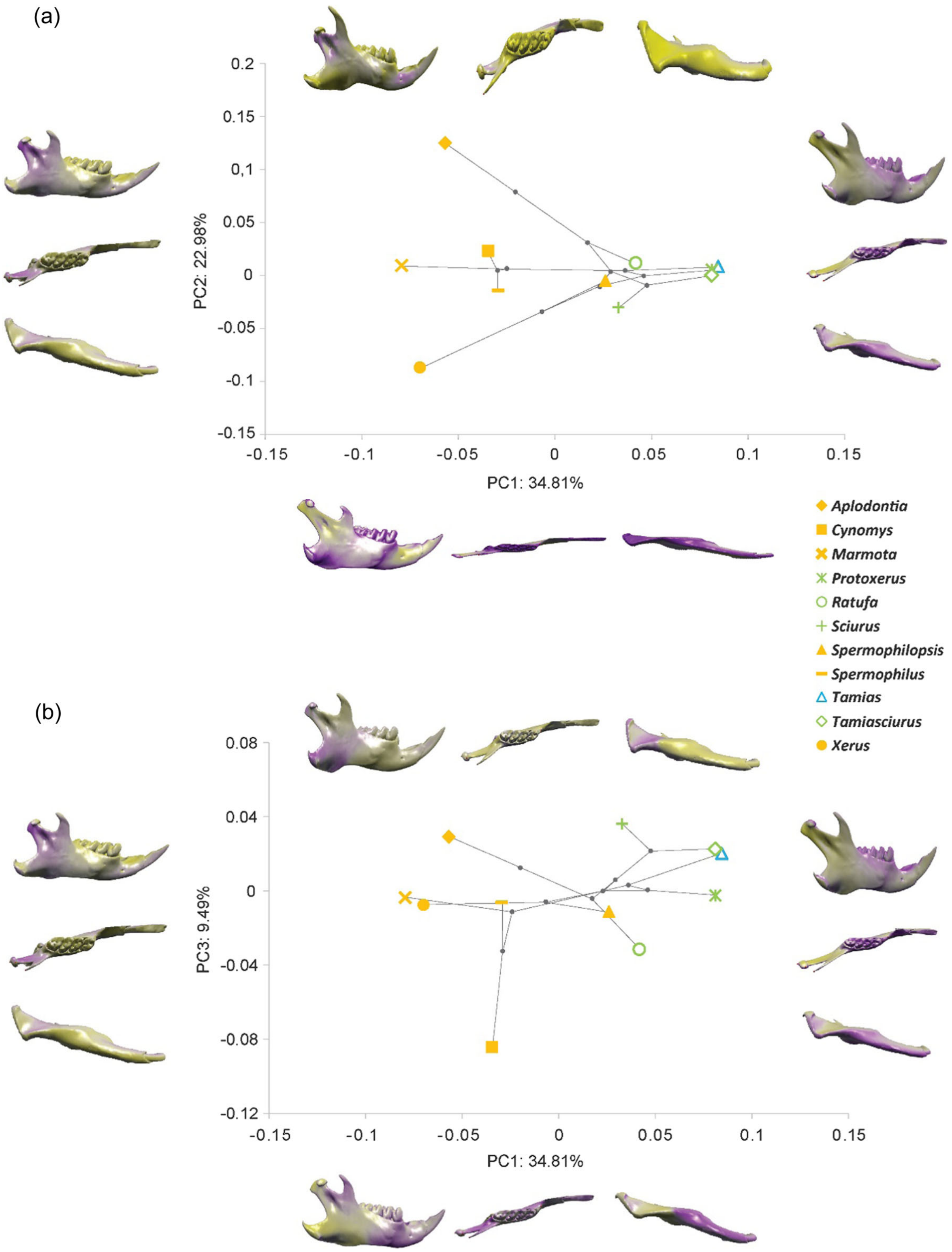


FIGURE 4 Principal component analyses realized on hemi-mandibles of Sciuromorpha (mean specimens for each genus) with phylogenetic relationships and associated virtual deformation on the extreme sides of each axis. Yellow and violet code for increases and decreases in surface area, respectively. In orange: fossorial taxa, in blue: arboreal/fossorial taxa, in green: arboreal taxa.

character found in many extant and extinct fossorial rodents (Gomes Rodrigues et al. in press). As with most fossorial rodents, they also show a braincase relatively reduced contrary to arboreal species (Bertrand et al., 2021).

