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RESEARCH PAPER

Ecomorphological characteristics of Afroalpine rodent communities

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Abstract. Rodents comprise around half of all mammalian species, showcasing their remarkable adaptability to thrive in almost all terrestrial habitats. Their evolutionary success is exemplified by a wide range of morphological features reflecting various feeding and locomotory adaptations. This study examines the functional variation in cranial and mandibular traits as well as locomotion indices in rodent communities within the high-altitude Afroalpine environment of the Ethiopian Highlands. The findings reveal two distinct patterns in cranial and mandibular traits. One pattern is associated with dietary differences, distinguishing the primarily herbivorous species *Otomys helleri*, *Arvicanthis abyssinicus* and *Lophuromys melanonyx*, which are characterised by relatively long molar rows, massive mandibles, and likely enhanced bite force, from the generally omnivorous genus *Stenocephalemys* and the more faunivorous *Lophuromys flavopunctatus*. The second pattern indicates that species in the Afroalpine ecosystem have adapted to life in distinct habitats across different elevational zones. Species from the highest elevational zones within the genera *Stenocephalemys* and *Lophuromys* exhibit convergent morphological adaptations for life in open habitats, characterised by their larger size, narrower interorbital constriction, and larger orbits. Regarding locomotion, our study emphasises the unique morphology of *Otomys*, which is characterised by equally long forelimbs and hindlimbs. This corresponds to its predominant fast quadrupedal running. In contrast, *Stenocephalemys* species are likely to rely more on saltatory locomotion. Among them, the forest-dwelling *S. albipes* likely demonstrates the most advanced form of this locomotory style. The study highlights significant functional diversification in rodent assemblages from the Ethiopian Highlands, primarily driven by foraging and locomotor ecologies. This morphological variation has likely contributed to shaping the rich rodent communities integral to the Eastern Afromontane Biodiversity Hotspot, globally recognized for its significance in mammal endemism.

Key words: skull, mandible, foraging ecology, locomotion, mammals, Ethiopian Highlands, rodents

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Introduction

Rodents represent almost half of the extant mammalian diversity, making them the largest group of mammals. Their remarkable adaptability to various niches allows them to inhabit virtually all terrestrial habitats. Rodents possess unique autapomorphic morphological features that distinguish them from other mammal groups (e.g. Cox & Hautier 2015). These features include continuously growing chisel-like incisors with enamel restricted to their anterior face, complex cranial musculature, a long diastema between the incisors and cheek teeth and many other characters defined mainly on the skull (e.g. Samuels 2009, Hautier et al. 2012, Hedrick et al. 2020). The evolutionary success of rodents can be attributed to acquiring these key evolutionary novelties (Cox & Hautier 2015).

The high degree of ecomorphological diversification of rodents is exemplified by their wide range of feeding, locomotory, and behavioural adaptations. Among them, the most prominent are those related to craniodental morphology. Rodents employ chisel-like incisors for various tasks, such as collecting vegetation, capturing and cutting prey, territorial behaviour, and digging shelters (e.g. Samuels 2009, Rodrigues et al. 2023). The shape and size of the incisors, as well as the molariform cheek teeth of rodents, reflect differences in feeding ecologies. Herbivorous rodents possess deeper, longer, and mesodistally broader incisors than faunivorous rodents (e.g. Croft et al. 2011, Martin et al. 2016). Additionally, they have longer maxillary tooth rows, deeper molars, blunter posteriorly angled cusps, and more expanded laterally oriented occlusal cusps (e.g. Samuels 2009, Verde Arregoitia et al. 2017, Grossnickle 2020). Fossorial rodents have short, flat, deep, and broad skulls compared to epigeic rodents. In many of these rodents, their highly procumbent and strengthened incisors serve as a powerful digging tool (reviewed in Rodrigues et al. 2023).

Another example is the elevation-related functional differentiation of rodent skull and mandible. Research has shown that highland species in the Ethiopian Highlands and the Rwenzori Mountains have a narrower interorbital constriction and a prolonged rostrum compared to their mid- and low-elevation counterparts (Peterhans et al. 1988, Mizerovská et al. 2023). Modifications to the orbits and insertion areas of masticatory muscles suggest an adaptive shift towards living in open Afroalpine habitats, where intense selection pressure facilitates rapid morphological evolution (Šumbera et al. 2018, Mizerovská et al. 2023). The shift from closed, typically forested habitats to more open ones may lead to notable morphological changes in mammals. This phenomenon has been observed in rodents and lagomorphs during the Cenozoic environmental transition to a more open landscape in North America (Samuels & Hopkins 2017).

Locomotion is another fundamental functional capacity of mammals. Rodents exhibit a wide range of locomotion modes, including fossorial, aquatic, scansorial, arboreal, gliding, and saltatorial forms (Samuels & Van Valkenburgh 2008). These modes possess adaptive modifications of the postcranial skeleton (e.g. Howel 1965, Hildebrand et al. 1985, Carvalho Coutinho & Alves de Oliveira 2017). For example, a study of ten species of caviomorph rodents found differences in functional indices, indicating functional differentiation for speed and force during the transition from cursorial to digging forms (Elissamburu & Vizcaíno 2004). Arboreal rodents have relatively longer humeri and digits and equally proportioned fore and hind limbs, whereas saltatory rodents display disproportionate limbs, longer tibiae, and hind feet (Samuels & Van Valkenburgh 2008). Functional adjustments of femoral traits reflect the evolutionary transition from the ancestral arboreal form to fossorial and gliding behaviour in sciuromorph rodents (Wölfer et al. 2019).

The interplay between morphology and species ecology has mainly been studied on a broader scale, including multiple taxa from either rodent subfamilies, the entire order (e.g. Carvalho Coutinho & Alves de Oliveira 2017, Samuels 2009) or even multiple vertebrate groups (e.g. Grossnickle 2020). However, much less attention has been devoted to investigating the ecomorphological structure of local communities. For instance, Pounds (1988) studied the *Anolis* community from Costa Rica, Onditi et al. (2022) examined the small mammals of Mt. Kenya and Villalobos-Chaves & Santana (2022) Neotropical free-tailed bats. This study focuses on the ecomorphology of rodent communities inhabiting a specific environment of the high-elevation Afroalpine ecosystem in the Ethiopian Highlands.

The Afroalpine ecosystem spans an altitude range of 3,200 to 4,620 meters above sea level (a.s.l.) and is widespread in Ethiopia, encompassing approximately 73% of the sub-Saharan region above 3,200 m a.s.l. (Williams et al. 2004). It is characterised by a mosaic structure, predominantly composed of open

grasslands and moorlands, occasionally interspersed with shrublands of tree heaths (*Erica*) (e.g. Fetene et al. 2006, Asefa et al. 2020). The considerable expanse of this ecosystem, coupled with climatic changes during the Pleistocene, has contributed significantly to the evolution of a remarkably diverse and unique range of flora and fauna, particularly among mammals and amphibians (Williams et al. 2004, Lavrenchenko & Bekele 2017, Bryja et al. 2019b). The Ethiopian Afroalpine ecosystem is home to diverse rodent genera, including narrow-headed rats (*Stenocephalemys*), brush furred rats (*Lophuromys*), grass rats (*Arvicanthis*), African vlei rats (*Otomys*), and African root-rats (*Tachyoryctes*) (Šumbera et al. 2018, Bryja et al. 2019b, Mizerovská et al. 2020, 2023). Importantly, rodents play a crucial role in maintaining the structural integrity and natural functioning of the Afroalpine ecosystem (e.g. Sillero-Zubiri et al. 1995, Šklíba et al. 2017, Atickem & Stenseth 2022). Therefore, investigating ecomorphological adaptations is essential to comprehend the mechanisms that facilitate the coexistence of such diverse rodent communities in this ecosystem.

