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RESEARCH ARTICLE

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

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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 (Buchholtz & 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; Matherne 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 vertebral 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 diprodont 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.

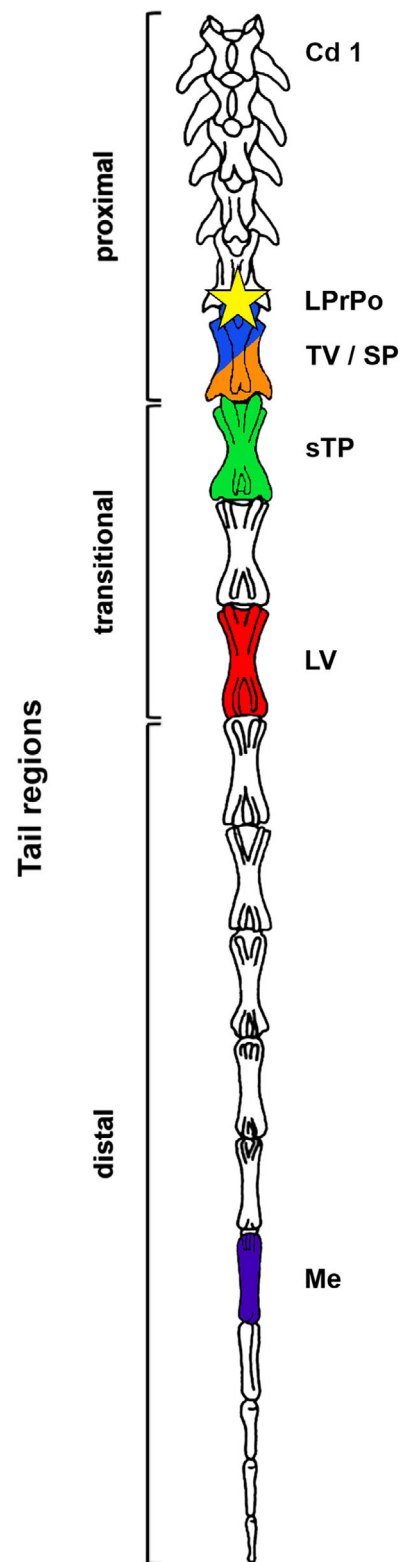
The vertebral column of vertebrates has been divided into different series (i.e., cervical, thoracic, lumbar, sacral and caudal), defined by a well-established set of characters (see Buchholtz, 2012). The mammalian caudal series (i.e., bony tail) has been further divided into the proximal, transitional 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 (LPrPo—star in Figure 1) between two consecutive vertebrae can be situated either on TV or cranial to TV. Hence, whereas proximal vertebrae cranial to LPrPo 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 <i>m. sacrocaudalis dorsalis medialis/extensor caudae medialis</i> and <i>mm. sacrocaudalis dorsalis lateralis/extensor caudae lateralis</i>
SP	The last caudal vertebra displaying a spinous process	Provide muscle attachment sites for basal tail extensor muscle (<i>m. sacrocaudalis dorsalis medialis/extensor caudae medialis</i>); leverage of the tail
sTP	The first caudal vertebra with two pairs of transverse processes	Transverse processes are the main attachment sites for <i>mm. intertransversarii caudae</i> (lateral and dorsoventral flexors, and rotators of the tail); origins of <i>m. sacrocaudalis ventralis lateralis/flexor caudae longus</i> and <i>sacrocaudalis ventralis medialis/flexor caudae brevis</i> (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



the transitional region is demarcated by the longest vertebra (LV), defined as the vertebra with the absolute longest measurable craniocaudal vertebral body length occurring caudal to TV. The caudal vertebrae of the distal region show the same discrete characters as the ones from the transitional region (e.g., transverse processes and metapophyses), but these features are progressively reduced toward

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 metapophyses 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, Pilosa, 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'Elia 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; Thorington 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 previously studied arboreal Primates and 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 & Thorington, 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 carnivorans 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 postsacral 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; Youlatos, 2003) for 10 primate and seven carnivoran 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

TABLE 2 Investigated species of Rodentia (Sciuromorpha), primates and Carnivora sorted alphabetically by family, subfamily and tribe. Species were assigned one of the following three different locomotor categories. (A) Arboreal Sciuromorpha are skilled climbers; mostly forage, shelter and escape in trees. (G) Gliding Sciuromorpha are capable of gliding through the use of a patagium; mostly forage in trees; seldom found on the ground. (S) Semifossorial Sciuromorpha regularly dig to build burrows for shelter, but do not forage underground and do not have a fossorial (subterranean) lifestyle. For the tangent space analyses we further assigned the main habitat to each species being either arboreal (a) or terrestrial (t). Taxonomy, ecology, locomotor category and habitat follow definitions of Nowak and Wilson (1999), Samuels and van Valkenburgh (2008), Thorington and Hoffmann (2005), Wilson et al. (2016) and Wilson and Reeder (2005)