The use of incisors in ground squirrels does not seem at first glance to be optimized for burrowing when looking at the mandible. Ground squirrels, mainly Marmotini, show a reduced condyle combined with an elongated dental row and a widened angular

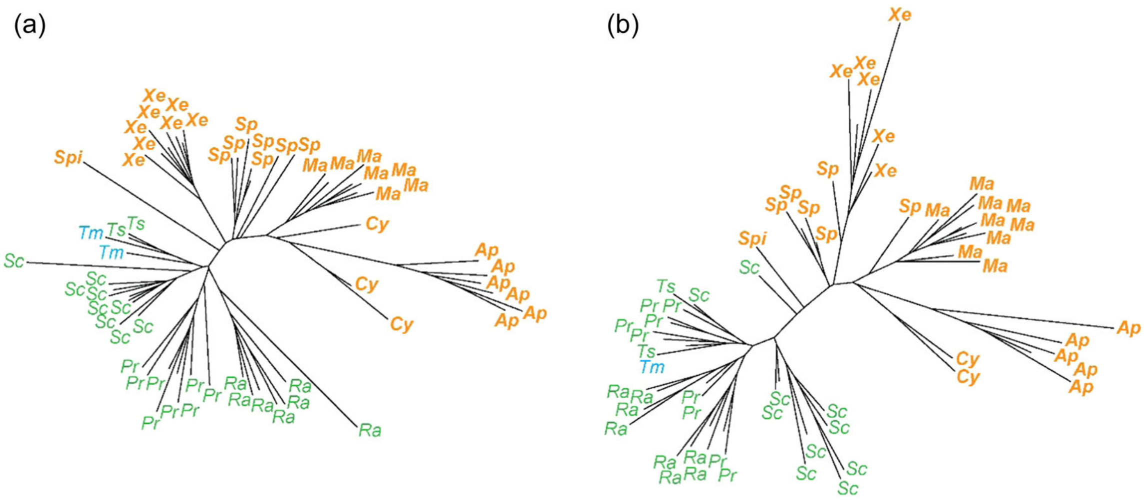


FIGURE 5 Trees illustrating morphological distances between Sciuromorpha resulting from neighbor joining analyses based on coordinates from the PCAs, and performed on crania (a) and hemi-mandibles (b). Ap, *Aplodontia*; Cy, *Cynomys*; Ma, *Marmota*; Pr, *Protoxerus*; Ra, *Ratufa*; Sc, *Sciurus*; Sp, *Spermophilus*; Spi, *Spermophilopsis*; Tm, *Tamias*; Ts, *Tamiasciurus*; Xe, *Xerus*. In bold and orange: fossorial taxa, in blue: arboreal/fossorial taxa, in green: arboreal taxa.

process allowing the insertion of a large superficial masseter. This configuration might improve the mastication of more fibrous and tough plants and roots (e.g., grasses and forbs; Koprowski et al., 2016) probably at the expense of incisor gnawing and biting force (Casanovas-Vilar & Van Dam, 2013; Cox et al., 2012). Conversely, tree squirrels have a shorter mandible but an enlarged coronoid process for the insertion of a massive temporal muscle, and therefore a high output force at the incisors, in relation to the consumption of hard items (e.g., nuts and fruits; Ball & Roth, 1995; Casanovas-Vilar & Van Dam, 2013; Cox et al., 2012; Freeman & Lemen, 2008; Velhagen & Roth, 1997). This latter configuration was described in many chisel-tooth digging rodents, which have large temporal muscles to improve both jaw closing and the incisor output force for digging (e.g., Echeverria et al. 2017; Gomes Rodrigues et al., 2016, in press; Marcy et al., 2016). However, a wide mandible with short condyles, and proodont incisors is observed in fossorial Marmotini and in chisel-tooth digging rodents, meaning that these characters might facilitate the occasional use of incisors for digging (e.g., bathyergids, ctenomyids, some octodontids, some cricetids, and some spalacids, Gomes Rodrigues et al., 2016; Kryštufek et al. 2016, Fournier et al., 2021). As a result, the mandible of ground squirrels, especially Marmotini, is likely impacted by their fossorial lifestyle, but to a lesser extent relative to the cranium, as suggested by Lu et al. (2014).