This study aimed to investigate the functional variation in cranial and mandibular traits and locomotion indices within rodent communities in the high-altitude Afroalpine environment of the Ethiopian Highlands. The aim was to understand how the Afroalpine rodent communities are structured from an ecomorphological perspective. Multivariate analyses and analyses of variance were used to identify independent patterns in the studied morphospace reflecting differences in species ecologies. We hypothesise that within Afroalpine rodent communities, genera/species with more similar foraging ecology and/or locomotion patterns will be closer to each other within the given morphospace. We predict that the shape of the skull and mandible would reflect 1) the biomechanical consequences of higher bite force in herbivorous species compared to omnivorous and/or insectivorous ones (e.g. Verde Arregoitia et al. 2017, Grossnickle 2020) and 2) the adaptation to life in different habitats within the Afroalpine ecosystem – rodents living in open grasslands and moorlands will be characterized by a narrower interorbital constriction and larger orbits than those from the Ericaceous belt, which reflects their need for better and faster detection of predators in open habitats (Peterhans et al. 1998, Beolchini & Corti 2004, Mizerovská et al. 2023). In relation to locomotion, differences in locomotory indices will reflect the predominant locomotory modes in studied rodents, specifically differences between quadrupedal hopping and running locomotion types (Samuels & VanValkenburgh 2008).

Material and Methods

Study area
Rodents were collected from five mountain massifs in Ethiopia: four located west of the Great Rift Valley (Aboye Gara, Borena Saynt, Mt. Choqa, and Guassa Community Conservation Area, hereafter referred to as Guassa) and one located east of the Rift (Bale Mountains). The five sites are covered by Afroalpine habitats at high elevations (above 3,000 m a.s.l.). Additionally, an Afromontane Ericaceous belt occurs in transitional elevation zones, while various types of forests are found at lower elevations (Fig. 1, see Lillesø et al. 2011, Bryja et al. 2019b for further details).

The five mountain massifs are situated in the Eastern Afromontane Biodiversity Hotspot, which extends from Ethiopia's highlands in the north to Mozambique in the south (Mittermeier et al. 2004, CEPF 2012). This hotspot is primarily composed of high-altitude plateaus and isolated mountain peaks and exhibits notable levels of species endemism. For example, approximately 21% of the approximately 490 mammalian species discovered in this hotspot are endemic (CEPF 2012).

Taxon sampling
The study analysed 138 individuals from the following ten species across four rodent genera. For details about the capturing sites, altitude range, number of captured females and males, mean body mass, and mean standard body measurements, refer to Table 1. Five out of the six species from the genus *Stenocephalemys* were included: white-tailed Ethiopian rat *S. albocaudatus*, Zima's Ethiopian rat *S. zimai*, Sokolov's Ethiopian rat *S. sokolovi*, gray-tailed Ethiopian rat *S. griseicauda*, and white-footed Ethiopian rat *S. albipes*. All species are nocturnal and considered predominantly herbivorous, with 80% plant matter in their diet (information available for *S. albipes* only, Bantihun & Bekele 2015). *Stenocephalemys albipes* is the smallest and most widespread species of the genus. It prefers forest types at lower elevations (Bryja et al. 2019b). *Stenocephalemys albocaudatus* is the largest species of the genus (Mizerovská et al. 2020) and highly specialised for life in open Afroalpine grasslands in Bale and Arsi Mountains and Guassa (3,000-4,500 m a.s.l.). *Stenocephalemys griseicauda* is only found on the eastern side of the Rift Valley in the Bale and Arsi Mountains at 3,000-3,800 m a.s.l., where it inhabits mainly *Erica* shrublands. *Stenocephalemys*
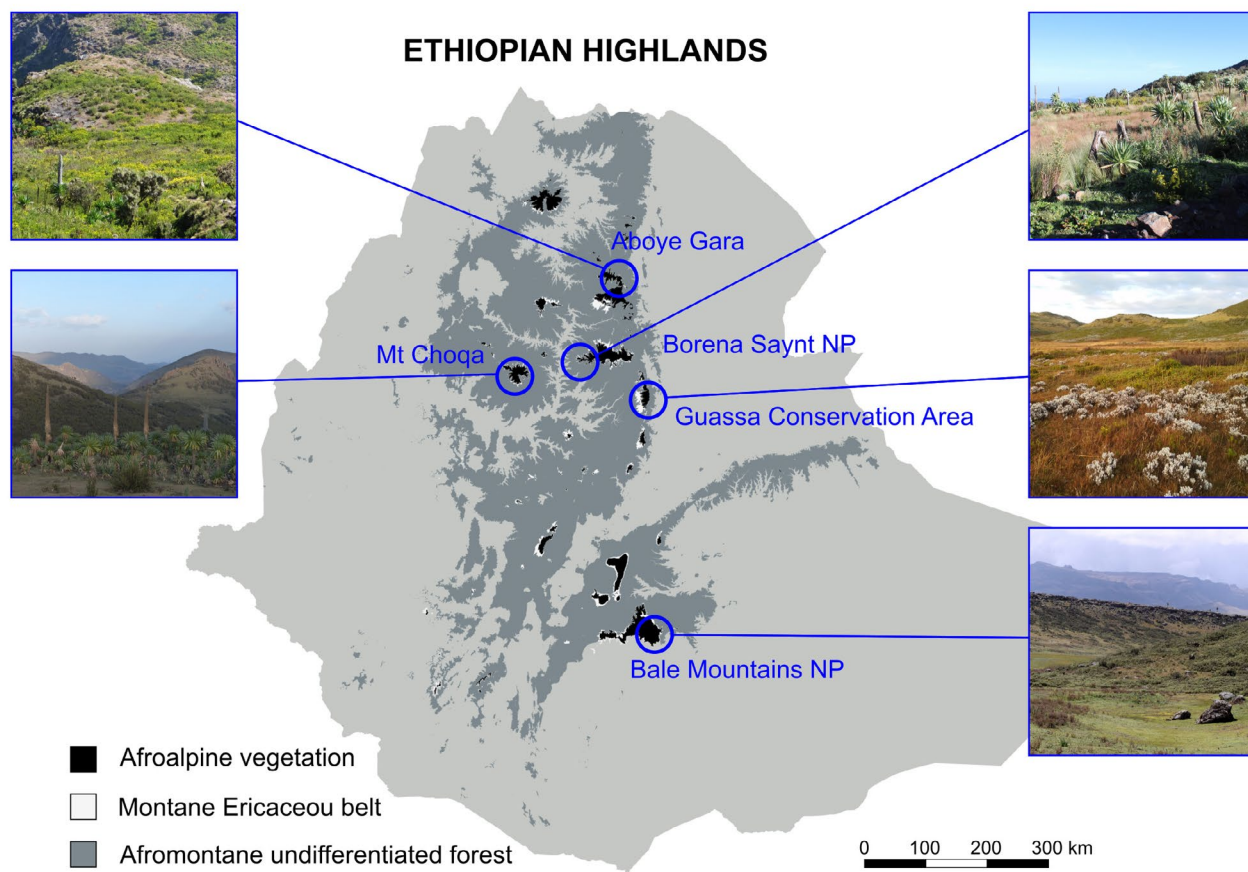
Fig. 1. Map showing sampling localities (depicted as blue circles) in the Ethiopian Highlands where rodents were captured for this study. Each photo shows a typical habitat found in a particular locality.