Rodentia (Sciuromorpha)		Primates		Carnivora	
Gliridae	<i>Dryomys nitedula</i> (Aa)	Strepsirrhini		Caniformia	
	<i>Eliomys quercinus</i> (Aa)	Cheirogaleidae	<i>Microcebus murinus</i> (Aa)	Ailuridae	<i>Ailurus fulgens</i> (Aa)
	<i>Glis glis</i> (Aa)	Catarrhini		Procyonidae	
	<i>Graphiurus microtis</i> (Aa)	Cercopithecidae		<i>Bassariscus</i> sp. ^a (Aa)	<i>Procyon</i> sp. ^a (Aa)
	<i>Graphiurus murinus</i> (Aa)	<i>Macaca mulatta</i> (Aa)		Feliformia	
	<i>Muscardinus avellanarius</i> (Aa)	<i>Macaca nemestrina</i> (Aa)		Eupleridae	<i>Cryptoprocta ferox</i> ^a (Aa)
Sciuridae		<i>Nasalis larvatus</i> (Aa)			
Callosciurinae	<i>Callosciurus finlaysonii</i> (Aa)	Platyrrhini		Nandiniidae	<i>Nandinia binotata</i> ^a (Aa)
	<i>Callosciurus notatus</i> (Aa)	Aotidae		Viverridae	
	<i>Callosciurus prevostii</i> (Aa)	<i>Aotus trivirgatus</i> ^a (Aa)		<i>Genetta</i> sp. ^a (Aa)	<i>Paradoxurus</i> sp. ^a (Aa)
	<i>Funambulus pennantii</i> (Aa)	Callitrichidae			
	<i>Rubrisciurus rubriventer</i> (Aa)	<i>Callithrix jacchus</i> (Aa)			
	<i>Tamiops mccllellandii</i> (Aa)	<i>Saguinus oedipus</i> ^a (Aa)			
Ratufinae	<i>Ratufa indica</i> (Aa)				
Sciurinae (Pteromyini)	<i>Glaucomys volans</i> (Ga)	Cebidae	<i>Saimiri boliviensis</i> (Aa)		
	<i>Hylopetes sagitta</i> (Ga)	<i>Saimiri sciureus</i> ^a (Aa)			
	<i>Petaurista petaurista</i> (Ga)				
Sciurinae (Sciurini)	<i>Sciurus anomalus</i> (Aa)	Pitheciidae	<i>Pithecia</i> sp. ^a (Aa)		
	<i>Sciurus vulgaris</i> (Aa)				
Xerinae (Marmotini)	<i>Cynomys ludovicianus</i> (St)				
	<i>Ictidomys tridecemlineatus</i> (St)				
	<i>Marmota marmota</i> (St)				
	<i>Spermophilus dauricus</i> (St)				
	<i>Tamias sibiricus</i> (St)				
Xerinae (Protoxerini)	<i>Paraxerus ochraceus</i> (Aa)				
Xerinae (Xerini)	<i>Atlantoxerus getulus</i> (St)				
	<i>Spermophilopsis leptodactylus</i> (St)				

^aData marked with the footnote refers to data taken from Organ (2010) and Youlatos (2003).

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 Sciuromorpha

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 “sciuriform” 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 macrotis*) 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; Stranding, 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 postsacral 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), $r_s = \pm 0.20$ to ± 0.39 (weak correlation), $r_s = \pm 0.40$ to ± 0.69 (modest correlation), $r_s = \pm 0.70$ to ± 0.89 (strong correlation) and $r_s = \pm 0.90$ 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

