The squirrel is in the detail: Anatomy and morphometry of the tail in Sciuromorpha (Rodentia, Mammalia)

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Abstract
In mammals, the caudal vertebrae are certainly among the least studied elements of their skeleton. However, the tail plays an important role in locomotion (e.g., balance, prehensility) and behavior (e.g., signaling). Previous studies largely focused on prehensile tails in Primates and Carnivora, in which certain osteological features were selected and used to define tail regions (proximal, transitional, distal). Interestingly, the distribution pattern of these anatomical characters and the relative proportions of the tail regions were similar in both orders. In order to test if such tail regionalization can be applied to Rodentia, we investigated the caudal vertebrae of 20 Sciuridae and six Gliridae species. Furthermore, we examined relationships between tail anatomy/morphometry and locomotion. The position of selected characters along the tail was recorded and their distribution was compared statistically using Spearman rank correlation. Vertebral body length (VBL) was measured to calculate the proportions of each tail region and to perform procrustes analysis on the shape of relative vertebral body length (rVBL) progressions. Our results show that tail regionalization, as defined for Primates and Carnivora, can be applied to almost all investigated squirrels, regardless of their locomotor category. Moreover, major locomotor categories can be distinguished by rVBL progression and tail region proportions. In particular, the small flying squirrels Glaucomys volans and Hylopetes sagitta show an extremely short transitional region. Likewise, several semifossorial taxa can be distinguished by their short distal region. Moreover, among flying squirrels, Petaurista petaurista shows differences with the small flying squirrels, mirroring previous observations on locomotory adaptations based on their inner ear morphometry. Our results show furthermore that the tail region proportions of P. petaurista, phylogenetically more basal than the small flying squirrels, are similar to those of bauplan-conservative arboreal squirrels.

KEYWORDS
axial skeleton, caudal vertebrae, ecomorphology, locomotion

1 | INTRODUCTION

In recent decades, the mammalian vertebral column has been the focus of renewed interest among functional morphologists, with an emphasis on developmental and genetic background of this structural complex (Böhmer, 2017; Burke et al., 1995; Deane et al., 2014; German, 1982; Narita & Kuratani, 2005; Organ, 2010; Organ et al., 2009; Russo, 2015; Shapiro, 1993; Tojima, 2013, 2014; Youlatos, 2003; Young et al., 2009). However, most recent studies on the mammalian vertebral column focused on presacral vertebrae. In
part, this is because postsacral vertebrae are widely considered to be intraspecifically highly variable, both in terms of number and length, and because they show a rather “simple” morphology (e.g., Narita & Kuratani, 2005; Starck, 1979, 1995). Furthermore, these vertebrae are frequently missing in museum specimens and thus are usually excluded from analyses (Buchholz & Stepien, 2009; Pilbeam, 2004).

In many mammals, the tail fulfills a wide range of significant functions from balancing and steering during locomotion, to thermoregulatory functions and signaling as part of their behavioral repertoire (Bopp, 1954; Delgado & Jacobs, 2016; Dunbar & Badam, 2000; Emmons & Gentry, 1983; Fatjó et al., 2007; Hickman, 1979; Mathene et al., 2018; Schmitt et al., 2005; Stankowich, 2008; Thorington, 1966; Walker et al., 1998; Young et al., 2021).

Studies on the association between relative tail length and vertebra anatomy are scarce (e.g., Russo, 2015). In contrast to short tails, long tails display features that enhance the flexibility of the proximal tail region (e.g., craniocaudally longer vertebral bodies), the range of motion at the intervertebral body joints (e.g., more circularly shaped articular surfaces), and the leverage of tail musculature (e.g., longer spinous processes; Russo, 2015). However, it is the specific function of the tail as a “fifth limb” in prehensile-tailed mammals (Emmons & Gentry, 1983) that has attracted the interest of most researchers working on the postsacral axial skeleton. These researchers have primarily studied this adaptation in Primates and Carnivora (Deane et al., 2014; Garber & Rehg, 1999; German, 1982; Lemelin, 1995; Organ et al., 2009; Russo & Young, 2011; Schmitt et al., 2005; Shapiro, 1993; Youlatos, 2003). Interestingly, both orders show similar morphological and biometrical differences between prehensile and non-prehensile tails (German, 1982; Organ, 2010; Russo, 2015; Youlatos, 2003). Anatomical features that distinguish the prehensile tail of Primates and Carnivora from non-prehensile-tailed species are: (a) a relatively longer (both in length and number of vertebrae) proximal tail region permitting greater flexibility in the proximal part of the tail, (b) relatively higher neural arches and spinous processes in the proximal region which provide increased attachment area for tail musculature, (c) more robust distal caudal vertebrae, which show a higher expansion of the transverse processes and a more ventral projection of the hemal processes (Ankel, 1965, 1972; Dor, 1937; Lemelin, 1995; Organ, 2007; Schmitt et al., 2005; Shapiro, 1993; Youlatos, 2003). Studies on the prehensile tail of small-sized mammals (< 100 g) are scarce. However, Maniakas and Youlatos (2019) observed that the tail anatomy of small prehensile-tailed muroid rodents as well as didelphid and dipoiodont marsupials follow the same pattern as large-sized mammals (i.e., long proximal tail region, the longest vertebra lies proximally, as well as short, robust vertebrae in the distal tail region).

A few additional studies of mammalian tail morphology focused on tail length and its correlation with locomotor categories (e.g., gliding, saltatorial, scansorial, semi-aquatic) (Essner, 2003; Hatt, 1932; Hayssen, 2008; Horner, 1954; Russo, 2015; Stein, 1988; Thorington & Heaney, 1981). Hayssen (2008) observed that ground squirrels display a shorter tail than tree squirrels, whereas flying squirrels have among the longest tails. Further, large flying squirrels possess proportionately longer tails than small flying squirrels (Thorington & Heaney, 1981). However, the tail of large tree squirrels (e.g., *Ratufa*) is absolutely and proportionately the longest among Sciuridae. Mincer and Russo (2020) found that substrate use correlates significantly with tail length. In particular, they observed that arboreal mammals possess longer tails compared to non-arboreal species, which display varying tail lengths. They also found that tail length is secondarily influenced by locomotion, diet, and climate. However, aside from arboreal Primates and arboreal Carnivora the tail of most other non-aquatic mammals has not been subject to detailed morphological investigations yet.

The vertebral column of vertebrates has been divided into different series (i.e., cervical, thoracic, lumbar, sacral and caudal), defined by a well-established set of characters (see Buchholtz, 2012). The mammalian caudal series (i.e., bony tail) has been further divided into the proximal, transitional and distal regions. The osteological characters used to identify these regions have been primarily defined and described in arboreal Primates, and have been subsequently corroborated in arboreal Carnivora (Ankel, 1965, 1972; Deane et al., 2014; Flower, 1876; German, 1982; Lemelin, 1995; Organ, 2007, 2010; Organ et al., 2009; Russo, 2015; Schmidt, 1886; Schmitt et al., 2005). The following general overview of tail anatomy builds on these studies and the position of morphofunctionally relevant characters along the tail (i.e., from the first caudal vertebra after the sacrum to the tip of the tail) as well as their functional properties are given in Table 1 and Figure 1.

The proximal tail region consists of caudal vertebrae usually displaying a neural arch bearing a spinous process, a single pair of transverse processes, and anterior as well as posterior articular processes (metapophyses and anapophyses, respectively) supporting the articular surfaces (pre- and postzygapophyses, respectively). The last vertebra included in the proximal tail region is called the transition vertebra (TV), because it possesses metapophyses with prezygapophyses, but is the first vertebra of the caudal series missing anapophyses and the associated postzygapophyses (Figure 1). However, the last functional pre- and postzygapophyseal articulation (LPnPo—star in Figure 1) between two consecutive vertebrae can be situated either on TV or cranial to TV. Hence, whereas proximal vertebrae cranial to LPnPo are connected by two types of intervertebral joints (both the plane synovial joints between zygapophyses and the secondary cartilaginous joints between the vertebral bodies), subsequent intervertebral articulations only occur by vertebral body joints. This is always the case between TV and the first vertebra of the transitional region. Neural arches and the spinous process regularly disappear cranial to or on TV. The last appearance of a spinous process is defined as SP.

Caudal vertebrae of the transitional region are characterized by the presence of one or two pairs of transverse processes and articulate with one another via vertebral body joints only. The cranial-most caudal vertebrae usually bear one pair of transverse processes. But, along the tail, a split in these processes occurs causing subsequent vertebrae to bear an anterior and a posterior pair of transverse processes. The first vertebra in the caudal series to show such a split (sTP) is usually positioned in close proximity to TV, and therefore belongs either to the proximal or the transitional region. The end of
TABLE 1  Characters with significant morphofunction for the mobility of the tail that have been considered for anatomical analyses. Definition of the functional properties follow the studies of Vallois (1922), Shapiro (1993), Lemelin (1995), Organ (2010) and Russo (2015)

| Character | Anatomical definition | Functional properties |
|-----------|-----------------------|-----------------------|
| LPrPo     | Last pre- and postzygapophyseal articulation of caudal vertebrae | Zygapophyses allow for a certain degree of sagittal flexion and extension in the proximal tail region; restriction to dorsoventral movement of the tail |
| LV        | Caudal vertebra with the longest measurable vertebral body length (demarcating the end of the transitional region) | Subject to highest degree of bending and torsion within vertebrae tail series |
| Me        | The last caudal vertebra displaying metapophyses | Provide muscle attachment sites for m. sacrocaudalis dorsalis medialis/extensor caudae medialis and mm. sacrocaudalis dorsalis lateralis/extensor caudae lateralis |
| SP        | The last caudal vertebra displaying a spinous process | Provide muscle attachment sites for basal tail extensor muscle (m. sacrocaudalis dorsalis medialis/extensor caudae medialis); leverage of the tail |
| sTP       | The first caudal vertebra with two pairs of transverse processes | Transverse processes are the main attachment sites for mm. intertransversarii caudae (lateral and dorsoventral flexors, and rotators of the tail); origins of m. sacrocaudalis ventralis lateralis/flexor caudae longus and sacrocaudalis ventralis medialis/flexor caudae brevis (primary flexors of tail) |
| TV        | Transition vertebra; first caudal vertebra missing postzygapophyses (demarcating the end of the proximal region) | Zygapophyseal joint at the anterior end and intervertebral disc articulation only at the posterior end |

FIGURE 1  Tail regionalization in mammals: proximal, transitional and distal region. The tail model illustrates the pattern of characters found in Primates and is assumed to be applicable to other mammals (Ankel, 1962, 1972; German, 1982; Organ, 2007; Russo, 2015). Cd1, first caudal vertebra; LV, longest vertebra; Me, last metapophyses; SP, last spinous process; yellow star, last pre- and postzygapophyseal articulation; sTP, split of transverse processes; TV, transition vertebra
the tip of the tail. The last vertebra bearing metaphyses is defined as Me, and is followed by the typical cylindrical-shaped caudal vertebrae.