zimai is an Afroalpine specialist that inhabits moorland and grassland habitats (3,600-4,000 m a.s.l.) in the northern part of the Highlands (Bryja et al. 2019b, Mizerovská et al. 2020). *Stenocephalemys sokolovi* inhabits grasslands and mosaic Afroalpine habitats with *Erica* shrubs in the western part of the Rift Valley (Mizerovská et al. 2020). *Arvicanthis abyssinicus* is a diurnal (100% of captures by the end of the daylight phase, Lövy et al. 2023), exclusively herbivorous species (Wilson et al. 2017) adapted to high-elevation open habitats (Bryja et al. 2019a, b). The Heller's vlei rat *Otomys helleri* is a true herbivore with prevailing diurnal activity (80% of captures occurring by the end of the daylight phase, Lövy et al. 2023). The last three species belong to the genus *Lophuromys*. The buff-spotted brush-furred rat *L. flavopunctatus* inhabits elevations from 2,600 to 3,300 m a.s.l. in central Ethiopia (Komarova et al. 2021). It is primarily diurnal (71%, Lövy et al. 2023) and likely omnivorous with a prevailing invertebrate diet (38% and 52% plant matter in the diet during the wet and dry season, respectively: Bantihun & Bekele 2015). The black-clawed brush-furred rat *Lophuromys melanonyx* is a highland diurnal, primarily herbivorous (98 [95-100]% plant matter in diet: Yalden & Largen 1992)

that inhabits Afroalpine moorland above 3,200 m a.s.l. in Bale Mts. (Wilson et al. 2017). The Simien brush-furred rat *Lophuromys simensis* is mostly found at higher elevations above 3,000 m a.s.l. but has also been captured at 1,800 m a.s.l. (see Bryja et al. 2019b) and its biology is largely unknown. As *L. simensis* skulls were not available for this study, the species was only included in the analyses of long bones (see below). Our sampling does not cover all species that comprise the Afroalpine rodent communities at the study sites. Some species, such as the genera *Dendromus*, *Megadendromus*, and some *Otomys* species, are relatively rare. Trapping success depends on the season or the type of traps used. Finally, no truly fossorial species from the genus *Tachyoryctes* were included in the study due to their distinct morphology reflecting their fossorial life, in contrast to the species analysed, which exhibit regular surface activity.

To summarise, the species included in the study primarily inhabit open Afroalpine grassland habitats, with some also found in neighbouring ericaceous vegetation. For comparison, we included a single forest species, *S. albipes*. The species of the individuals were

Table 1. Capture sites, the number of captured animals, and their mean body mass for nine species of Ethiopian rodents were used for this morphological study of craniodental and long bone morphology.

| Species	Locality	Altitude (m a.s.l.)	Sex (F, M)	Body mass (g)	LC (mm)	LCd (mm)	LTp (mm)	LA (mm)
Stenocephalemys albipes	Bale Mts.	2,123-3,203	3, 4	39 ± 8	121.6 ± 8.3	153.3 ± 10.1	26.6 ± 1.1	22.3 ± 1.2
Stenocephalemys albocaudatus	Bale Mts.	3,524-4,134	10, 2	130 ± 17	163.8 ± 11.1	139.1 ± 7.0	32.3 ± 0.8	26.8 ± 1.4
	Guassa	3,273-3,350	10, 8	106 ± 22	153.4 ± 14.6	134.7 ± 16.8	30.8 ± 1.4	25.8 ± 2.0
Stenocephalemys griseicauda	Bale Mts.	3,608	1, 2	93 ± 13	142.7 ± 11.0	135.3 ± 7.6	27.4 ± 0.3	23.4 ± 0.6
Stenocephalemys sokolovi	Guassa	3,315-3,375	5, 8	71 ± 15	136.1 ± 10.2	143.3 ± 7.5	27.3 ± 1.0	22.1 ± 1.1
Stenocephalemys zimai	Mt. Choqa	3,421-3,780	4, 0	91 ± 15	152.3 ± 7.2	139.5 ± 5.9	28.3 ± 1.0	27.0 ± 2.5
	Aboye gara	3,533-3,783	2, 3	105 ± 12	154.2 ± 12.6	122.2 ± 10.2	26.5 ± 1.3	26.1 ± 2.3
Arvicanthis abyssinicus	Mt. Choqa	3,780	1, 3	108 ± 21	160.8 ± 11.1	101.3 ± 13.1	28.1 ± 0.8	21.4 ± 1.4
	Aboye Gara	3,783	1, 0	99	148.0	102	26.6	20.6
	Guassa	3,298-3,319	3, 4	100 ± 18	146.8 ± 8.8	95.7 ± 7.3	27.9 ± 0.8	17.1 ± 0.9
Otomys helleri	Aboye Gara	3,783	0, 1	120	166.0	84	21.7	21.8
	Guassa	3,294-3,361	9, 6	105 ± 27	153.9 ± 14.3	79.0 ± 7.9	25.6 ± 1.3	21.3 ± 1.3
	Borena Saynt	3,273	1, 2	153 ± 12	166.0 ± 13.5	79.3 ± 5.0	27.5 ± 1.4	24.0 ± 2.0
Lophuromys flavopunctatus	Guassa	3,310-3,362	12, 13	57 ± 8	123.0 ± 7.0	60.0 ± 6.0	21.1 ± 0.6	17.3 ± 0.7
Lophuromys melanonyx	Bale Mts.	3,524	2, 5	101 ± 14	NA	NA	NA	NA
Lophuromys simensis	Aboye Gara	3,783	0, 2	68 ± 7	126.5 ± 0.7	68.3 ± 6.0	22.8 ± 2.5	17.6 ± 0.8
	Borena Saynt	3,273	1, 0	76	127.0	64.0	20.6	19.1
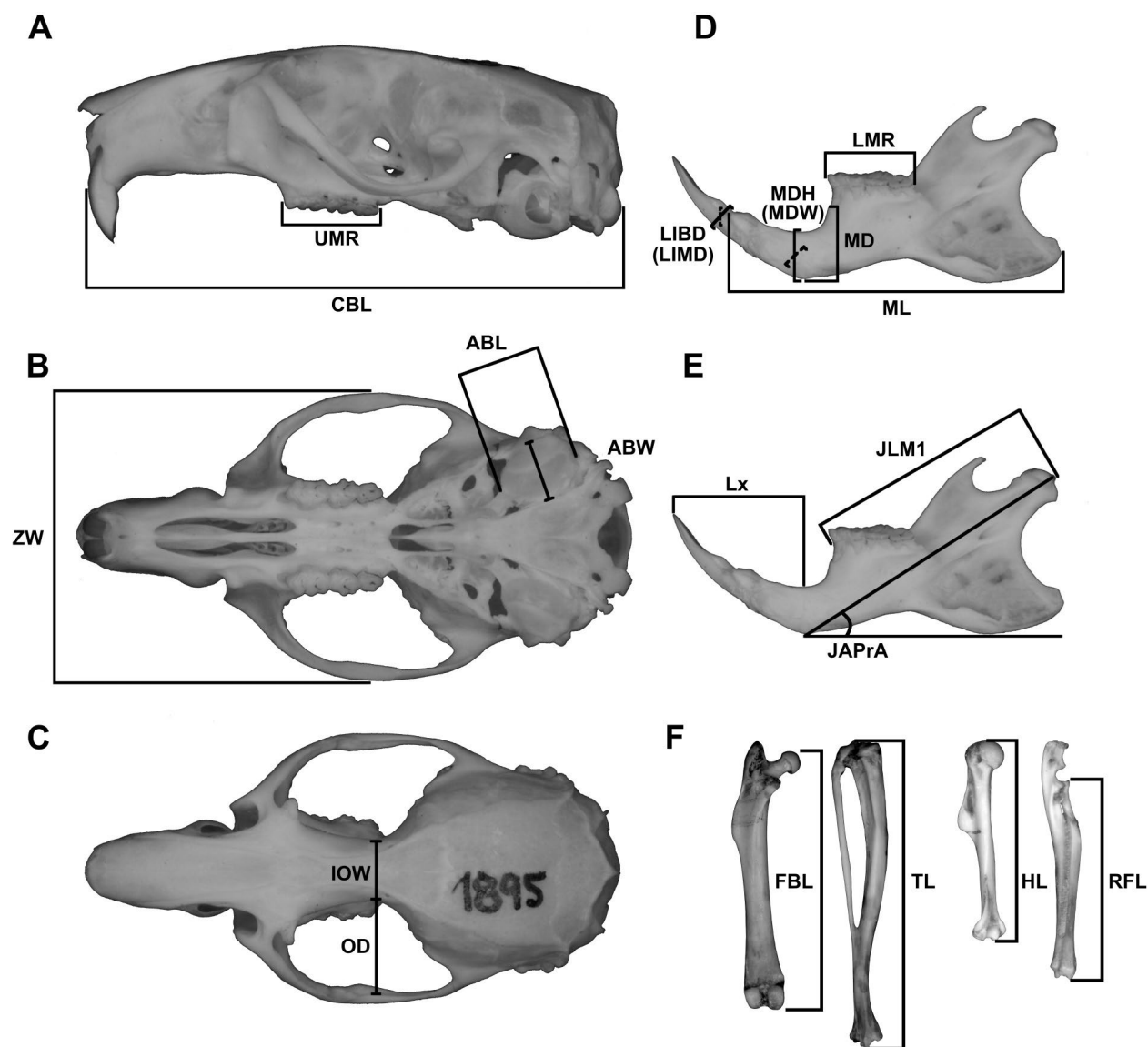
Fig. 2. Cranial, mandibular, and front and hind limb morphological traits examined in this study. For a detailed description of each trait, see Table S1.