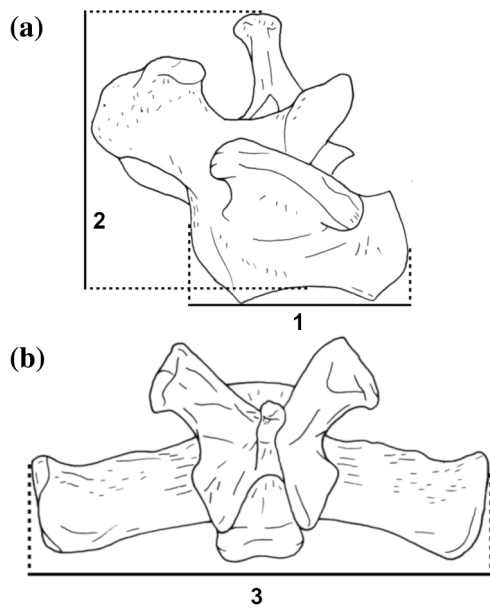


FIGURE 2 Proximal caudal vertebra in lateral (a) and dorsal view (b) with linear measurements taken. (1) VBL—craniocaudal vertebral body length (mm); (2) SPmax—maximum dorsoventral spinous process height (mm); (3) TPBmax—maximum transverse processes breadth (mm)

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 minimize the effect of body size when comparing different species, variables were normalized using the anteroposterior midshaft diameter of the femur as proxy for size, an estimate that is mainly associated with the body mass and only little affected by locomotor style (Wölfer et al., 2019). Although commonly used (Aiello, 1981; Alexander et al., 1979; Biknevicius et al., 1993; Christiansen, 2002; Egi, 2001; Gingerich, 1990; Hopkins, 2008; Reynolds, 2002; Ruff, 1990), femur length was not chosen as proxy for body size, because scaling differences between different locomotor categories have been observed in Sciuromorpha

(Wölfer et al., 2019). Furthermore, we did not use body mass as frequently been done in other studies (Fleagle, 1985; Organ, 2010; Organ et al., 2009; Russo, 2015; Schmidt-Nielsen, 1984; Youlatos, 2003), because intraspecific body mass within Rodentia can vary immensely according to, for example, seasonality (Yang et al., 2014). For consistency and due to its frequency in the collections, the left femur was preferred over the right one. Missing femoral data in two specimens of *S. vulgaris* (SMF 57960 and ZFMK 1984.0008) were replaced by the average anteroposterior femoral midshaft diameter measured on the other nine *S. vulgaris* specimens. The standardized variables (rVBL, rSPmax and rTPBmax) and their respective functional relevance are listed in Table 3. Likewise, the tail length has been standardized using the anteroposterior femoral midshaft diameter (relative tail length; 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” (Lüdtke, 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., $SD \leq 1$) with up to four missing vertebrae. Estimates based on more than four missing caudal vertebrae become 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; Youlatos, 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

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 trans-verse 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			

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 *Graphiurus 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 `gpgen` 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 (ppls) analyses using function “`procD.ppls`” 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.ppls`” 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.pcomp` (`geomorph` 3) functions. Details of these analyses are