The morphology and position of characters observed in Primates and Carnivora have largely been assumed to be applicable to all mammalian orders (Ankel, 1962, 1965, 1972; Flower, 1876; Schmidt, 1886; Starck, 1979, 1995). Russo (2015) performed one of the few studies including representatives of orders outside of Primates and Carnivora (i.e., Diprotodontia, Pliosa, Rodentia, Scandentia). She also included species with reduced tails (and even without external tails) beside prehensile- and long-tailed species, and did not limit her sample to arboreal taxa. However, the anatomical descriptions and comparative analyses involving these species were limited to a few characters. Therefore, the occurrence of the morphological patterns found in the tail of arboreal Primates and arboreal Carnivora still needs to be tested in other orders of mammals and in different locomotor categories.

Here, we investigate the anatomy and morphometry of the tail vertebra series within Rodentia, an order that constitutes almost half of the extant mammalian species and shows a high diversity of adaptations to a wide array of different ecologies (Fabre et al., 2012; Wilson et al., 2016; Wilson et al., 2017; Wilson & Reeder, 2005). For this study, the focus was set on the Sciuromorpha (sensu D’Elía et al., 2019). We decided to stay within one monophyletic clade of Rodentia to minimize the impact of the phylogenetic signal on the results and to place special emphasis on the different locomotor categories present in Sciuromorpha. In particular, the families Sciuridae and Gliridae cover different types of locomotion from semifossorial, cursorial to arboreal and gliding (Nowak & Wilson, 1999; Wilson et al., 2016; Wilson & Reeder, 2005). Moreover, Sciuromorpha have been the object of various ecomorphological studies dealing with their locomotor behavior (Bryant, 1945; Essner & Scheibe, 2000; Gambaryan, 1974; Hayssen, 2008; Mielke et al., 2018; Parsons, 1894; Peterka, 1936; Polyakova & Sokolov, 1965; Scheibe & Essner Jr., 2000; Stalheim-Smith, 1984; Swiderski, 1993; Thornton et al., 1997; Thorington & Santana, 2007; Wölfer et al., 2019). Further, since Sciuromorpha harbor a high number of species adapted to an arboreal lifestyle, they represent a good comparative group with the arboreal Primates and arboreal Carnivora (Hayssen, 2008; Koprowski et al., 2016).

Previous studies on Sciuromorpha revealed correlations between shape and morphometry with locomotor category in brain size (Bertrand et al., 2021; Meier, 1983; Roth & Thornton, 1982), inner ear morphometry (Pfaff et al., 2015), myology (Thorington et al., 1997), long bones (Polk et al., 2000; Samuels & van Valkenburgh, 2008; Scheibe et al., 2007; Wölfer et al., 2019) as well as body proportions (Thorington & Heaney, 1981) and with kinematics during locomotion (Essner, 2003). To the best of our knowledge, Hayssen (2008) is the only author who looked at the tail in Sciuromorpha in more detail. However, this author only focused on its overall length, showing that the tail was the shortest in ground squirrels, longer in arboreal squirrels and the longest in gliding squirrels.

Thus, the objectives of our study are: (a) the osteological description of the tail in Sciuromorpha, (b) the comparison of the distribution patterns of key osteological features with those in arboreal Primates and arboreal Carnivora in order to test the degree of applicability of tail regionalization, and (c) testing for correlations between tail anatomy/morphometry and the different types of locomotion in Sciuromorpha.

We hypothesize that Sciuromorpha species, adapted to an arboreal environment, should exhibit a tail anatomy similar to that in arboreal non-prehensile-tailed primates and carnivors due to similar constraints set by their lifestyle. In particular, we expect that the arboreal (but also gliding) Sciuromorpha show relatively longer tails, with an absolutely longer proximal tail region, than their terrestrial relatives. It has been shown that the tail is used by arboreal mammalian species for counterbalance and stabilization when leaping and jumping as well as for landing on the ground afterwards (Essner, 2003; Hildebrand & Goslow Jr., 2001; Horner, 1954; Larson & Stern, 2006; Preuschoft et al., 1996; Stevens et al., 2008; Walker et al., 1998). The movements of the tail associated with arboreal locomotion are linked with osteological features, which are expected to be found not only in Primates and Carnivora, but in other mammalian orders like Rodentia as well. The interplay between characters and their pattern of distribution in the tail are crucial for understanding locomotor functions.

2 | MATERIAL & METHODS

2.1 | Material

For the purpose of this study, we described osteological characters of the tail and took morphometric measurements in a total of 37 dried postscapal vertebral series of 20 sciurid species and six glirid species (Rodentia; see Table 2, and Supporting Information, Table A1). With our sample we strived to not only cover a broad range of species within Sciuromorpha, but also to include the most common locomotor categories found within this clade: arboreal, gliding and semifossorial. We also wanted to test for intraspecific variability, and therefore sampled 11 specimens of Sciurus vulgaris (from different regions across Germany). Species taxonomy, ecology and locomotor categories follow previous studies (Nowak & Wilson, 1999; Samuels & van Valkenburgh, 2008; Thorington & Hoffmann, 2005; Wilson et al., 2016; Wilson & Reeder, 2005). For a detailed ecological profile of the species consult Supporting Information, Table S1. For the purpose of comparison, we further sampled and included data from the literature (Organ, 2010; Yoolatos, 2003) for 10 primate and seven carnivorans species for some of the analyses (Table 2).

Sampled specimens are housed in the mammalogy collections of the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt (Frankfurt am Main, Germany)—SMF, Museum der Universität Tübingen Zoologische Sammlung (Tübingen, Germany)—ZSTÜ, Zoologisches Forschungsmuseum Alexander Koenig (Bonn, Germany)—ZFMK. Data were collected from articulated and disarticulated tails of dry skeletons. Complete caudal series were preferred, but specimens for which measurements of single vertebrae in
the proximal, transitional or distal region could not be taken, or for which the exact number of distalmost vertebrae is unknown, were still considered for analyses (see Methods). We selected osteologically mature specimens only. Maturity was determined by the complete to almost complete fusion of the epiphyseal plates of the long bones (the femora in particular). While fusion of the epiphyseal plates of the long bones was complete in all specimens, many still showed visible sutures of the epiphyseal plates in their respective vertebral bodies in the caudal series. Maturity was still assumed since incomplete fusion of the epiphyseal plates of tail vertebrae is not a disqualifier for osteological maturity of an individual. The timing of fusion in caudal vertebrae is still unknown and may even vary (Organ, 2010), but it seems well-supported that the timing of ossification occurs later in caudal vertebrae than in long bones (Beyerlein et al., 1951; Johnson, 1933; Petri, 1935; Sánchez-Villagra, 2002; Strong, 1925).

2.2 Methods

2.2.1 Phylogeny of Sciromorpha

In order to place the discussion of the results in a systematic and evolutionary context, we used the phylogeny of Zelditch et al. (2015) and Montgelard et al. (2003). These phylogenies are based on
mitochondrial and nuclear genes and cover about 66% of all known extant sciurid species for the former, and the glirid species for the latter. The combined phylogenetic tree used for the present paper was trimmed to include only the rodent species sampled in this study (Supporting Information, Figure A1). With exceptions of two species (Tamias sibiricus and Ictidomys tridecemlineatus) we followed the taxonomy of Wilson and Reeder (2005). Within the genus Tamias, three subgenera (Tamias, Eutamias and Neotamias) have been recognized (Patterson & Norris, 2016). However, for our specimen we utilized the sole genus name Tamias as used in Zelditch et al. (2015), since taxonomy is not the scope of our study and we only have one specimen of Tamias at hand. Further, the species “Spermophilus” tridecemlineatus has now been recognized as a member of the genus Ictidomys (Helgen et al., 2009).

Throughout our paper, we use “sciuromorph” as an informal name for the taxon Sciuromorpha. In order to make the text easier to read, we use the full scientific names only the first time a species is mentioned; afterwards only the genus name is used, unless several species of a genus are mentioned.

### 2.2.2 Locomotor categories in Sciuromorpha

For the purpose of our study, we classified the species into one of three locomotor categories found in our sampled Sciuromorpha (see Table 2), following the work of Samuels and van Valkenburgh (2008) and Samuels et al. (2013). The assignment of a locomotor category is based on the most frequent locomotor behavior displayed by the animal: arboreal (A), gliding (G) or semifossorial (S). Note that there are no prehensile-tailed, fossorial, ricochetal, semiaquatic and terrestrial taxa within Sciuromorpha (Nowak & Wilson, 1999). We were not able to get access to specimens of the two cursorial squirrels (Epixerus, Rheithrosciurus mackrotis) for our analysis. A gradation between locomotor categories is possible and will be taken into consideration in the discussion. The locomotion of arboreal squirrels has been further split in two categories: squirrels that walk, scramble and leap, and squirrels that mainly claw cling (Youlatos, 1999; Youlatos et al., 2015; Youlatos & Samaras, 2011). For the purpose of our analysis, and given our sample, we kept the broader locomotor categories. However, we consider the finer categories when discussing positional behaviors. All primate and carnivoran species considered here are arboreal (Nowak & Wilson, 1999). In order to distinguish arboreal-bound animals (i.e., arboreal as well as gliding species) from terrestrial-bound animals (i.e., ground living and semifossorial species) in the tangent space analyses, we introduced the category “habitat” (Table 2).