determined using a combination of morphometric diagnostic traits (Monadjem et al. 2015), molecular barcoding based on the mitochondrial gene for cyt*b* (Bryja et al. 2019a, Mizerovská et al. 2020, Komarova et al. 2021), and their locality of origin (cf. Bryja et al. 2019b).

Morphological traits studied

The study analysed two sets of functional traits: skull and mandible dimensions, which mainly reflect sensory perception and diet, and limb bone lengths, which reflect locomotion style. A total of 15 cranial and mandibular traits and four limb bone traits were analysed (see Table S1 for the complete list and Fig. 2 for their definition). As the species differ in their body size, we standardized by the condylobasal length of the skull and mandible length, respectively.

Zygomatic width, for instance, is a proportional width of the skull relative to its length. The mandible length was standardised by dividing by the skull length. The only variables left in their original units were the condylobasal length of the skull, which measures body size, and the joint-to-angular process angle of the mandible. Two mandible variables (Z_I and A_D) were designed as proxies of bite force (Freeman & Lemen 2008). They were calculated from cross-sectional dimensions of the lower incisor and the mandible at its diastema (the gap between incisors and molars). These dimensions are defined in Table S1.

Three locomotory indices were calculated based on the lengths of limb bones: the brachial index (BI), the crural index (CI), and the intermembral index (IMI).
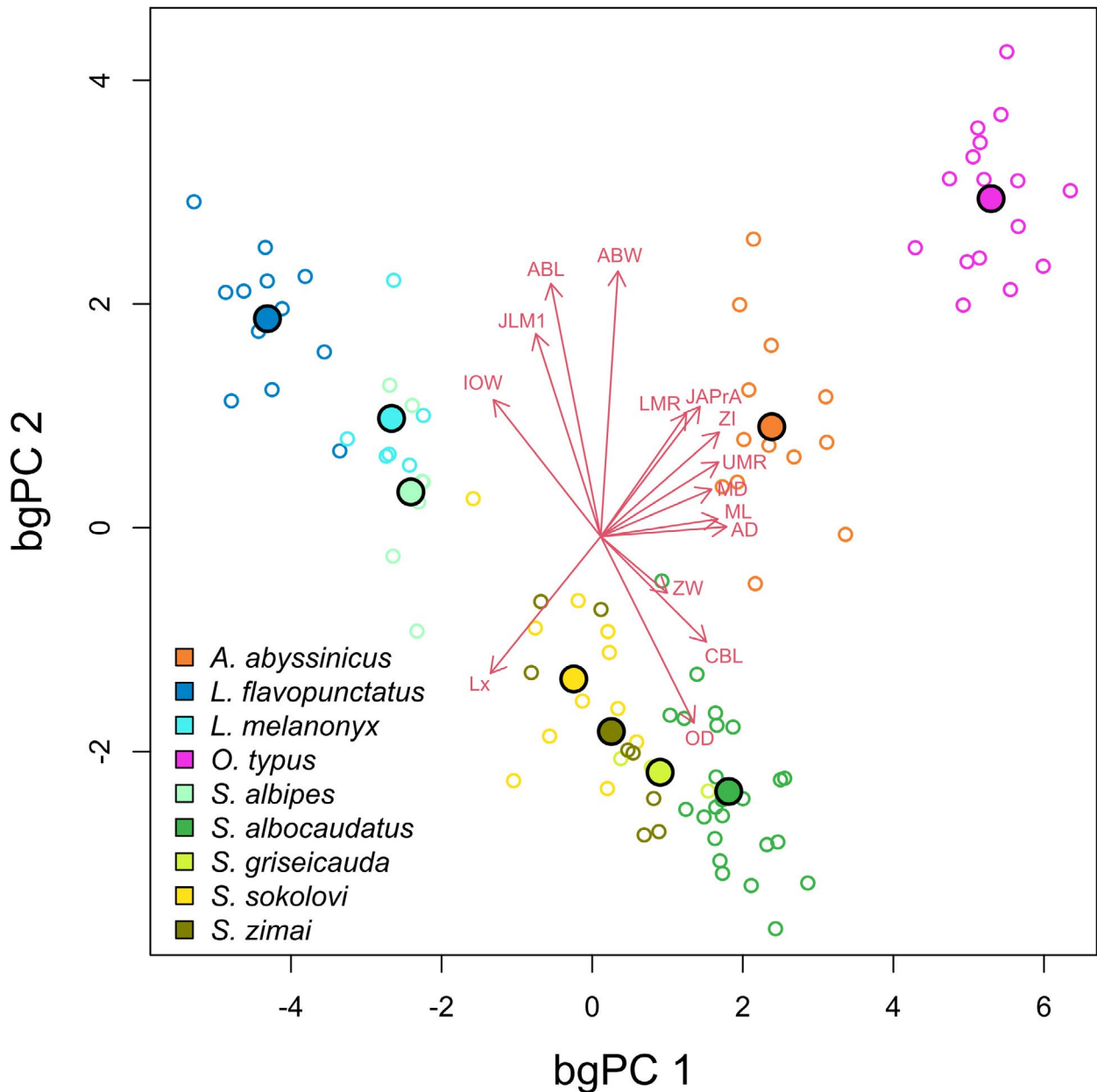
Fig. 3. The ordination of species in the space of skull and mandible traits reduced to the bgPC1,2 plane. The large, filled circles indicate species means; the small, empty circles are individuals, *post hoc* projected to the axes. The arrows represent variable loadings (magnified three times for better visibility). The colour legend is provided in the figure; variable abbreviations correspond to those in Table S1.