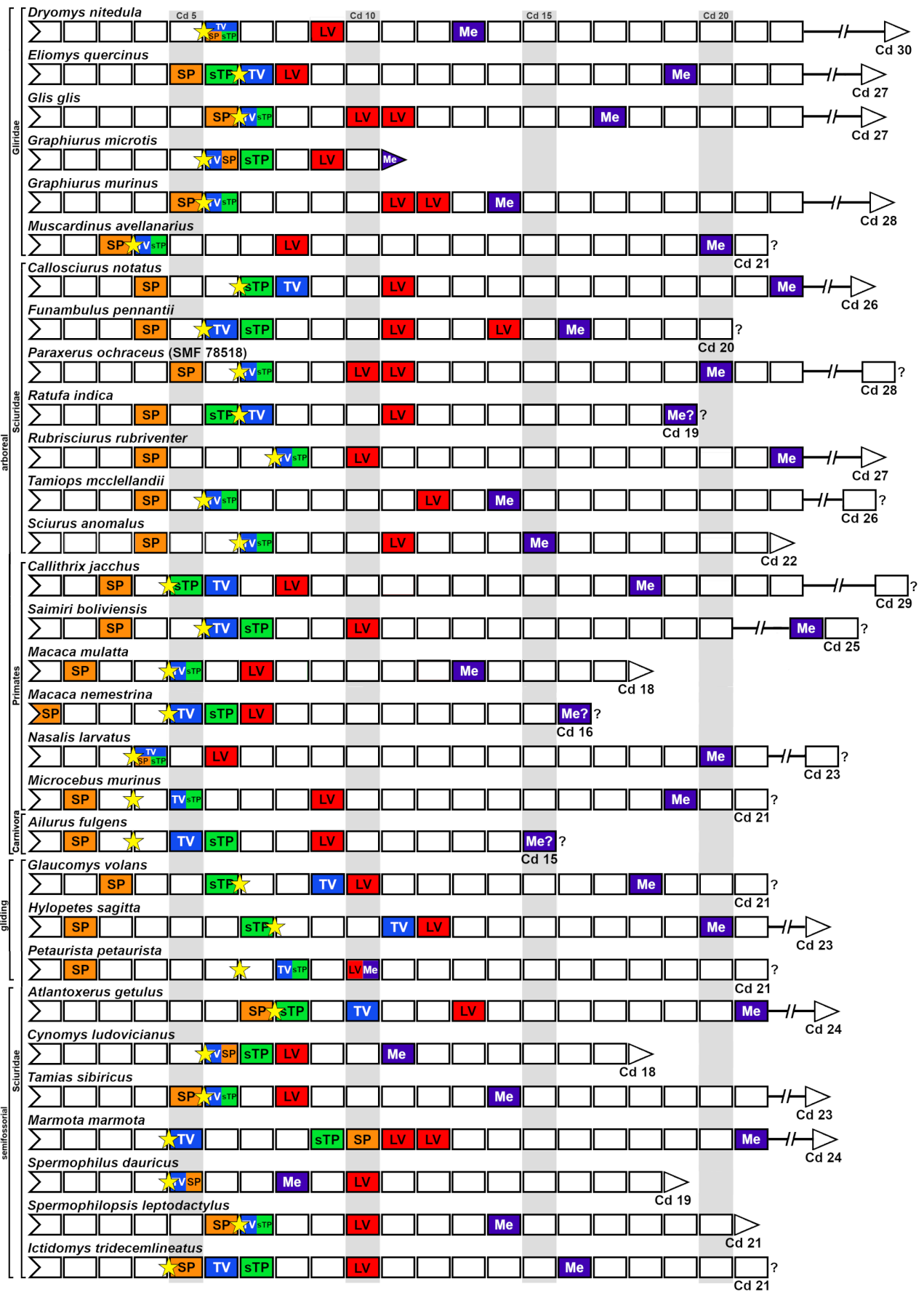


FIGURE 3 Legend on next page.

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 petaurista*, *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* SMF 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 some cases (*Cynomys ludovicianus*, *Spermophilus dauricus*, *Graphiurus murinus*), and is even present on TV together with sTP (split of transverse processes) in *Dryomys nitedula*. Apart from *Atlantoxerus getulus* and *Marmota marmota*, SP is

always located on one of the first six caudal vertebrae of the proximal tail region. Interestingly, *Marmota* is the only species of our sample to show SP positioned caudal to TV (Figure 3). The placement of TV is rather consistent throughout all tails and often overlaps in position with sTP. The last contact between pre- and postzygapophysis (yellow star) always appears proximal to TV. In 42 out of 45 rodent and primate specimens (93.3%), the last zygapophyseal contact can be found between TV and the penultimate vertebra of the proximal region, or between the penultimate and antepenultimate vertebrae of that region. However, in the gliding small flying squirrels *Glaucomys* and *Hylopetes* and the semifossorial *Atlantoxerus*, TV is positioned more caudally than in any other species. The occurrence of sTP is rather consistently located on the 6th to the 8th caudal vertebra (exceptions: *Muscardinus avellanarius*, *Nasalis* (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

FIGURE 3 Osteological tail anatomy of arboreal and gliding Sciuromorpha studied. Specimens were sorted by locomotor category and family in alphabetical order. For the osteological anatomy of specimens not displayed here refer to Table S2. Each box represents a single caudal vertebra from the root (left) to the tip (right) of the tail. A triangle at the end of a caudal series represents a complete tail series, while a question mark indicates the absence of an unknown number of distalmost caudal vertebrae. The boxes are not to scale and the figures serve morphological comparisons only. Characters defined in Figure 1 and Table 1 were marked on the respective vertebra on which they have been found

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 significant 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 carnivora 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