### 2.2.3 Anatomical description and analysis

This study only concerns mobile tail vertebrae and their biomechanical functions. A vertebra was identified as caudal vertebra, and not part of the sacrum, when no sacral fusion was present (Schultz & Straus, 1945; Standring, 2005; Tague, 2017; White et al., 2012). The anatomical description follows the definitions of vertebral characters used in previous studies (Ankel, 1962, 1972; German, 1982; Organ, 2007; Russo, 2015). However, these studies focused primarily on the morphometry and position of the “key-vertebrae” TV and LV, and did not give detailed anatomical descriptions or the position of other features. In this study, we extended the number of characters used as pertinent anatomical features to six (see Figure 1 and Table 1 for definition and functional properties). Furthermore, the total number of post sacral vertebrae as well as the number of vertebrae of each tail region was documented. The characters were recorded and schematically visualized for each species (see Results). We were not able to record the position of these characters for the primate and carnivoran specimens from the literature (Organ, 2010; Youlatos, 2003) since several were not described or their position on the tail was not given.

To statistically assess the degree of similarity between the distribution patterns of these characters in different species, we performed a Spearman rank correlation analysis with the software PAST 3.12 (Hammer et al., 2020). We assigned ranks/positions to all of the six anatomical features described in accordance to the order they appear on the caudal series. If x characters occur at the same rank/position P, they are given the average rank,

\[ \frac{\sum_{k=0}^{x-1}(P+k)}{x} \]

and the next available rank/position is then \((P + x)\) (Fowler et al., 1998).

This gave us a pattern of ranked features for each tail. Spearman rank correlation analysis compares the distribution pattern of each specimen against each other and measures the strength of their similarities. Spearman’s rank correlation coefficient \(r_S\) ranges from \(-1\) (i.e., exactly reversed patterns) to \(+1\) (i.e., identical patterns), with absolute values closer to zero indicating weaker relationships. Following Fowler et al. (1998) the strength of the association is categorized into:

- \(r_S = 0.00 \) to \(±0.19\) (very weak correlation),
- \(r_S = ±0.20\) to \(±0.39\) (weak correlation),
- \(r_S = ±0.40\) to \(±0.69\) (modest correlation),
- \(r_S = ±0.70\) to \(±0.89\) (strong correlation),
- \(r_S = ±0.90\) to \(±1.00\) (very strong correlation).

Furthermore, we tested the statistical significance of the correlation coefficients to determine whether two patterns are more similar to one another than expected by chance (i.e., \(p < .05\); Fowler et al., 1998). Another advantage of such correlation analysis is that we take several important features of the tail into account at the same time instead of considering and comparing only one “key-vertebra” (TV or LV) between specimens as previous studies on the prehensile tail did (Deane et al., 2014; German, 1982; Organ, 2007, 2010; Organ et al., 2009; Russo, 2015; Russo & Young, 2011; Tojima, 2013; White et al., 2012; Williams & Russo, 2015).

### 2.2.4 Morphometry

Three linear measurements were taken on each single vertebra of a specimens’ caudal series, using a HELIOS dial caliper with an accuracy of \(±0.05\) mm (see Figure 2). The craniocaudal vertebral body
length (VBL) was measured on the ventral side of the centrum of a vertebra. We added up all VBL to estimate the total length of the tail and the VBL of the vertebrae involved in the proximal, transitional and distal regions to calculate the respective proportions of each tail region. Accordingly, when a tail length is mentioned in the text, it is not based on measures on living or stuffed individuals and does not include intervertebral discs or soft tissues. The maximum transverse processes breadth (TPBmax) is measured from the tip of one lateral projection of the transverse processes to the other one for each vertebra. For bifurcated transverse processes we measured along the longest lateral projection. If one side of the transverse processes was broken, we measured the preserved lateral projection up to the middle of the vertebral centrum and multiplied by two to obtain TPBmax. The maximum dorsoventral spinous process height (SPmax) was measured between the ventral side of the vertebral body perpendicularly up to the highest point of the spinous process. All measurements for VBL, TPBmax and SPmax can be found in Table S2 (sheet VBL, SPmax, TPBmax).

In order to estimate missing data (e.g., measurements as well as vertebral counts, primarily for the distal part of the tail) we developed a new method by fitting models to the available vertebrae and extrapolating length distributions as a function of vertebral position. We used generalized additive models (GAMs) in R (R Core Team, 2014; Version 3.4.1) using packages “ggeffects” (Lüdecke, 2018; Version 0.9.0) and “mgcv” (Wood, 2021; Version 1.8–36). For each specimen, we fit a model of vertebral length as a function of position using a thin plate spline smoother. We extrapolated using these GAMs to reconstruct the unobserved portion of the tail (i.e., positions beyond those observed), and estimated the end of the tail to occur where the projected vertebral length was either equal to or less than zero. The use of this method assumes that vertebral length changes in a relatively smooth fashion that is consistent within the part of the tail where the data is missing. We cannot test this assumption in the species for which data is being imputed, so to test the robustness of this new method we applied it to complete tail series (see Supporting Information, Table S2, sheet Empirical Test of GAMs). We did this by removing some of the distalmost vertebrae (2, 3, 4, 5, 7 and 9 caudal vertebrae) to simulate missing data. We then compared the estimated results from GAMs with the original complete series. We found that, regardless of the number of removed vertebrae, the total number of vertebrae is never underestimated. Moreover, the estimations are reliable (i.e., SD ≤1) with up to four missing vertebrae. Estimates based on more than four missing caudal vertebrae became more uncertain, with reliability decreasing as more vertebrae are missing. We assume that this is related to and influenced by the steeper decrease in the length between two consecutive vertebrae toward the tip of the tail.

We excluded the primate Microcebus murinus from all morphometric analyses since the distalmost caudal vertebrae were not assessable with the methods we used to estimate the lengths of missing measurements. As with the anatomical description, the published measurements for Primates and Carnivora (Organ, 2010; Yoolatos, 2003) could not be used for our morphometric analyses, because they are not given for each caudal vertebra. However, the morphometric data found in literature (e.g., lengths of tail regions...
and the respective region proportions) were included into the tail region proportion analysis.

### 2.2.5 Tail region proportion analysis

The relative proportion of each region of the tail, in terms of vertebrae count and length (the sum of the VBL for that region), in relation to the entire tail were visualized in ternary diagrams, where each corner represents either the proximal, transitional or distal tail region. Results were generated in R (R Core Team, 2014; Version 3.4.1) using the package “Ternary” (Smith, 2017; Version 1.1.0).

Among the rodent sample, our *Graphiumus microtis* specimen, showing a pathological fusion of an unknown number of distalmost caudal vertebrae, and the *Funambulus pennantii* specimen, missing a high number of vertebral measurements, were excluded from the analysis.

The tail region proportions of the 11 specimens of *S. vulgaris* have been tested for normality (e.g., Shapiro–Wilk) with the software PAST 3.12 (Hammer et al., 2020). This allowed to verify if the tail region proportions show no deviation from a unimodal distribution (i.e., a low intraspecific variability), and in turn support the use of one individual per species in this study.

### 2.2.6 Length progressions of rVBL, rSPmax and rTPBmax (Tangent space analyses)

Due to differences in tail length and number of caudal vertebrae, vertebral length progressions (from the root to the tip of the tail) are not directly comparable between species. To compensate for this, we standardized the estimated tail measurements for each species by using interpolated estimates for each anatomical feature. To do this, we constructed a GAM fitting the anatomical measurement of each vertebra as a function of its proportional distance from the base to the tip of the tail. To convert this model to approximations that could be compared across species, we then projected this model across the range from 0 (indicating the base of the tail) to 1 (indicating the tip of the tail), in increments of 0.1, resulting in 11 values per species. This means, e.g., a rVBL measurement at Pos = 0.1 represents the approximate rVBL of a vertebra located 10% of the distance from the base to the tip of the tail, based on a model of how rVBL changes as a function of tail position for that species.

We used these interpolated linear measurements and relative tail position as landmarks to conduct a two-dimensional procrustes analysis using the gpanel function in the geomorph R package (Adams et al., 2020; Version 3.1.0). We used the resulting values to test for phylogenetic signal using the “physignal” function, finding that rTPBmax and rVBL showed highly significant phylogenetic signal (p < .001). rSPmax did not show significant phylogenetic signal, likely because overall variance was low. We therefore conducted phylogenetic generalized least squares (pgls) analyses using function “procD.pglss” to determine whether the distribution of shapes of tail vertebrae were affected by habitat and locomotion. Exploratory “procD.lm” models indicated significant interactions between the total number of vertebrae and the effects of the other predictors, indicating that the effects of habitat and locomotion on tail vertebra shape are modified by the total number of vertebrae. The “procD.pglss” models were therefore modified to include these effects.