The BI was calculated as the length ratio of the distal and proximal parts of the forelimbs and hindlimbs. The CI was calculated as the maximal length of the tibia (measured from the proximal border to the most distal part of the medial malleolus) divided by the length of the femur (measured from the femoral head to the distal condyles). The IMI was calculated as the ratio of the forelimb (the length of the ulna plus the length of the humerus) to the hindlimb (the length of the tibia plus the length of the femur) lengths. For the reference see Samuels & Van Valkenburgh (2008).

Statistical analyses

The morphological traits measured were subjected to between-group principal component analysis (bgPCA); PCA performed on group (= species) mean values. With K species, such PCA defines up to $K - 1$ principal components, and individual data are then projected onto them *post hoc* (Yendle & MacFie 1989). To account for the heterogeneous nature of the variables, all were scaled so that the variance of species means was unity. The number of retained principal components was estimated using the elbow method of Salvador & Chan (2004). The ordination of
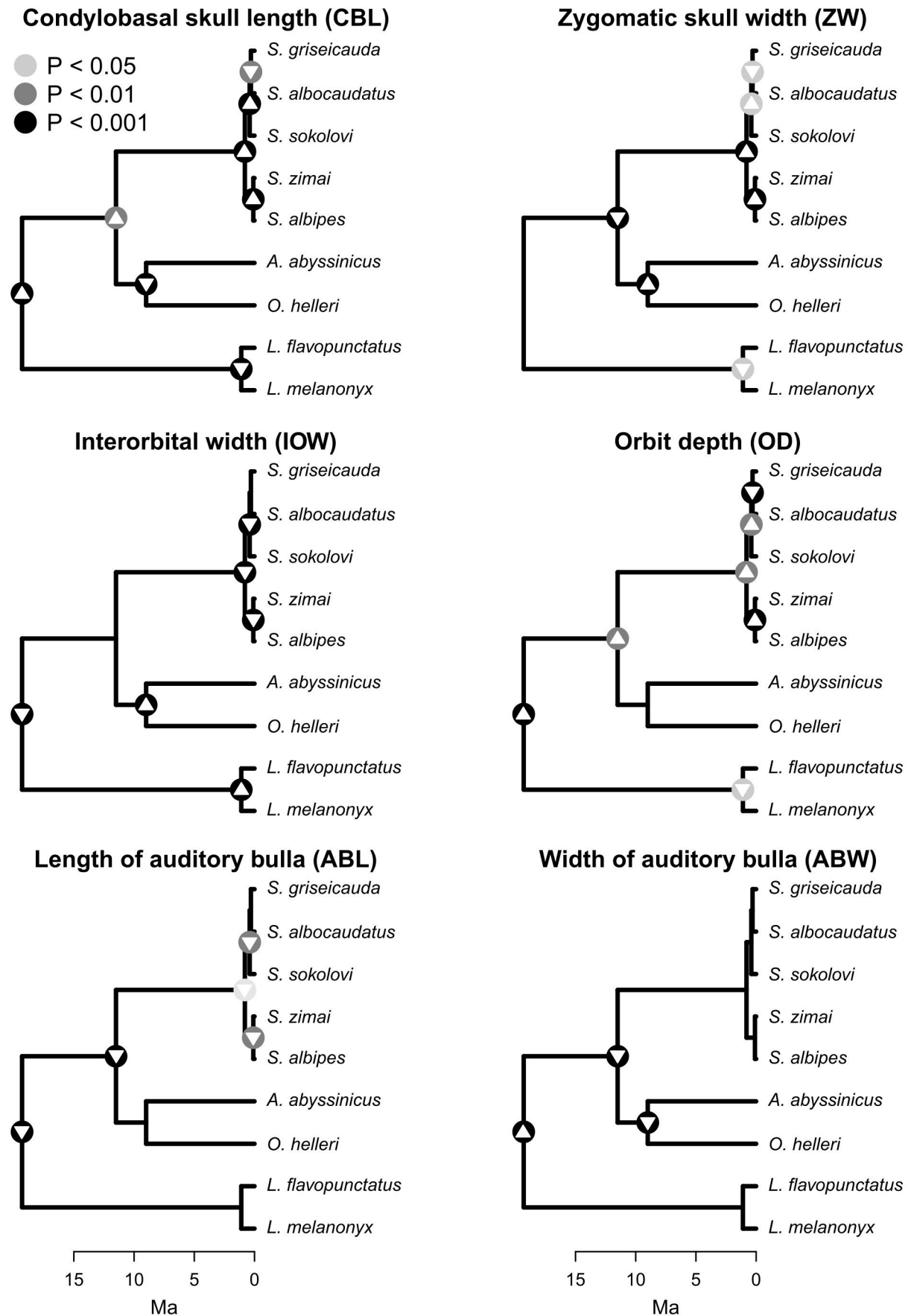
Fig. 4. Differences in CBL, ZW, IOW, OD, ABL and ABW in the studied Afroalpine rodents. Black, dark grey and light grey circles indicate significant results for the comparison between two sister branches of the phylogenetic tree at $P < 0.001$, 0.01 and 0.05, respectively; white arrows indicate the relative increase of the respective trait for a given sister pair.
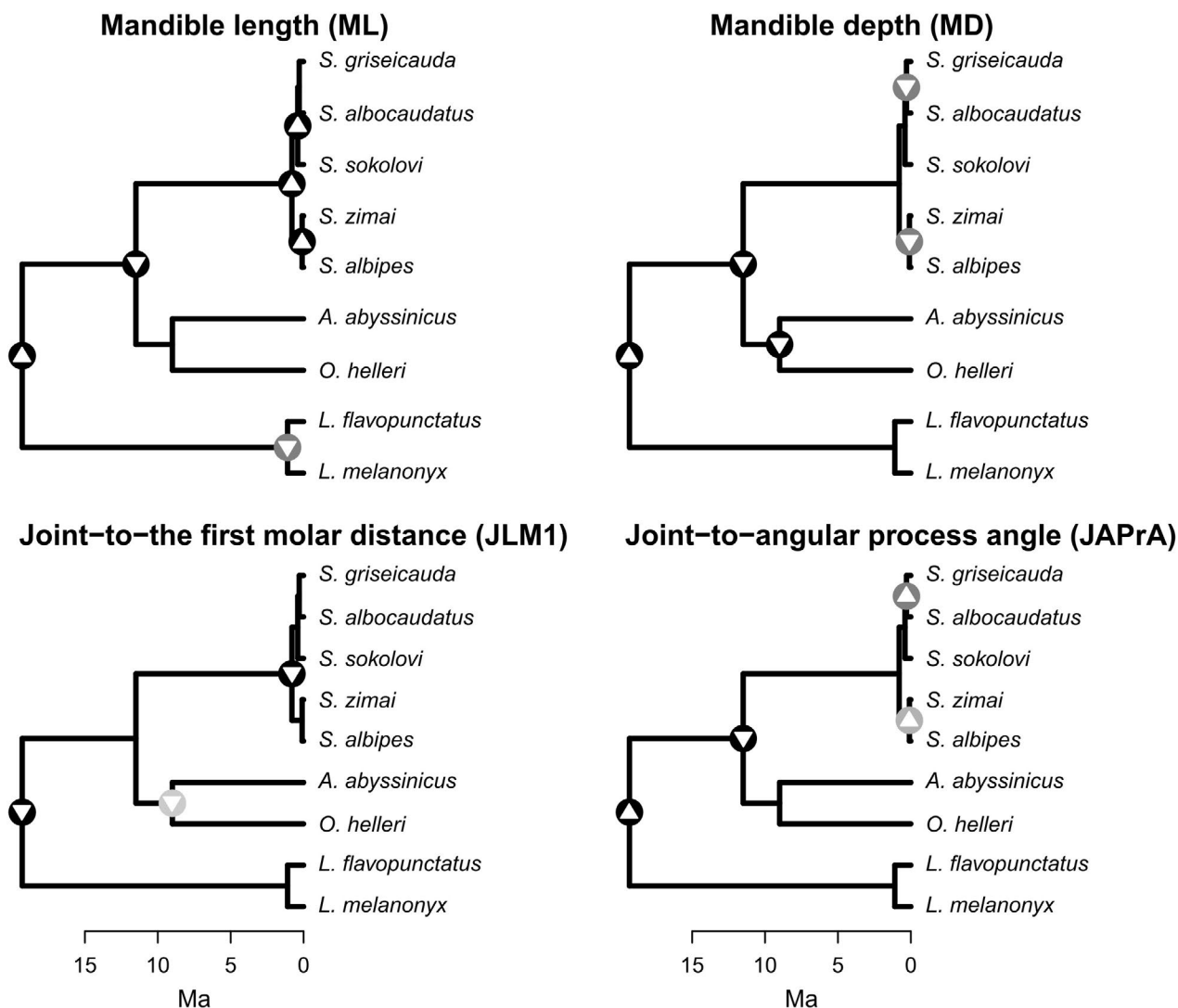
Fig. 5. Differences in ML, MD, JLM1 and JAPrA in the studied Afroalpine rodents. Black, dark grey and light grey circles indicate significant results for the comparison between two sister branches of the phylogenetic tree at $P < 0.001$, 0.01 and 0.05, respectively; white arrows indicate the relative increase of the respective trait for a given sister pair.