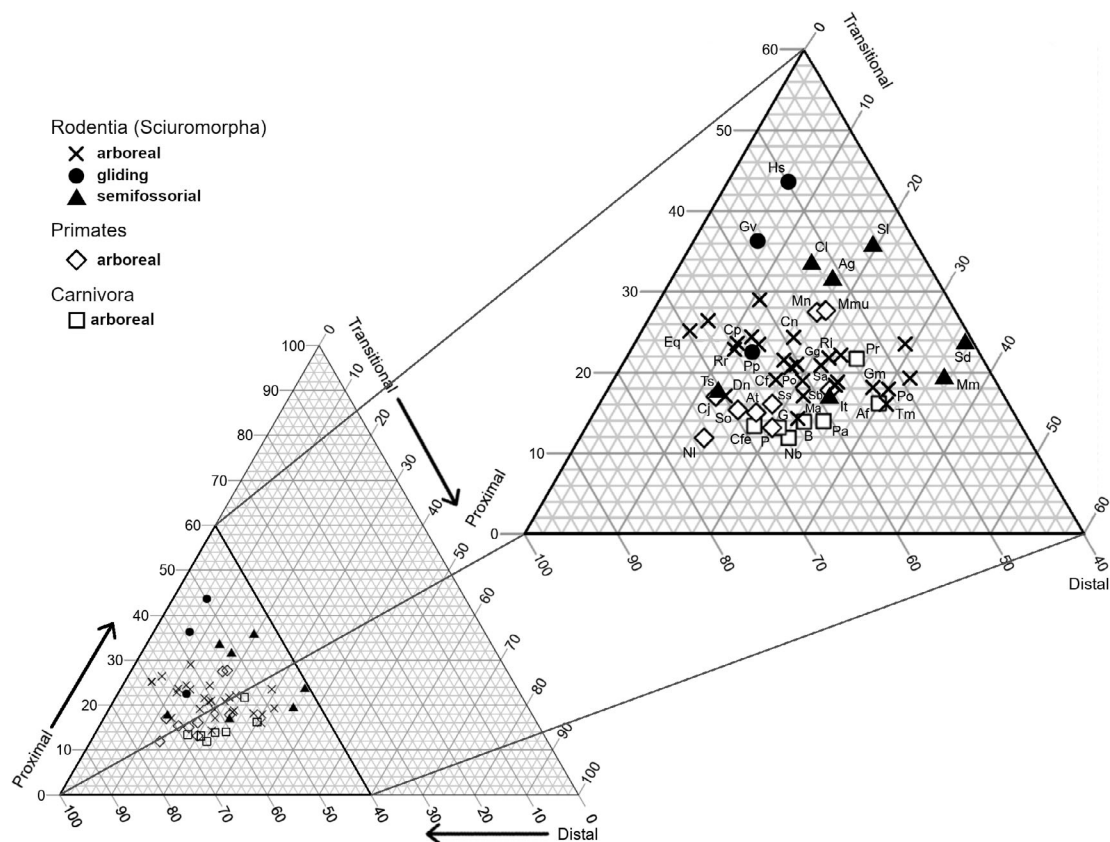


FIGURE 4 Ternary plot of the proportion of each tail regions length (proximal, transitional and distal) in tails of arboreal, gliding and semifossorial sciuriform rodents (except *Funambulus pennantii* and *Graphiurus microtis*), arboreal Primates (except *Microcebus murinus*), also including data from literature (Organ, 2010), as well as data of arboreal Carnivora from the literature (Youlatos, 2003). Abbreviations: **Rodentia**; Dn, *Dryomys nitedula*; Eq, *Eliomys quercinus*; Gg, *Glis glis*; Gm, *Graphiurus murinus*; Ma, *Muscardinus avellanarius*; Ag, *Atlantoxerus getulus*; Cf, *Callosciurus finlaysonii*; Cn, *Callosciurus notatus*; Cp, *Callosciurus 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, *Rubrisciurus rubriventer*; Sa, *Sciurus anomalus*; 11 *Sciurus vulgaris* specimens were not assigned an ID for reasons of clarity in the diagram; Sl, *Spermophilopsis leptodactylus*; Sd, *Spermophilus dauricus*; Ts, *Tamias sibiricus*; Tm, *Tamiops mccllellandii*; **Primates**; At, *Aotus trivirgatus*; Cj, *Callithrix jacchus*; So, *Saguinus oedipus*; Sb, *Saimiri boliviensis*; Ss, *Saimiri sciureus*; Mmu, *Macaca mulatta*; Mn, *Macaca nemestrina*; Ni, *Nasalis larvatus*; P, *Pithecia* sp.; **Carnivora**; Af, *Ailurus fulgens*; B, *Bassariscus* sp.; Pr, *Procyon* sp.; Cfe, *Cryptoprocta ferox*; G, *Genetta* sp.; Nb, *Nandinia binotata*; Pa, *Paradoxurus* sp