To visualize the variation in morphometric measurements we conducted phylogenetically aligned principal components analyses on our interpolated landmark data using the plotTangentSpace (geomorph 2) and gm.prcomp (geomorph 3) functions. Details of these analyses are

### Table 3

List of linear measurements taken on caudal vertebrae. Definitions of measurements follow the study by Russo (2015) and are illustrated in Figure 2. Each row in the table represents which linear measurements were made, the derived characters (variables) used in the morphometric analyses, its functional relevance, and how it was calculated. MapD = midshaft anteroposterior diameter of the femur. All measurements were calculated in mm.

| Measurements | Variables for analyses | Functional relevance | Calculation |
|--------------|------------------------|----------------------|-------------|
| VBL measures from the ventral side of the vertebral body from proximal to distal | rVBL (relative vertebral body length) | influences potential flexibility of the tail | VBL/MapD |
| SPmax measures between the ventral side of the vertebral body perpendicularly up to the apex of the spinous process | rSPmax (relative spinous process height) | influences leverage and surface area of attachment for basal tail extensor musculature | SPmax/MapD |
| TPBmax measures laterally from the apex of the left transverse process to the apex of the right transverse process | rTPBmax (relative maximum transverse processes breadth) | influences leverage and surface area of attachment for abductors muscles in the proximal region and for ventral flexor muscles at the level of the transitional vertebra | TPBmax/MapD |

MapD measures the anteroposterior diameter in the middle of a femur
FIGURE 3  Legend on next page.
given in the Supporting Information. These functions reduce the dimensionality of high-dimensional morphological data, to simplify the presentation and analysis of morphological variation. Again, G. microtis and Funambulus were excluded from the analysis due to the large number of missing measurements. The rSPmax data of four rodents was not usable for the tangent space analysis due to insufficient data.

Three specimens (i.e., Hylopetes sagitta, Petaurista petarura, S. vulgaris ZFMK MAM 2004.0029) only display two spinous processes on their caudal series, so that not enough data is available for a PCA. Even though three spinous processes are present on the specimen S. vulgaris SM 57960, we could not use the data because only two could be measured directly, while the third was estimated. The data of two further S. vulgaris specimens was not sufficient for a PCA on rSPmax (SMF 48690, ZFMK MAM 2005.0382).

Since only one Carnivora (Ailurus fulgens) was sufficiently documented for inclusion in such an analysis, the whole order was excluded from the analysis. We suggest that this order should be the object of a separate study. For Primates, we could only rely on the five species we measured ourselves: Callithrix jacchus, Saimiri boliviensis, Macaca nemestrina, Macaca mulatta, and Nasalis larvatus. Although all five could be used for rVBL and rTBPmax progression analyses, the Macaca species could not be used for rSPmax analysis because they show only up to two spinous processes on their caudal series.

3 | RESULTS

3.1 | Anatomical description

Figure 3 displays the schematized anatomy of the tail for the studied species. S. vulgaris and Sciurus anomalus show the same tail pattern and are, therefore, represented together. Only one representative is shown here. The same applies to the three different Callosciurus species and the two Paraxerus ochraceus specimens, too. Refer to Supporting Information, Table S2 (sheet Tail Anatomy) for the complete data set. Moreover, only minor intraspecific variations have been noticed (e.g., total number of vertebrae, position of LV) in our sample of S. vulgaris specimens (see Supporting Information, Figure A2) that will be discussed.

In almost all species studied, SP (the last appearance of a spinous process) is the first of our six osteological features encountered along the tail. It falls on TV (the transition vertebra) in most cases (exceptions: Muscardinus avellanarius, Nasalis larvatus (4th caudal vertebra); Callithrix, Macaca mulatta, Microcebus (5th caudal vertebra); Marmota (9th caudal vertebra)). LV (longest vertebra) is always the second to last of our features found in the caudal series, but it shows a high variability in its specific vertebral placement within the tail (from the 6th to the 14th caudal vertebra). In three out of 45 specimens LV directly follows TV, which causes the transitional region to consist of only one vertebra (viz. LV; Glaucomys, Hylopetes and Eliomys quercinus). The feature with the highest variability in its specific vertebral position is Me (last vertebra bearing metapophyses). Yet, it is also the most caudally positioned of our characters on the tail in every species of the sample.

3.2 | Spearman rank correlation

With only a few exceptions, the analysis of the distribution patterns of our six osteological characters shows remarkable correlations in Sciuromorpha (see Supporting Information, Table S3). Almost all arboreal species display strong to very strong correlation with each other. Likewise, the gliding species are very strongly correlated with each other. In semifossorial species, the correlations are less distinct.

In contrast to other arboreal sciuriforms, the two glirids Dryomys and G. microtis are only significantly correlated with about half of the other arboreal species (46.2% and 57.7%, respectively, contra >90% for other arboreal species). Accordingly, their degree of correlation with these species is usually only strong, sometimes even modest. In fact, these two species are responsible for most of the discordance among arboreal taxa. For instance, G. microtis shows a non-significant modest correlation \( r_s = 0.64/p = .19 \) with Ratufa indica, four specimens of S. vulgaris (and non-significant strong correlation with further three) and Hylopetes.

The distribution pattern in gliding squirrels is strongly to very strongly correlated with that of all arboreal animals. However, here again Dryomys and G. microtis show different correlations with the...
three gliding squirrels. Whereas their correlation with the giant flying squirrel Petaurista is significantly strong ($r_s = 0.83/p = .05$ and $r_s = 0.87/p = .04$, respectively), it is non-significant and modest with the small gliding squirrels Glaucomys and Hylopetes ($r_s = 0.70/p = .15$ and $r_s = 0.64/p = .19$, respectively).

The semifossorial species Marmota and Spermophilus display non-significant modest correlations with most of the other semifossorial and the arboreal sciuriform species. However, Marmota shows significant strong correlations with the semifossorial Spermophilus and Ictidomys ($r_s = 0.72/p = .11$ and $r_s = 0.83/p = .03$, respectively), and even very strong correlations with Cynomys (semifossorial), as well as Dryomys, and G. microtis (arboreal; $r_s = 0.90/p = .03$; $r_s = 0.94/p = .02$; $r_s = 0.90/p = .03$, respectively). Spermophilus has a strong correlation with four S. vulgaris specimens, Dryomys and Eliomys (arboreal; $r_s = 0.77/p = .10$ and $r_s = 0.70/p = .14$, respectively), but also with Glaucomys and Hylopetes (gliding; $r_s = 0.70/p = .14$ for both), as well as with Marmota (semifossorial; $r_s = 0.72/p = .11$). Yet, these correlations are not statistically significant.

With the exception of Nasalis, Primates and Carnivora are significantly correlated at a strong to very strong degree with each other. Likewise, besides Nasalis, all primates and carnivorns of our sample (all arboreal species) are significantly strongly or very strongly correlated with the investigated arboreal (except sometimes Dryomys and G. microtis) and gliding sciuriform species. The primate genus Nasalis is only significantly (strongly to very strongly) correlated with 21 out of 43 specimens (i.e., 15 out of 33 arboreal specimens; 1 out of 3 gliding species; 5 out of 7 semifossorial species (all orders combined). This taxon is only significantly very strongly correlated with the arboreal Dryomys and G. microtis ($r_s = 1.00/p = .01$ and $r_s = 0.95/p = .07$, respectively), as well as with the semifossorial Cynomys, Marmota, and Ictidomys ($r_s = 0.95/p = .01$; $r_s = 0.94/p = .02$; $r_s = 0.94/p = .02$, respectively). The other arboreal

**FIGURE 4** Ternary plot of the proportion of each tail regions length (proximal, transitional and distal) in tails of arboreal, gliding and semifossorial sciuriform rodents (except Funambulus pennantii and Graphiurus microtis), arboreal Primates (except Microcebus murinus), also including data from literature (Organ, 2010), as well as data of arboreal Carnivora from the literature (Youldos, 2003). Abbreviations: Rodentia: Dn, Dryomys nitedula; Eq, Eliomys quercinus; Gg, Glis glis; Gm, Graphiurus murinus; Ma, Muscardinus avellanarius; Ag, Atlantoxerus getulus; Cf, Collosciurus finlaysonii; Cn, Collosciurus notatus; Cp, Collosciurus prevostii; Cl, Cynomys ludovicianus; Gv, Glaucomys volans; Hs, Hylopetes sagitta; It, Ictidomys tridecemlineatus; Mm, Marmota marmota; Po, Paraxerus ochraceus; Pp, Petaurista petaurista; Ri, Ratufa indica; Rr, Rubriscius rubriventer; Sa, Scirius anomalus; 11 Scirius vulgaris specimens were not assigned an ID for reasons of clarity in the diagram; Sl, Spermophilops leptodactylus; Sd, Spermophilus dauricus; Ts, Tamias sibiricus; Tm, Tamias meskilandi; Primates: At, Aotus trivirgatus; Cj, Callithrix jacchus; So, Saginus oedipus; Sb, Saimiri boliviensis; Ss, Saimiri sciureus; Mm, Macaca mulatta; Mn, Macaca nemestrina; Nl, Nasalis larvatus; Pp, Pithecia sp.; Carnivora: Af, Allurus fulgens; B, Bassariscus sp.; Pr, Procyon sp.; Cfe, Cryptoprocta ferox; G, Genetta sp.; Nb, Nandinia binotata; Pa, Paradoxurus sp.
FIGURE 5  Tangent space analysis of the length progressions in sciuromorph caudal series for the variable rVBL. Since only one Carnivora (Ailurus fulgens) was available, we excluded the whole order from this analysis. Inset: Tangent space analysis including rodents and all measured primates (refer to Table S2, sheet Tangent Spaces with Primates for a more detailed graph). The polarity of the PC 1 axis is inversed. Here, rodents were colored according to their respective locomotor category (i.e., arboreal-green, gliding-blue, semifossorial-red). Abbreviations: Rodentia: Dn, Dryomys nitedula; Eq, Eliomys quercinus; Gg, Glis glis; Gv, Graphiurus murinus; Ma, Muscardinus avellanarius; Ag, Atlantoxerus getulus; Cf, Callosciurus finlaysonii; Cn, Callosciurus notatus; Cp, Callosciurus prevostii; Cl, Cynomys ludovicianus; Gv, Glaucomys volans; Hs, Hylotris sagitta; It, Ictidomys tridecemlineatus; Mm, Marmota marmota; Po78, Paraxerus ochraceus (SMF 78518); Po86, P. ochraceus (SMF 86333); Pp, Petaurista petaurista; Ri, Ratufa indica; Rr, Rubrisciurus rubriventer; Sa, Sciurops anomalus; Sv48, Sciurus vulgaris (SMF 48690); Sv57, S. vulgaris (SMF 57960); Sv78, S. vulgaris (SMF 78866); Sv87, S. vulgaris (SMF87580); Sv93, S. vulgaris (SMF 93777); Sv08, S. vulgaris (ZFMK MAM 1984.0008); Sv27, S. vulgaris (ZFMK MAM 2004.0027); Sv29, S. vulgaris (ZFMK MAM 2004.0029); Sv61, S. vulgaris (ZFMK MAM 2004.0061); Sv81, S. vulgaris (ZFMK MAM 2005.0381); Sv82, S. vulgaris (ZFMK MAM 2005.0382); Sl, Spermophilopsis leptoedactylus; Sd, Spermophilus dauricus; Ts, Tamias sibiricus; Tm, Tamiops mcclellandii; Primates; Cj, Callithrix jacchus; Sb, Saimiri boliviensis; Mmu, Macaca mulatta; Mn, Macaca nemestrina; Ni, Nasalis larvatus