species means and the size and shape of individual scatters reveal the packing of species in this reduced phenotype space. The variable loadings, which define the principal components, allow for the functional interpretation of directions in this space.

Finally, we subjected the functional traits to separate univariate analyses. In each of them, we used an analysis of variance (ANOVA) with a particular trait as a response variable and species as the only categorical predictor. If the effect of species was significant, we followed the hierarchy of their phylogenetic relationships, and for each split in the tree (reported in Fig. S1), we tested for the differences between sister clades. We achieved this by setting up a priori contrasts to compare each pair of sister branches while excluding the rest of the species. The first contrast, the deepest one, was between

Lophuromys and the murine genera, with no species left aside, and the last contrast was the shallowest one, between *S. albipes* and *S. zimai*. Topology and divergence times in the tree (Fig. S1) were obtained from previously published phylogenies (Aghová et al. 2018, Komarova et al. 2021, Mikula et al. 2021, Nicolas et al. 2021). All tests were performed in R (R Core Team 2023).

Results

Among the studied species, *S. albocaudatus*, *S. griseicauda*, *S. zimai*, *A. abyssinicus*, *O. helleri* and *L. melanonyx* were the largest representatives, whereas *S. sokolovi*, *L. flavopunctatus*, *L. simensis* were intermediate-sized and *S. albipes* was the smallest species (Table 1). All *Stenocephalemys* species have relatively longer tails, hind feet, and ears than other

Fig. 6. Differences in UMR, LMR, Zi, AD and Lx in the studied Afroalpine rodents. Black, dark grey and light grey circles indicate significant results for the comparison between two sister branches of the phylogenetic tree at $P < 0.001$, 0.01 and 0.05, respectively; white arrows indicate the relative increase of the respective trait for a given sister pair.
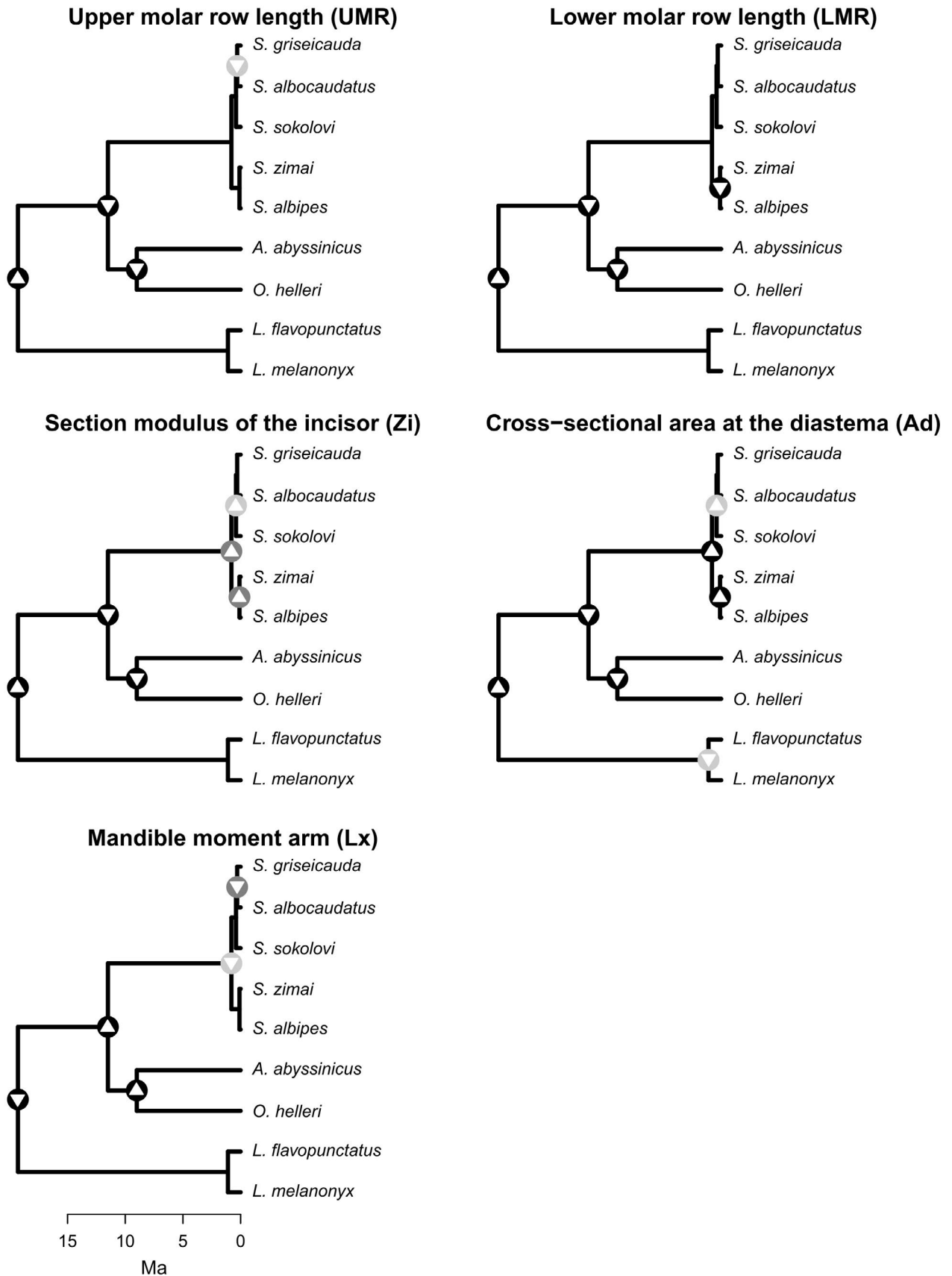
species, with these characteristics being relatively longer in *S. albipes* than in its congeners.