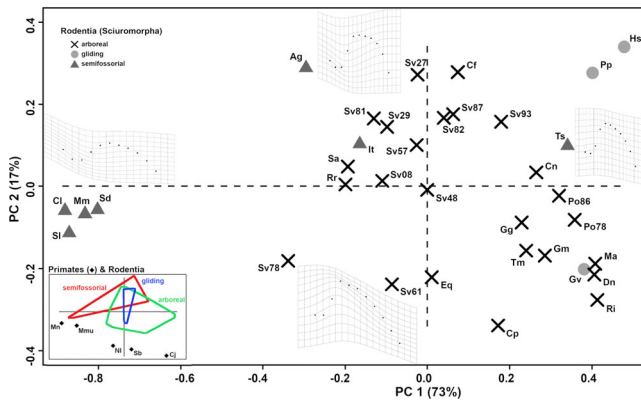


FIGURE 5 Tangent space analysis of the length progressions in sciromorph caudal series for the variable rVBL. Since only one Carnivora (*Ailurus fulgens*) was available, we excluded the whole order from this analysis. Inset: Tangent space analysis including rodents and all measured primates (refer to Table S2, sheet Tangent Spaces with Primates for a more detailed graph). The polarity of the PC 1 axis is inverted. 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*; Gm, *Graphiurus murinus*; Ma, *Muscardinus avellanarius*; Ag, *Atlantoxerus getulus*; Cf, *Callosciurus finlaysonii*; Cn, *Callosciurus notatus*; Cp, *Callosciurus prevostii*; Cl, *Cynomys ludovicianus*; Gv, *Glaucomys volans*; Hs, *Hylopetes 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, *Sciurus anomalus*; Sv48, *Sciurus vulgaris* (SMF 48690); Sv57, *S. vulgaris* (SMF 57960); Sv78, *S. vulgaris* (SMF 78868); 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 leptodactylus*; Sd, *Spermophilus dauricus*; Ts, *Tamias sibiricus*; Tm, *Tamiops mccllellandii*; **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* ($r_s = 0.81/p = .07$), 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 ($r_s \geq 0.90/p \leq 0.3$) 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

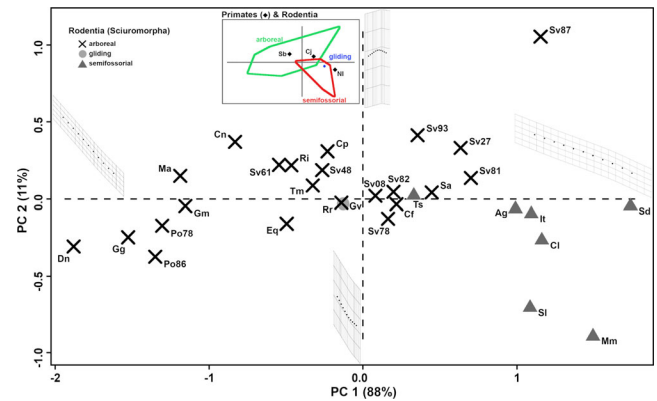


FIGURE 6 Tangent space analysis of the length progressions in sciromorph caudal series for the variable rSPmax. It includes all rodents (except *Hylopetes*, *Petaurista*, and four *Sciurus vulgaris* specimens [SMF 48690, SMF 57960, ZFMK MAM 2004.0029, and ZFMK MAM 2005.0382]). Inset: tangent space analysis 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 inverted. 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*; Gm, *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, *Sciurus anomalus*; Sv78, *S. vulgaris* (SMF 78868); Sv87, *S. vulgaris* (SMF87580); Sv93, *S. vulgaris* (SMF 93777); Sv08, *S. vulgaris* (ZFMK MAM 1984.0008); Sv27, *S. vulgaris* (ZFMK MAM 2004.0027); Sv61, *S. vulgaris* (ZFMK MAM 2004.0061); Sv81, *S. vulgaris* (ZFMK MAM 2005.0381); Sv82, *S. vulgaris* (ZFMK MAM 2005.0382); Sl, *Spermophilopsis leptodactylus*; Sd, *Spermophilus dauricus*; Ts, *Tamias sibiricus*; Tm, *Tamiops mccllellandii*; **Primates**; Cj, *Callithrix jacchus*; Sb, *Saimiri boliviensis*; NI, *Nasalis larvatus*

(Figure 4 and Supporting Information, Table S2, sheet Tail Region Proportion Analyses). Arboreal Sciromorpha are grouped closely with the arboreal Primates and Carnivora. However, primate and carnivoran species show tendencies toward a shorter proximal region than the rodents under study. Among the gliding squirrels *Petaurista* plots within the arboreal sciurids/gliroids point cloud, whereas *Glaucomys* and *Hylopetes* are segregated from this cloud, displaying the longest proximal region (except for *Spermophilopsis leptodactylus*) 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 *Hylopetes*), primate and carnivoran species by their proportionally shortest distal region (40.97%–52.5%). Among these five semifossorial species *Marmota* and *Spermophilus* can be further