FIGURE 6  Tangent space analysis of the length progressions in sciuromorph caudal series for the variable rSPmax. It includes all rodents (except Hylotris, Petaurista, and four Sciurus vulgaris specimens [SMF 48690, SMF 57960, ZFMK MAM 2004.0029, and ZFMK MAM 2005.0382]). Inset: tangent space analysis including rodents and all measured primates, except Macaca species (refer to Table S2, sheet Tangent Spaces with Primates for a more detailed graph). Since only one Carnivora (Ailurus fulgens) was available, we excluded the whole order from this analysis. The polarity of the PC 1 axis is inversed. Here, rodents were colored according to their respective locomotor category (i.e., arboreal-green, gliding-blue, semifossorial-red). Abbreviations: Rodentia: Dn, Dryomys nitedula; Eq, Eliomys quercinus; Gg, Glis glis; Gv, Graphiurus murinus; Ma, Muscardinus avellanarius; Ag, Atlantoxerus getulus; Cf, Callosciurus finlaysonii; Cn, Callosciurus notatus; Cp, Callosciurus prevostii; Cl, Cynomys ludovicianus; Gv, Glaucomys volans; It, Ictidomys tridecemlineatus; Mm, Marmota marmota; Po78, Paraxerus ochraceus (SMF 78518); Po86, P. ochraceus (SMF 86333); Ri, Ratufa indica; Rr, Rubrisciurus rubriventer; Sa, Sciurops anomalus; Sv48, Sciurus vulgaris (SMF 48690); Sv57, S. vulgaris (SMF 57960); Sv78, S. vulgaris (SMF 78866); Sv87, S. vulgaris (SMF87580); Sv93, S. vulgaris (SMF 93777); Sv08, S. vulgaris (ZFMK MAM 1984.0008); Sv27, S. vulgaris (ZFMK MAM 2004.0027); Sv29, S. vulgaris (ZFMK MAM 2004.0029); Sv61, S. vulgaris (ZFMK MAM 2004.0061); Sv81, S. vulgaris (ZFMK MAM 2005.0381); Sv82, S. vulgaris (ZFMK MAM 2005.0382); Sl, Spermophilopsis leptoedactylus; Sd, Spermophilus dauricus; Ts, Tamias sibiricus; Tm, Tamiops mcclellandii; Primates; Cj, Callithrix jacchus; Sb, Saimiri boliviensis; Mmu, Macaca mulatta; Mn, Macaca nemestrina; Ni, Nasalis larvatus

Primates and Carnivora are significantly strongly or very strongly correlated with our semifossorial species. Exceptions are Callithrix that shows a non-significant strong correlation with Cynomys ($r_5 = 0.81/p = .07$), as well as Marmota and Spermophilus, which show only modest non-significant correlations. Finally, our 11 specimens of S. vulgaris show a very strong and significant correlation ($r_5 \geq 0.90/p \leq 0.3$) with each other, which suggests only minor intra-specific variation.

3.3 Tail region proportion analyses

The ternary plot of the tail region proportions calculated with the VBL shows a rather compact distribution of the data, in one of the corners of the diagram consisting of 10%–50% of proximal region, 0%–40% of transitional region and 40%–80% of distal region (Figure 4 and Supporting Information, Table S2, sheet Tail Region Proportion Analyses). Arboreal Sciuriformes are grouped closely with the arboreal Primates and Carnivora. However, primate and carnivore species show tendencies toward a shorter proximal region than the rodents under study. Among the gliding squirrels Petaurista plots within the arboreal sciurids/glirids point cloud, whereas Glaucomys and Hylotris are segregated from this cloud, displaying the longest proximal region (except for Spermophilopsis leptoedactylus) and shortest transitional region (except a specimen of S. vulgaris) in our sample. Moreover, the two small flying squirrels have a shorter distal region than Petaurista.

Five out of seven semifossorial rodents can be separated from the arboreal rodents (except two S. vulgaris specimens and Hylotris), primate and carnivore species by their proportionally shortest distal region (40.97%–52.5%). Among these five semifossorial species Marmota and Spermophilus can be further
distinguished from Atlantoxerus, Cynomys and Spermophilopsis, as well as from all other taxa in our sample, by their proportionally longest transitional region (35.39% and 35.5%, respectively). The two remaining semifossorial species, Ictidomys and Tamias, plot within the arboreal specimens.

Primates and carnivores plot very closely to one another, and only four taxa break ranks. Among the primate species, two outliers can be identified: *M. mulatta* and *Macaca nemestrina* as they display a distinctively longer proximal and shorter distal region than the other Primates (proximal 27.6%/distal 53.87% and proximal 27.46%/distal 54.86%, respectively). Within Carnivora *Ailurus* and *Procyon* sp. show the longest proximal and shortest distal regions (proximal 16.22%/distal 53.86% and proximal 21.70%/distal 53.50%, respectively), while their transitional region is longer than in most other Carnivora species (the exception is *Paradoxurus* sp.: 25.10%). Besides these four taxa, the primate *Nasalis* is also noteworthy, as it shows the proportionally longest distal region of the whole sample (74.76%).

Among the 11 specimens of *S. vulgaris*, two show the shortest distal region for arboreal taxa, whereas one has even the shortest transitional region for our whole sample. Yet, the proportions of each region follow a normal distribution within the species (Supporting Information, Table A2). Hence, the variation of the tail region proportions in *S. vulgaris* are homogenous and vary continuously (i.e., unimodal distribution), supporting a low intraspecific variability.

The ternary plot of tail region proportions based on the number of vertebrae in each tail region does not depart substantially from the one using VBL (see Supporting Information, Figure A3 and Table S2). The data points are also located in the short proximal region/long distal region corner of the graph, and arboreal taxa are associated. The semifossorial genera *Marmota* and *Spermophilus* stand out again for their highest number of vertebrae in the transitional region. However, one gliding squirrel (*Hylopetes*) and one semifossorial rodent (*Atlantoxerus*), which show the relative highest number of vertebrae in the proximal region and a comparably low number of vertebrae in the distal region, stand out of the main point cloud. Likewise, primates are more clearly separated from the rodents (except *S. vulgaris* specimens) in having a higher number of vertebrae in the distal and a lower number in the proximal region. Again, the two *Macaca* species are separated from the other primates in possessing more vertebrae in the proximal and less in the distal region, so that they plot among the arboreal rodents. Also, three carnivoran species (*Procyon, Bassariscus* sp. and *Ailurus*), all belonging to the Caniformia, lie outside the space occupied by other carnivorans and primates. They show more vertebrae in the proximal and less in the distal region than other Carnivora, which happen to all belong to the Feliformia (*Cryp toprocta ferox, Genetta sp.*, *Nandinia binotata, Paradoxurus*). Both carnivoran groups show relatively similar transitional region proportions though. Finally, the primate *Nasalis* stands out of the whole sample as the taxa with the proportionally highest number of vertebrae in the distal, but lowest number in the proximal region (76.92% and 15.38%, respectively).

### 3.4 | Tangent space analyses of rVBL, rSPmax and rTPBmax progressions

The tangent space variation of the progression of rVBL (relative vertebral body length), rSPmax (relative maximum spinous process height) and rTPBmax (relative maximum transverse processes breadth) in caudal series of different species is represented in Figures 5–7. Consult Supporting Information, File S4 (Rodentia only) and File S5 (Rodentia and Primates) to see a description of the statistical approach, the first 11 principal components and for detailed results of ANOVAs.

On the x axis the shape of rVBL progression with positive PC 1 score values (0.0 up to 0.5) shows a compression of the rVBL progression curve with vertebrae reaching greater lengths. Here, the length differences between each standardized vertebral position are higher than what can be seen for negative PC 1 score values (0.0 up
to −0.9) on the x axis (Figure 5). Toward negative values the shape of the rVBL progression leads to a stretching of the tail with lower length differences of rVBL. The y axis displays a stretching of the rVBL progression curve for negative PC2 values (0.00 up to −0.4) and higher length differences for positive PC 2 score values (0.00 up to 0.4). The shape of rVBL progression with negative PC 2 score values shows a slight decrease in length in the cranial-most part of the proximal region followed by a plateau and a steep increase in length up to the longest rVBL. After this peak, the rVBL slowly decreases toward the tip of the tail. Conversely, along the positive PC 2 score values the shape of rVBL progression shows a distinct decrease followed by a sudden increase in length within the proximal tail region, until reaching the longest rVBL. After a plateau, rVBL then decreases rapidly toward the tip of the tail. Despite the detailed change in the shape of rVBL progression, the overall trend of shape is the same. The rVBL of the first caudal vertebrae slightly decrease in length, followed by an increase in length toward the longest vertebra and a continuous decline until reaching the tip of the tail.