The studied species show considerable differentiation in the analysed functional traits. The species-specific means and standard deviations are summarized in Table S2-S5 and visualized by violin plots in Figs. S2-S6. The interspecific differences in skull and mandible variables showed two prominent patterns, both visible in the space of the first two between-group principal components (Fig. 3). The first pattern is the separation of *Otomys* from *Stenocephalemys* and *Lophuromys* with *Arvicanthis* in between. The bgPC loadings indicate that the separation is attributed to a cluster of traits, including dimensions of the mandible, molar rows and both proxies of bite force. *Otomys*, a prominent herbivore, occupies the end of the gradient characterised by relatively long molar rows, a massive (long and deep) mandible, a wide joint-to-angular process angle and strong bite force. Conversely, *Stenocephalemys* and *Lophuromys* exhibit the opposite trends.

The second prominent pattern revealed in the bgPC1,2 space is the interspecific differentiation between species within the *Stenocephalemys* and *Lophuromys* genera (Fig. 3). This differentiation reflects adaptation to different habitats along the altitudinal gradient within the Afroalpine ecosystem. The differentiation primarily involves the relative size and position of orbits, as well as skull size. *Stenocephalemys albipes* has a relatively shorter skull (condylobasal length), with small, short, and shallow orbits separated by a wide interorbital constriction. On the other hand, *S. albocaudatus*, *S. zimai*, and *S. griseicauda* are larger, with a narrower interorbital constriction and relatively larger orbits. *Stenocephalemys albocaudatus* is slightly different from *S. zimai* and *S. griseicauda*, as its average skull is larger and relatively broader. *Stenocephalemys sokolovi* occupies an intermediate position between the two extremes. The two species of *Lophuromys* are differentiated along the same line as the five species of *Stenocephalemys*, but they are distinguished from the *Stenocephalemys* species by their relatively smaller skulls. *Lophuromys melanonyx* from Bale Mts. has a relatively larger skull with a wider interorbital constriction than *L. flavopunctatus* from Guassa.

The elbow criterion suggested retaining three bgPCs. However, the third component, which is not presented graphically, only distinguishes *S. albipes* from other species. It shows *S. albipes* as having a smaller mandible and a smaller and narrower skull but a relatively longer lower molar row, deeper orbits, and a relatively longer joint-to-the-first lower molar distance.

The interspecific differentiation was highly significant ($P < 0.0001$) for all skull and mandibular traits, with the coefficient of determination ($R2$) ranging from 0.36 to 0.96 (median 0.82) (Table S6). The phylogenetically defined contrasts revealed a variety of differentiation patterns that are shown in Figs. 4, 5, and 6. Some traits, such as CBL, ZW, OD, and AD, showed significant differences at inter-generic and inter-specific levels. However, the significance was mainly limited to the contrasts involving whole genera in others, such as ABW, UMR, and LMR. Regarding the comparison of sister species pairs, the smallest differences were observed between *L. flavopunctatus* and *L. melanonyx*, with *L. melanonyx* having a more robust skull with deeper orbits, a narrower interorbital constriction and a larger cross-sectional area of the diastema. In the next pair, *S. albocaudatus* has a more robust skull with deeper orbits and mandible, a longer upper molar row and Lx than *S. griseicauda* (Table S6). In contrast, two other pairs of sister species in the dataset, *A. blicki* and *O. typus* and *S. albipes* and *S. zimai*, both differed in 11 out of 15 traits (see Table S6).

The interspecific differentiation in locomotory indices is characterised by the presence of three clusters in the space of the first two between-group principal components (see Fig. 7). One cluster corresponds to *Otomys*, which is separated from the rest by its large values of IMI. The other two clusters are defined by the different values of BI and CI. Although *Stenocephalemys* tends to have relatively longer proximal parts in both limbs (and hence both indices), the opposite is true for *Lophuromys* and *Arvicanthis*.

The interspecific differentiation was highly significant ($P < 0.0001$) for all three locomotory indices. The $R2$ values were 0.48, 0.81 and 0.85 in BI, CI and IMI, respectively (Table S7). From a phylogenetic perspective, the differentiation was mostly significant at the inter-generic level, although the IMI was also significantly different in some internal contrasts of *Lophuromys* and *Stenocephalemys* (see Fig. 8).