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* (Sl), *Spermophilus* (Sd), and all Gliridae, are the only ones to occupy the area with high negative PC 1 and moderate negative PC 2 values of 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 *Petaurista* (Pp) and *Hylopetes* (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* (Sl) 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 sciuriforms. 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 glirid species are found in the positive PC1 and negative PC2 quadrant, along with the arboreal sciurid species *P. ochraceus* (Po78, Po86), *Tamiops mccllellandii* (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 sciurid 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 sciurid genus *Callosciurus* (*C. finlaysonii*, *C. notatus*, *C. prevostii*) are widely separated along PC 2, but not along PC 1.

Sciuriforms 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 ($\kappa = 0.21$; $p = .001$). 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 Sciuriforms (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 sciuriforms 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 Sciuriforms (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 gliroids *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 semifossorial species, *Marmota* (Mm), show positive PC 2 values. *Tamias* (Ts) and *Marmota* (Mm) are separated from the other semifossorial species and their shape coordinates are rather dispersed. Most semifossorial species (*Atlantoxerus* (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 *Hylopetes* (Hs) are found close to the arboreal gliroid species, *Petaurista* (Pp) plots with the main group of semifossorial 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 ($\kappa = 0.35$; $p = .001$). 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 rSPmax 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 causes again 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 platyrrhine primates (i.e., New World monkeys) *Callithrix* and *Saimiri* plot among the sciuiromorph 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 sciuiromorph rodents, (b) the comparison of distribution patterns of key osteological features with those in arboreal primates 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 Sciuiromorpha.

4.1 | Intraspecific variability

Before drawing conclusions about the interspecific differences in tail morphology among Sciuiromorpha, 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 sciuiromorph Rodentia, morphofunctional parameters taken from a single specimen are sufficient to stand in for the entire species.

4.2 | Tail anatomy in Sciuiromorpha

Overall, we confirm that the same osteological tail characters and tail patterns are present within our sciuiromorph sample, irrespective of their relative tail length and locomotor category. However, among our sample two exceptions were evident. The semifossorial marmotines *Marmota* and *Spermophilus* are the only species with anatomical tail patterns that deviate from the other sciurid and gliroid 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 sciuiromorph 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 interspinales 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 zygapophyseal 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 sciuiromorph 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. Likewise, behavioral studies focusing on the usage of 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 eutherian 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 plesiomorphic 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. Catharrhini (*Macaca* species, *Nasalis*) can be separated from the Platyrrhini (*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 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 sciurids and arboreal glirids, that differ in their bias angle of the semicircular canals, which detect angular acceleration of the head. These arboreal sciurids 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 *Hylopetes* 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 manoeuvrability.” Despite this added wing surface, the wing loading of *Petaurista* is still high (about 81 N/m²; Andō & Shiraishi, 1993) and makes it less agile than smaller gliders (Andō & 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 (Andō & 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 *Hylopetes* 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 locomotory 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 sciuriforms. 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 Sciuromorpha. 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 *Spermophilopsis* 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 Sciuromorpha 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 sciuriform 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 high 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 sciuriforms. 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 sciuriform rodents under study.

It has been observed that some semifossorial sciuriforms (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 sciuriforms (or ground squirrels; e.g., *Ictidomys*) do not climb trees, yet show an “arboreal tail pattern” in our analyses. Therefore, following Emry and

Thorington (1984), ground squirrels should not be defined by their inability to climb trees, but rather by their ability to dig and use burrows.

Our study focused on differences between taxa using broad locomotor categories within the Sciuromorpha. Yet it has been observed that postural and behavioral differences can be observed within arboreal squirrels (e.g., Youlatos, 1999; Youlatos et al., 2015; Youlatos & Samaras, 2011). These differences may be correlated to body-size, since small-bodied squirrels tend to use clawed locomotion on various vertical supports from the lower parts of the canopy to the ground, whereas larger squirrels engage more frequently in quadrupedal walk and leaping, and use mainly small horizontal supports (Stafford et al., 2003; Thorington & Thorington, 1989; Youlatos, 1999; Youlatos & Samaras, 2011). Detailed positional behavior studies for our sampled taxa being scarce, we could only tentatively test for a signal based on their general body-size. The smaller-sized animals in our sample (*Dryomys*, *Eliomys*, *Glaucomyss*, *Glis*, *Graphiurus*, *Hylopetes*, *Muscardinus*, *Paraxerus*, *Tamias*, *Tamiops*) indeed seem to be clustered in the tangent space analyses, but the larger-sized rodents, for example, *Cynomys*, *Marmota*, *Petaurista*, *Ratufa*, are not. Hence, it is more cautious to wait until more detailed observations on the positional behavior of our taxa are available, before drawing any conclusions based on their tail anatomy.