Among rodents, the four semifossorial taxa Cynomys (Cl), Marmota (Mm), Spermophilopsis (Si), Spermophilus (Sd), and all Gliridae, are the only ones to occupy the area with high negative PC 1 and moderate negative PC 2 values in the morphospace. The arboreal rodents are spread out along a diagonal running from the [negative PC 1/positive PC 2] quadrant to the [positive PC 1/negative PC 2] quadrant. Exceptions are two S. vulgaris specimens (Sv61, Sv78), which are found in the morphospace with negative PC 1 and negative PC 2 values.

The gliding squirrels cannot be distinguished from one another on PC 1, but are far apart along PC 2. For instance, Glaucomys (Gv) plots among the arboreal rodents with a negative PC 2 value, whereas Petarista (Pp) and Hylomys (Hs) show high positive PC 2 values and fall outside of the arboreal species.

Scores for semifossorial rodents are quite widespread. Four out of seven species (Cynomys (Cl), Marmota (Mm), Spermophilopsis (Si) and Spermophilus (Sd)) cluster at the lowest range of PC 1 (values < −0.8) among Rodentia, and a moderately negative PC 2 score. This corresponds to a caudal series with low differences in vertebral length, and separates them from other semifossorial, but also arboreal and gliding sciurids. Among the other semifossorial rodents, Ictidomys (It) shows positive PC 1 and positive PC 2 scores and plots within the arboreal rodents. With the second highest positive PC 2 score of our sample, Atlantoxerus (Ag) shows a different shape than the other semifossorial species. Likewise, Tamias (Ts) stands out of the other semifossorial species with the most positive PC 1 value, and is found close to the arboreal group.

Interestingly, all glrid species are found in the positive PC1 and negative PC2 quadrant, along with the arboreal sciuroid species P. ochraceus (Po78, Po86), Tamlops mcelleanldii (Tm), Ratufa (Ri) and Callosciurus prevostii (Cp), as well as the gliding Glaucomys (Gv). Within Gliridae, Dryomys (Dn), Glis glis (Gg), G. murinus (Gm) and Muscardinus (Ma) plot close together among arboreal sciuroid species, whereas Eliomys (Eq) is set apart from this group with a PC 1 value close to 0. Gliridae cannot be distinguished based on their PC 2 scores. Conversely, the three different species of the sciuroid genus Callosciurus (C. finlaysonii, C. notatus, C. prevostii) are widely separated along PC 2, but not along PC 1.

Sciuromorpha differ significantly in their rVBL progression shape in habitat and locomotion (F = 19.79/p = .01, F = 4.79/ p = .01, respectively) as well as the maximum rVBL (F = 7.71/ p = .01) in the ANOVA. The phylogenetically informed ANOVA significantly supports the latter results (habitat: F = 1.89/p = .01, locomotion: F = 1.20/p = .01, maximum rVBL: F = 30.21/p = .01). The rVBL progression shape coordinates display a significant phylogenetic signal (κ = 0.21; p = .001). ANOVAs were applied to the residuals of the original data and corroborate the results of the original data. For detailed results on the ANOVAs refer to Supporting Information, File S4.

The position of primate species with respect to rodent species can be seen in the PCA inset of Figure 5. It seems that our observation pertains to Rodentia as well as Primates. However, inclusion of primate specimens in the tangent space analysis of rVBL causes the mirroring of the PC 1 axis’ polarity and is accompanied by positional changes in some Sciuromorpha (see figure in Supporting Information, Table S2, sheet Tangent Spaces with Primates). The group of arboreal rodents seems to plot more closely together. Furthermore, the gliding species are now plotting closer to each other along PC 1 (close to 0) and PC 2. The shape coordinates of Primates are widespread along PC 1, but are confined in the positive PC 2 values. M. mulatta (Mmu) and M. nemestrina (Mn) plot closer to semifossorial rodent species than to other primates.

The progression of rSPmax does not show any remarkable differences in shape among our studied specimens (Figure 6). The distribution is represented by a rather flat point cloud, with data points widely spread along PC 1, whereas PC 2 score values are not very variable and close to 0 with few exceptions, e.g., one S. vulgaris specimen (Sv87). Arboreal sciurids do not show any clustering, but semifossorial rodents plot preferentially in the positive PC 1 and negative PC 2 quadrant. However, this pattern was not found to be statistically significant for any criteria (see Supporting Information, File S4). Interestingly, all glirids show very high negative PC 1 scores.

The inclusion of primate specimens in the tangent space analysis of rSPmax causes the mirroring of the PC 1 axis’ polarity. The shape coordinates of Primates are spread along PC 1 with low variation along PC 2 and plot among the flat point cloud of Sciuromorpha (inset in Figure 6; see figure in Supporting Information, Table S2, sheet Tangent Spaces with Primates).

Along PC 1, the rTPBmax progression stays similar in shape with the highest breadth in the proximal part of the tail, followed by a decline toward the distal tail region (Figure 7). The decrease in breadth is more gradual for species with a negative PC 1 value. Along PC 2 however, the breadth decreases gradually in the negative values, whereas in the positive values, the breadth of the transverse processes increases at first in the proximal third of the tail before slowly decreasing. Most of the arboreal rodent species show
a negative PC 2 score, while their PC 1 scores are widespread. Nonetheless, the bulk of them occupies the [positive PC 1/negative PC2] quadrant of the morphospace. Only the arboreal glirids Dryomys (Dn), Glis (Gg), G. murinus (Gm) and Muscardinus (Ma) and two arboreal sciurids (P. ochraceus (Po78), S. anomalus (Sa)) show positive PC 2 scores. Conspicuously, all but one semisossorial species, Marmota (Mm), show positive PC 2 values. Tamias (Ts) and Marmota (Mm) are separated from the other semisossorial species and their shape coordinates are rather dispersed. Most semisossorial species (Atlantoerus (Ag), Cynomys (Cl), Ictidomys (It), Spermophilopsis (Sl), Spermophilus (Sd)) can be found in the quadrant with negative PC 1 and positive PC 2 score values. While the small gliding squirrels Glaucomys (Gv) and Hylometes (Hs) are found close to the arboreal glirid species, Petarurista (Pp) plots with the main group of semisossorial species, presenting negative PC 1 and positive PC 2 values.

As with rVBL, the rTPBmax progression shape differs significantly in habitat and locomotion (F = 3.69/p = .02, F = 4.90/p = .01, respectively) as well as the maximum rTPBmax (F = 5.85/p = .01) in the ANOVA. The phylogenetically informed ANOVA significantly supports the latter results (habitat: F = 0.34/p = .01, locomotion: F = 0.47/p = .01, maximum rTPBmax: F = 3.48/p = .05). The rVBL progression shape coordinates display a significant phylogenetic signal (κ = 0.35; p = .001). ANOVAs were applied to the residuals of the original data and corroborate the results of the original data. For detailed results on the ANOVAs refer to Supporting Information, File S4.

Results of the tangent space analyses show a rather compact S. vulgaris cluster (for rSPTmax and rTPBmax). In the PCA of rVBL, nine out of 11 S. vulgaris specimens were clustered. These results again suggest limited intraspecific variability.

The inclusion of primate specimens in the tangent space analysis of rTPBmax again causes the mirroring of the PC 1 axis' polarity. Primates are spread along PC 1 with all five species showing positive PC 1 values (inset in Figure 7). Remarkably, the platyrhine primates (i.e., New World monkeys) Callithrix and Saimiri plot among the sciromorph point clouds, whereas the catarrhine primates (i.e., Old World monkeys) M. mulatta, M. nemestrina and Nasalis appear as outliers, displaying the highest positive PC 1 values of all specimens in the study (see figure in Supporting Information, Table S2, sheet Tangent Spaces with Primates).

### 4 | DISCUSSION

This study aims to give insights into (a) the osteological tail anatomy in sciromorph rodents, (b) the comparison of distribution patterns of key osteological features with those in arboreal pri-mates and carnivorans in order to test the degree of applicability of tail regionalization, and (c) tests for correlations between tail anatomy/morphometry and the different types of locomotion in Sciuromorpha.

#### 4.1 | Intraspecific variability

Before drawing conclusions about the interspecific differences in tail morphology among Sciuromorpha, we wanted to assess the variability of our observations within one species. Our sample of 11 S. vulgaris specimens showed no significant intraspecific difference in tail anatomy, no polymorphism in the tail region proportions, and rather compact clusters in the tangent space analyses. Furthermore, no major variability between the tail anatomy of rodents with different locomotor categories is present. Finally, all specimens were wild-caught and collected in Hesse and North Rhine-Westphalia (Germany), but are not otherwise related to each other. Thus, we confidently conclude that, at least for sciromorph Rodentia, morphofunctional parameters taken from a single specimen are sufficient to stand in for the entire species.