4.2 | From scratch digging to chisel-tooth digging

Marmotini shows fossorial characters more distinctive than in Xerini (e.g., cranium with wide zygomatic arches and occipital plate, proodont incisors), and closer to the specialized morphology of *Aplodontia* (Calede & Hopkins, 2012; Druzinsky, 2010). It is interesting to note that these characters are only incipient in *Spermophilopsis* (see Casanovas-Vilar & Van Dam, 2013 for similar observation on the mandible) showing the most elongated claws, which may improve its scratch digging activity in soft sandy soils (Ognev, 1966; Ružić, 1967), where the use of incisors is not necessary for burrowing. Wölfer and Nyakatura (2019) on femoral traits mentioned that Xerini are much closer to the arboreal condition than most Marmotini. This result might be based on diverse functional demands since that Xerini spend less time underground than most Marmotini, which can build burrows in soft to hard soils (e.g., Hoogland, 1996; Janderková et al., 2011; Ponomarenko, 2007). Digging abilities in hard soils are more important in chisel-tooth diggers than in scratch diggers (Echeverria et al., 2017; Giannoni et al., 1996; Lessa & Thaeler, 1989; Marcy et al., 2016; Mora et al., 2003). The use of incisors for digging has often been observed in *Marmota*, *Cynomys* and *Spermophilus* (Agrawal, 1967; Burns et al., 1989; Ramos-Lara et al., 2014), contrary to *Xerus*, *Spermophilopsis*, and the arboreal/fossorial *Tamias*, which mainly use their incisors for seed and fruit processing, like tree squirrels (Koprowski et al., 2016). This observation might also explain both the adaptability of fossorial Marmotini to dig in different types of soil and their more pronounced fossorial morphologies.

Some rodent species, even if they are not highly fossorial or not adapted to dig with their incisors, can use them occasionally, as observed, for instance, in juveniles of laboratory rats to compensate the lower strength in their forelimbs (Gobetz, 2007). Fossorial ground squirrels do show some specializations for chisel-tooth digging (e.g., wide cranium with widened occipital plate, wide mandible, and proodont incisors) even if they are not strongly adapted to do so. The use of incisors in addition to forelimbs to break the soil, especially in hard soil conditions, has been reported in other scratch-digging species, such as degus (*Octodon*; Ebensperger & Bozinovic, 2000). To date, there are many other lines of evidence suggesting that the use of incisors for digging in rodents is primarily driven by the soil hardness, as noticed in some Marmotini. For instance, pocket-gophers (Geomyidae) and tuco-tucos (Ctenomyidae) show different modes of digging depending on the nature of the soil, and some species can use both modes alternately (e.g. Echeverría et al., 2017; Marcy et al., 2016). In African mole-rats (Bathyergidae), the only scratch digger (*Bathyergus*) lives in sandy soil contrary to other South African chisel-tooth digging genera occupying more consolidated soils (i.e., *Georychus* and *Cryptomys*; Cuthbert, 1975; Gomes Rodrigues et al., in press). It is likely the case in Rhizomyinae (Spalacidae), in which the African root-rat (*Tachyoryctes*) uses only its incisors for digging and occupies more arid areas than its South Asian counterparts, bamboo rats (*Rhizomys* and *Cannomys*; Fournier et al., 2021).

Consequently, if aridity and opening of environment generated the need to find shelter underground at the origin of the spread of fossorial habits (e.g., Jardine et al., 2012; Nevo, 1979), then frequent changes in the nature of the soil required a better efficacy to remove earth, and thus a more important use of incisors in rodents, as frequently observed in Marmotini. Conversely, the use of incisor for digging is not reported in Xerini, as mentioned above. They use to live in soft soils (Koprowski et al., 2016; Ognev, 1966), especially *Spermophilopsis*, but they do present cranial specializations, although minor, associated with fossorial life. It means that other behavioral or environmental parameters related to both burrowing and frequent life in burrows might impact their skull shape (e.g., brain size and auditory capacities), which does not extend to *Tamias*, which frequently climb trees. These different parameters related to the nature of the soil, the time spent underground, and the nature and length of the corresponding subterranean activities (e.g., digging, foraging, or dispersion) likely have a strong impact on both the degree of fossoriality (e.g., use of incisors or not for digging) and on the resulting skull shape, from scratch digging to chisel-tooth digging rodents.

The originality of ground squirrel compared to most fossorial rodents is definitely their morphology inherited from an arboreal condition. Despite their mosaic evolution, sciurids are generally viewed as constituting a morphologically conservative group, reinforced by their functionally versatile trophic morphology, which might limit ecomorphological convergences (see Zelditch et al., 2017). In the present case, the different examples of fossorial adaptations in sciurids (and aplodontiids) are exemplified by convergent skull traits related to departure from tree life and to the strong constraints on the whole skeleton imposed by digging, especially in hard soils (in addition to food foraging and processing). An accurate study of morphological variation of the skull combined with more data on the digging behavior in the different species of ground squirrels in relation to soil hardness will provide more information regarding their skull evolvability and adaptability compared to other fossorial rodents.

AUTHOR CONTRIBUTIONS

Helder Gomes Rodrigues: Conceptualization (lead); formal analysis (supporting); investigation (equal); methodology (lead); supervision (lead); validation (equal); visualization (equal); writing – original draft (lead). **Mathilde Damette**: Formal analysis (lead); investigation (equal); validation (equal); visualization (equal); writing – original draft (supporting).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The datasets generated and analyzed during the current study (i.e., Procrustes coordinate database) are available from the corresponding author upon reasonable request.

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