Finally, our study has shown that, while the overall anatomy of the tail in arboreal, gliding and semifossorial sciuromorphs follows a relatively stable pattern, differences are visible at the morphometrical level. This raises questions about the mechanisms involved and how fast tails can adapt to a different ecological niche (i.e., arboreal vs. semifossorial). Byron et al. (2011) studied the behavior and anatomical changes in living laboratory mice (*Mus musculus*). Mice were kept in a terrarium where they were forced to permanently climb, with no horizontal ground to walk on. At maturity “climbing” mice and control mice showed minor, but significant skeletal plasticity. Among other features, the “climbing” mice exhibited relatively longer transverse processes in the caudal vertebrae that is probably linked to the higher amount of balancing and grasping they had to perform with their tail while moving in the branches (Byron et al., 2011). This study shows that in Rodentia anatomical features of the tail can adapt relatively fast to environmental constraints. Moreover, it shows that the transverse processes are impacted significantly. Remarkably, in our study semifossorial species differ significantly from arboreal ones for the progression of their relative maximum transverse processes breadth (rTPBmax): semifossorial taxa have a positive PC 2 value (i.e., their transverse processes first become broader before getting narrower), whereas most arboreal taxa have negative PC 2 scores (i.e., continuously decreasing transverse process' breadth). Since transverse processes are the sites of attachment for muscles and ligaments responsible for the lateral and dorsoventral movement as well as the rotation of the tail (see Table 1), it stands to reason to assume that the different osteological patterns observed in semifossorial and arboreal taxa also involve myologic differences. Comparison of the gross anatomy of these rodents' tail would help identifying, which muscles (and thereby function) is affected the most by each pattern. It might

also be interesting to test experimentally, whether the breadth of the transverse processes in semifossorial Marmotini exposed from weaning to adulthood to an environment that require them to climb, would follow the regulatory decreasing pattern seen in climbing Sciuromorpha.

Genetic expression is another, deeper mechanism linked to the change in anatomical characters in the tail. Here too, many more genetic studies dealing with the vertebral column focused on the pre-sacral series rather than the postsacral series (Buchholtz & Stepien, 2009; Burke et al., 1995). However, Burke et al. (1995) showed that tail length in mice is regulated by the expression of paralog group Hoxd13 gene. Another study by Economides et al. (2003) observed that the loss of function of Hoxb13 causes an overgrowth of tail vertebrae. Rashid and Chapman (2021) discussed the trunk-to-tail boundaries in different amniotes and the underlying mechanisms for tail length. They concluded that many aspects of tail evolution and its developmental processes still need to be studied. Unfortunately, none of these studies offers a detailed description of the postsacral anatomical characters, which were used in our study. It would be interesting to compare the position (or loss) of the tail characters and the vertebral body length progression in genetically altered sciuromorphs with the wild types from the present study.

5 | CONCLUSIONS

The present study was a first excursion outside of the orders Primates and Carnivora in the analysis of a neglected yet complex organ: the tail. We verified the applicability of the tail characters and regionalization as defined for arboreal Primates and Carnivora, and observed the overall similar osteological tail anatomy and patterns within Sciuromorpha irrespective of locomotor category. But, this still needs to be tested for other rodents, especially for less arboreal species. Within Rodentia, taxa with a reduced tail (e.g., Caviomorpha) should be of particular interest, since it is not known which tail characters are still present and which regions of the tail become reduced. This could be linked to the aforementioned genetic studies showing tail reduction, as well as to developmental studies, using embryos.

Our morphometric methods (i.e., region proportion analysis on VBL and tangent space analyses on rVBL) enable distinctions between arboreal and semifossorial sciuromorph rodents. Likewise, a very short transitional region separates the flying squirrels from other Sciuromorpha in our sample. Furthermore, within the flying squirrels, the phylogenetically more basal giant flying squirrel *Petaurista* seems to have kept the plesiomorphic tail pattern of arboreal sciurids, whereas the small flying squirrels *Glaucomyss* and *Hylopetes* display modifications, especially in the proportions of their tail regions.

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); methodology (equal); 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); validation (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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