#### 4.2 | Tail anatomy in Sciuromorpha

Overall, we confirm that the same osteological tail characters and tail patterns are present within our sciromorph sample, irrespective of their relative tail length and locomotor category. However, among our sample two exceptions were evident. The semisossorial marmotines Marmota and Spermophilus are the only species with anatomical tail patterns that deviate from the other sciurid and glirid species (see Figure 3, Supporting Information, Table S3). On the one hand, SP usually wanes cranially to or on TV in Primates, Carnivora (e.g., Organ, 2010; Russo, 2015) and sciromorph rodents, but in Marmota it persists quite far caudally from TV, and disappears only just before LV. The spinous processes of the tail provide an extensive attachment site for the basal tail extensor muscles (musculus extensor caudae medialis and musculi interspinosae caudae; Shapiro, 1993). The further caudally these muscles extend on the tail, the more vertebrae are involved in the dorsal extension and leverage produced by these muscles. In Marmota, SP is positioned on the 10th caudal vertebra (out of 24), close to the middle of the tail. Thus, unlike any other taxa in our sample, the range of action of these muscles not only includes the proximal, but also the transitional region. Hence, compared to other taxa it should be possible for Marmota to extend dorsally a more distal part of its tail (Organ et al., 2009; Russo, 2015). The absence of zygapophysyal articulation in the transitional region possibly allows for an even higher degree of tail extension. Marmots have been observed to use their tail frequently as a tool for interindividual visual communication, which might be an explanation for the higher mobility of the tail (Waring, 1966). Further, considering that marmots are large-sized squirrels, the tail is short (about 30% of the head-body length), which might facilitate anatomical variability in the tail (Koprowski et al., 2016). On the other hand, the tail anatomy of Spermophilus mainly differs from other sciromorph rodents in having the last metapophyses (Me) in the transitional region (cranial to LV), not in the distal region. The more cranial disappearance of Me should
not have any influence on the mobility of the tail since LPrPo (i.e., the last functional pre- and postzygapophyseal articulation) still occurs more cranially than Me. To the best of our knowledge, Spermophilus has not been observed to use its tail in a specific way that could explain the unique pattern. However, the different species of the genus Spermophilus show a great variability in their tail length (between 10% and 45% of the head-body length; Kryštufek & Vohralík, 2012). We have no further functional explanations why the tail pattern is aberrant in these two semifossorial species. The study of further specimens of Marmota and Spermophilus may help testing the consistency of our observations on the tail in the latter species might help to explain our observations in their tail morphology.

No phylogenetic signal could be detected within Sciuromorpha either. Yet, among arboreal rodent species, most Gliridae (except Glis (Glirinae) and Eliomys (Leithiinae)) are separated from the S. vulgaris group (mainly Sciurini) in the tangent space of rVBL and rTPBmax and show higher negative PC 1 values in the tangent space of rSPmax. Hence, subtle phylogenetic differences might be detectable with a larger sample.

4.3 Comparison with arboreal Primates and Carnivora

Our study shows that the sciuromorph tail anatomy is comparable, both in terms of distribution patterns of key osteological features and of regionalization, with the anatomy found in Primates and Carnivora. Since every mammal possesses a tail regardless of its length or function (Mallo, 2019), the observed anatomical similarities within and between mammalian orders, but also across different locomotor categories (arboreal, gliding, semifossorial), suggest a conservative bauplan for the tail. Overall, the functional and biomechanical constraints on the mammalian tail seem to be similar across mammalian orders and locomotor categories, except perhaps for species with highly adapted tails, e.g., prehensile tails (Emmons & Gentry, 1983; Hickman, 1979). Moreover, with few exceptions the results of the Spearman rank correlation analyses show a remarkably high similarity of tail patterns (i.e., sequence of characters present along the tail) among sciuromorph rodents, but also between the latter (especially arboreal species) and Primates/Carnivora. The tail region proportion analyses show similar results for arboreal sciuromorph rodents and arboreal Primates/Carnivora. Arnold et al. (2017) observed that the neck vertebrae series in almost all mammals shows low variability of its internal organization due to structural constraints present in the mammalian neck. Likewise, with few exceptions (e.g., Afrotheria, Xenarthra, Carnivora and Perissodactyla showing high proportions of meristic deviations from median vertebral counts) the number of thoracolumbar vertebrae in eutharian orders is not random but the result of developmental constraints (Asher et al., 2009; Asher et al., 2011; Asher & Lehmann, 2008; Narita & Kuratani, 2005; Sánchez-Villagra et al., 2007). In that regard, rodents show the least intraspecific variation in presacral vertebral counts (both homeotic and meristic), and the majority of them maintain the pliesiomorphic number of thoracolumbar vertebrae (Asher et al., 2011; Sánchez-Villagra et al., 2007). Hence, according to Asher et al. (2011, p. 1085) “Rodents [...] appear to be among the most vertebrally constrained mammals” and even “the most vertebrally conservative mammals quantified thus far” (Asher et al., 2011, p. 1089). These developmental constraints observed on rodents presacral vertebrae may be different on their tail though, since our analyses reveal variations in proportion and structure that can be correlated with phylogeny and locomotion within Sciuromorpha.

Primates possess a lower number of caudal vertebrae in the proximal region of the tail than Sciuromorpha, which might represent a phylogenetic signal. Noteworthy among our primate sample are M. mulatta and M. nemestrina, which appear as outliers in our tail region proportion analyses and the tangent space analysis of rVBL. Separated from the other primates, both are nested within the Sciuromorpha and even group with the semifossorial species in some cases (e.g., rVBL). Both Macaca species possess, relatively to their body size (i.e., normalization using the anteroposterior femoral midshaft diameter), the shortest tails of the whole sample. The other Catarrhini, Nasalis, has an average relative tail length in our sample, and is distinct from the Macaca in the rVBL plot. As such, the reduction of tail length alone might be the reason for the separation of the macaques from the other primates in analyses related to tail length and proportions. Between different species of Macaca the tail length varies widely, which has been related to climate and terrestriality (Mincer & Russo, 2020). Further, the evolutionary rate in Macaca has been observed to be much higher than in other primates, indicating an increased level of phenotypic diversity within the genus (Mincer & Russo, 2020). Conversely, the distribution of primates in the tangent space analysis of rTPBmax shows a phylogenetic signal. Catharrini (Macaca species, Nasalis) can be separated from the Platyrhini (Callithrix, Saimiri) by the more gradual decrease in the breadth of their transverse processes along the tail. It is remarkable that Nasalis, which possesses a relatively longer tail than Macaca, follows the latter for the characteristics of the transverse process.

Interestingly, we were able to detect another phylogenetic signal among Carnivora in the tail region proportion analyses (especially for vertebrae count). The tail region proportions seem to separate the Feliformia (Cryptoprocta, Genetta, Nandinia, Paradoxurus; less proximal and more distal vertebrae) from the Caniformia (Ailurus, Bassariscus, Procyon; more proximal and less distal vertebrae). However, since the Feliformia and Caniformia species in our sample show similar length of their proximal region (i.e., sum of VBL; Supporting Information, Table S2), it means that these Caniformia possess more, but shorter vertebrae in the proximal region. This observation must be taken with reservations since our Caniformia taxa all belong to the Musteloidea. Moreover, our sample does only include arboreal species and does not cover the large range of morphofunctional adaptations seen in Carnivora. Yet, these preliminary results encourage more studies on the potential phylogenetic signal of the tail within Carnivora as well as Primates.
4.4 | Locomotor signal of the tail in Sciuromorpha

Overall, the same anatomical tail characters and tail patterns are present in all locomotor categories. Yet, as described above, within arboreal real rodent species Gliridae show some differences from the Sciurini. Our results mirror the phylogenetic signal observed by Pfaff et al. (2015) on the bony labyrinth (housing the hearing and the sense of balance) of arboreal sciuroids and arboreal glirids, that differ in their bias angle of the semicircular canals, which detect angular acceleration of the head. These arboreal sciuroids and arboreal glirids evolved different patterns under more or less similar functional constraints.

The small gliding squirrels show a longer proximal region than arboreal Callosciurinae, Protoxerini, Ratufinae and Sciurini (above 30%) and stand out from the entire sample (except Eliomys) with their extremely short transitional region (about 6%). Interestingly, a long proximal and a short transitional region is also characteristic for prehensile-tailed primates (Organ, 2010; Russo, 2015). But, unlike primates, Glaucomys and Hylomys show only one vertebra in the transitional region (i.e., TV is directly followed by LV). This is probably rare, as in our sample only Eliomys (described as ground-adapted species, preferring rocks and dense understory (Bertolino et al., 2003; Mori et al., 2020)) and one individual of S. vulgaris also present this pattern. This raises questions about the homology of this region, especially when it only consists of one transitional vertebra and if this region is still functional in those taxa. Furthermore, it challenges the classical definitions of tail regions (Organ, 2010; Russo, 2015). Whereas the separation between proximal and transitional region involves a change of articulation type, the shift from the transitional to the distal region is based on a more continuous parameter (i.e., a measurement of VBL), whose morphofunctional meaning is not well understood. Organ (2010: 734) stated that “LV is the longest vertebra of the sequence, thus bending (and torsion) would be highest in this vertebra among all caudal vertebrae.” Nonetheless, to the best of our knowledge, no study has tested the intraspecific variability of the position of LV along the tail, nor the morphofunctional differences cranial and caudal to LV.

Compared to the small flying squirrels, the giant flying squirrel Petaurista plots with the arboreal squirrels in terms of tail anatomy and tail region proportions. Petaurista is the basal-most Pteromyini, the sister tribe to the exclusively arboreal Sciurini (Blanga-Kanfi et al., 2009; Fabre et al., 2015; Zelditch et al., 2015). As arboreality is probably the plesiomorphic condition in Sciuromorpha (Ge et al., 2014), it can be assumed that Petaurista kept the plesiomorphic tail pattern (short proximal, long distal region), whereas the small flying squirrels modified the proportions of their tail regions (long proximal, shorter transitional region). While the proportion analyses show a clear separation between the two small and the large flying squirrel, the Spearman rank correlation only slightly supports this hypothesis, and the results of the tangent space analyses of rVBL and rTPBmax are ambiguous. This probably shows the range of possible variations within the caudal series (i.e., individual feature position, proportion, progression along the tail) and that the tail is more complex than assumed.

Gliding as mode of locomotion probably developed to save energy and time when traveling long distances (Krishna et al., 2016). Compared to small flying squirrels the giant flying squirrels (Petaurista) face the problem of an increased wing loading (i.e., total mass divided by wing area) that comes with their higher body weight and thus require a higher glide speed to maximize the gliding distance (Thorington & Heaney, 1981). Accordingly, the patagium of small and giant flying squirrels shows significant differences in the uropatagium (flying membrane between the hind limbs and connecting to the tail). It is highly reduced in small flying squirrels and well-developed in giant flying squirrels (Johnson-Murray, 1977; Thorington & Heaney, 1981). The uropatagium is well-developed in all gliding mammals that weigh more than 1 kilogram and the surface area of the uropatagium is positively correlated with weight (Jackson, 2012). Although few studies have focused on the aerodynamic properties of the uropatagium, in bats Gardiner et al. (2011) found that: “The tail membrane [...] is [...] an aid to flight control, specifically improving agility and maneuverability.” Despite this added wing surface, the wing loading of Petaurista is still high (about 81 N/m²; Ando & Shiraishi, 1993) and makes it less agile than smaller gliders (Ando & Shiraishi, 1993). This also results in some behavioral differences like favoring landing on larger tree trunks, or gliding (instead of non-gliding locomotion) only if the distance is not too short (Ando & Shiraishi, 1993). According to Thorington and Heaney (1981) large flying squirrels seem to be best adapted to open areas, where more turbulences are present, but less obstacles to maneuver around. On the other hand, small flying squirrels are found in forested areas, where turbulences rarely occur, but maneuverability is of importance. Reduction of the uropatagium in small flying squirrels might lead to a higher mobility of the hindlimb and the tail (hence their longer proximal regions), which in turn allows to more efficiently control their gliding (Bishop & Brim-DeForest, 2008). However, although the tail of small gliders is actively moving while turning, observations could not conclusively confirm its role as rudder (Bishop & Brim-DeForest, 2008). The tail of small flying squirrels possesses hairs that are distichously arranged and therefore provide considerable surface area for gliding, while the tail of the larger relatives has a much narrower gliding surface.

The differences in the tail pattern between small and giant flying squirrels revealed by our study mirrors differences observed in their morphofunction of the inner ear bony labyrinth. Based on morphometric analyses of the semicircular canals, Pfaff et al. (2015) propose that the inner ear (i.e., vestibular system) of flying and gliding mammals is less sensitive than in fossorial taxa to prevent overstimulation during motion of the animal. Yet, within flying squirrels the inner ear of Petaurista is less sensitive than the inner ear of Glaucomys and Hylomys because of the higher gliding speed the giant flying squirrel reaches. Conversely, small flying squirrels depend on their maneuverability and therefore a need for higher sensitivity is assumed (Pfaff et al., 2015).

Based on a large sample, Hayssen (2008) proposed that among Sciuridae, gliding species possess relatively longer tails than arboreal species and that ground squirrels have the shortest tails. Her results, however, are to be put in perspective, as the ranges of the relative tail
length for each locomotor category in this study are conspicuously overlapping and several species do not follow the proposed general pattern. Direct comparison of our results with those obtained by Hayssen (2008) was not possible as the author used tail measurements including skin, fur and the tuft of the tip of the tail, whereas we only took measurements on dried tail vertebrae. Yet, our study provides complementary observations that can help to identify locomotor distinctions. In our Sciuromorpha sample, Petaurista might show the absolute longest tail, but its normalized tail length (i.e., using the anteroposterior femoral midshaft diameter) is of average value, similar to that of the other flying squirrels as well as to that of all Sciurini and other arboreal sciurids. Since our sample includes only three Pteromyini genera and, most notably, does not include Aeromys, the species showing the longest tail in the aforementioned study, our study can neither confirm the observation of Hayssen (2008), nor test for further morphofunctional features associated with a very long tail and gliding. However, our study reveals the short transitional region of the flying squirrels in our sample, which separates them from other Sciuridae. It would therefore be interesting to test this pattern in other Pteromyini, including taxa with longer tails.

Furthermore, five out of seven semifossorial species in our Sciuromorpha sample show shorter relative tail lengths compared to gliding and arboreal species as suggested by Hayssen (2008). In particular, Cynomys, Marmota and Spermophilus stand out for having very short tails in our sample, whereas Tamias and Atlantoxerus show the longest tail among semifossorial taxa, as it also has been observed by Hayssen (2008). Accordingly, relative tail length alone is not sufficient to distinguish semifossorial taxa like Tamias and Atlantoxerus from arboreal Sciuridae as their tail length relative to body length overlap (e.g., 70%–74% for Tamias, 75%–80% for Atlantoxerus, but 65%–95% for arboreal Sciurini according to Hayssen (2008)). Conversely, we observed further differences between arboreal and semifossorial sciurid rodents, primarily in the tail region proportion analysis of VBL and the tangent space analysis of rVBL. In particular, semifossorial sciurids like Atlantoxerus have a longer proximal region (>30% of total length) and a shorter distal region (<57% of total length) than arboreal animals. The separation is even more obvious in the tangent space analysis of rVBL, where marmotine ground squirrels (Cynomys, Marmota, Spermophilus) and the xerine Spermophilopsis are clearly separated from arboreal squirrels in showing lower differences in vertebral length progression toward the tip of the tail (i.e., high negative PC 1 scores). In a different way, Atlantoxerus can be distinguished from arboreal (and other) taxa by showing a higher difference in vertebral length progression (i.e., positive PC 2 score). Since Atlantoxerus inhabits arid habitats, thermoregulatory functions of the tail (e.g., as parasol) might be a possible explanation for the results we see here (Muchlinski & Shump, 1979). Likewise, Tamias appears as an outlier in the tangent space analysis of rVBL with vertebrae showing greater length differences (i.e., positive PC 1 scores/negative PC 2 scores).

Thus, in general our study reveals patterns that distinguish semifossorial from arboreal sciurids. Yet, two exceptions among the marmotine tribe exist, which plot with the arboreal squirrels in all morphometric results: Tamias and Ictidomys. The chipmunk Tamias shows a semifossorial, but also somewhat arboreal lifestyle which might have an influence on the morphology of the tail. Living in arboreal coniferous forests (i.e., Taiga) in Asia and deciduous forests in Europe (where it has been introduced), this species digs and uses burrows as larders for food storage. Tamias also uses burrows for nesting, substantially more often than it uses tree nests (Kawamichi, 1989). Moreover, Tamias forages significantly more often on the ground than on trees, but can deftly climb trees and move on branches using claw climb locomotor mode (Kawamichi, 1989; Koprowski et al., 2016; Nowak & Wilson, 1999; Thorington et al., 2012; Youlatos et al., 2008). In that respect, it has been hypothesized that the most recent common ancestor of Marmotini was an arboreal species (Rocha et al., 2016). Moreover, Tamias represents one of the oldest ground squirrel genera with extant descendants and is found at the base of Marmotini (Ge et al., 2014). Based on observations of their climbing ability (claw climb; Youlatos et al., 2008), of their feeding strategy (73% of their food items are the products of trees; Kawamichi, 1989), and now of their anatomical tail pattern being more similar to arboreal than to semifossorial species, it seems that Tamias retained behavioral and morphological features associated with the ancestral arboreality of Marmotini, which in turn allow it to exploit diverse habitats as suggested by others (Emry & Thorington, 1984; Youlatos et al., 2008; Youlatos et al., 2021). Ictidomys is a mainly solitary species, which inhabits open and very short grasslands, meadows and shrublands in North America (with a northern distribution into south-central Canada), preferring dry and sandy soils, and not forested habitats (Koprowski et al., 2016; Nowak & Wilson, 1999; Thorington et al., 2012; Wistrand, 1974). While there is no ecological explanation as to why the anatomical tail pattern of Ictidomys is similar to that of arboreal species, some answers might be found in the locomotion and behavior of this species. Indeed, Ictidomys is known to make quick up-down motions with its tail, called tail-flicking (Wistrand, 1974). Interpreted as a form of communication, Ictidomys flicks the tail over its back after running or waves the tail in a circular arch. If many conspecifics are around, and especially during courtship period, tail-flicking increases considerably suggesting a reproductive communication function (Wistrand, 1974). Tail-flicking and especially arching the tail over the back is also commonly known in the behavior of the arboreal squirrel S. vulgaris (Koprowski et al., 2016; Thorington et al., 2012). So, the fulfillment of a behavioral repertoire might explain why Ictidomys’ tail displays similarities with the tail of arboreal squirrels. However, social behavior alone might not be sufficient to explain the overall tail patterns in sciurid rodents under study.

It has been observed that some semifossorial sciurids (e.g., Tamias, Cynomys, Spermophilus) climb bushes and trees occasionally (Emry & Thorington, 1984). Still according to our analysis, the tail pattern of these species does not exactly match that of an arboreal taxon, and can be dissimilar from each other (see for instance Figures 4, 5, 6, 7). In contrast, other semifossorial sciurids (or ground squirrels; e.g., Ictidomys) do not climb trees, yet show an “arboreal tail pattern” in our analyses. Therefore, following Emry and
The lack of significant intraspecific variation seen in our sample allows for investigation of a single or few specimens per species, at least in Sciuromorpha. Hence rare species and fossils that are often represented by only one individual could be studied morphofunctionally following the methods used here. Although tails in fossils are not often preserved, there are exceptions (e.g., fossils...
from the Messel Pit Fossil Site in Germany) and information provided by the tail could supplement what is known from other cranial and/or postcranial elements.

Future studies of the tail could benefit from the development of morphometric methods used in this study, in particular, methods to statistically compare curves (i.e., rVBL, rSPmax, rTPBmax). This is particularly important, as we showed that when working on the tail, it is crucial to not only look at single key tail vertebrae, but to consider the whole caudal series.

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AUTHOR CONTRIBUTIONS

Rebecca Hofmann: Conceptualization (equal); formal analysis (lead); investigation (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). Thomas Lehmann: Conceptualization (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (lead); supervision (equal); visualization (equal); writing – review and editing (equal). Dan Warren: Formal analysis (equal); investigation (equal); methodology (equal); writing – review and editing (equal). Irina Ruf: Conceptualization (equal); funding acquisition (equal); methodology (equal); project administration (equal); resources (equal); supervision (lead); writing – review and editing (equal).

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DATA AVAILABILITY STATEMENT

All data is included with the manuscript.

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