Discussion

To the best of our knowledge, this study is the first to examine in detail the functional variation in skull and mandible morphology, as well as locomotion-related indices, at both inter- and intraspecific levels within rodent communities inhabiting the high-altitude Afroalpine environment of the Ethiopian Highlands,
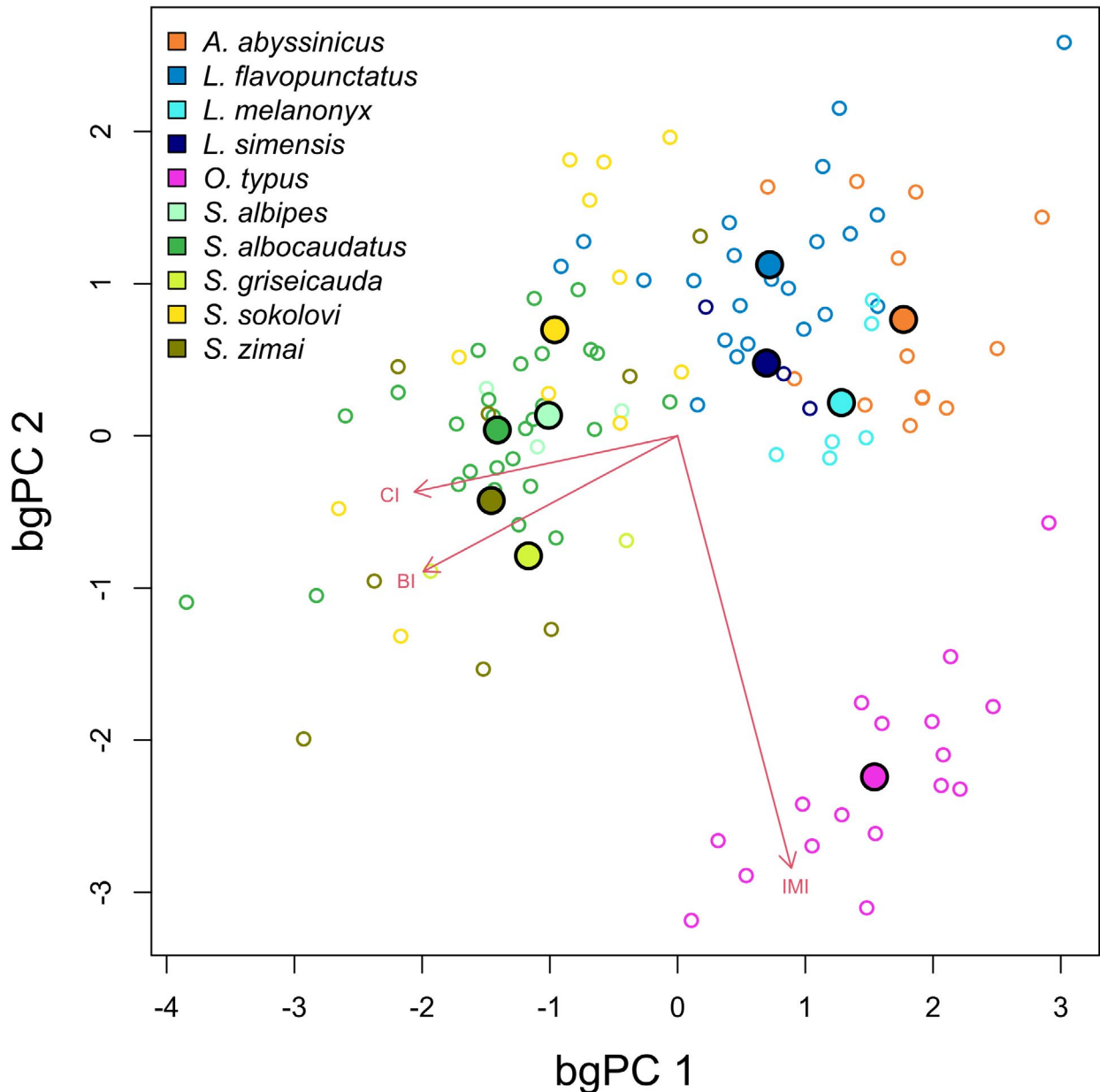
Fig. 7. The ordination of species in the space of three locomotory indices reduced to the bgPC1,2 plane. The large, filled circles indicate species means, and the small, empty circles are individuals, *post hoc* projected to the axes. The arrows represent variable loadings (magnified three times for better visibility). The colour legend is provided in the figure; variable abbreviations correspond to those in Table S1.

with a particular focus on characters reflecting differences in species ecologies. The results of both multivariate analysis and ANOVA tests applied to cranial and mandibular traits reveal a distinct differentiation among species that constitute the core of the Afroalpine rodent community in the Ethiopian Highlands. Two notable patterns emerge from the species ordination along the bgPC1,2 axes of skull and mandible variation. One pattern is associated with dietary differences, while the other reflects specialization for life in open moorland and grassland habitats primarily located at higher elevations within the Afroalpine ecosystem.

Morphological variation in skull and mandible shape

The first pattern distinguishes *O. helleri* from the genera *Stenocephalemys* and *Lophuromys*, with *A. abyssinicus* in between (Fig. 3). *Otomys helleri* and, to a much lesser extent, *A. abyssinicus*, differ from the others mainly due to their relatively long molar rows, massive (long and deep) mandible, wide joint-to-angular process angle, and strong bite force (indicated by higher values of the cross-sectional area at the diastema and the section modulus of the lower incisors). The observed morphological variations suggest dietary differentiation, as both *O. helleri*
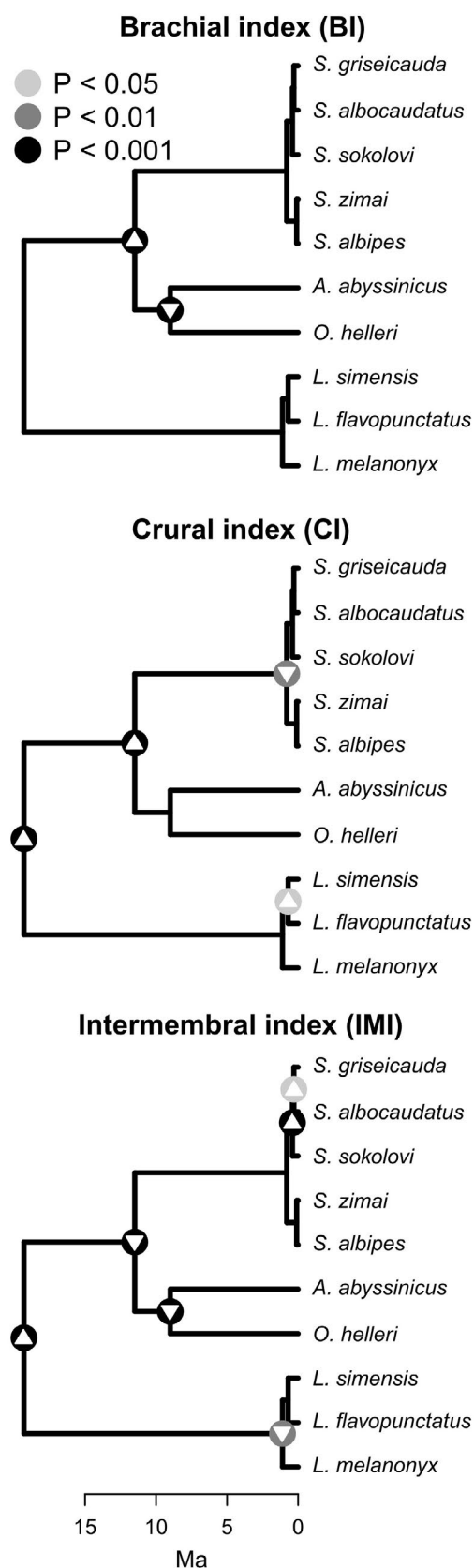
Brachial index (BI)

Crural index (CI)

Intermembral index (IMI)

Fig. 8. Differences in BI, CI, and IMI in the studied Afroalpine rodents. Black, dark grey and light grey circles indicate significant results for the comparison between two sister branches of the phylogenetic tree at $P < 0.001$, 0.01 and 0.05, respectively; white arrows indicate the relative increase of the respective trait for a given sister pair.

and *A. abyssinicus* are specialized herbivores. This finding aligns with prior studies on rodents, which have shown that herbivorous rodents typically have more robust mandibles (e.g. Michaux et al. 2007, Samuels 2009, Grossnickle 2020) and greater bite force compared to faunivorous taxa (Freeman & Lemen 2008, Verde Arregoitia et al. 2017). Differences in the joint-to-angular process angle are reflected in other cranial characteristics, such as gape angle, molar dimensions, and jaw articulation, that influence the insertion of chewing musculature (e.g. Verde Arregoitia et al. 2017). A similar correlation between prey hardness and bat cranial morphology was observed in a vespertilionid bat community inhabiting a mountain ecosystem in Mexico (Ayala-Berdon et al. 2023). This finding suggests that species feeding on harder prey have evolved a skull shape characterised by more developed muscle attachment areas (Nogueira et al. 2009).

The phylogenetic relationships among the examined taxa indicate functional similarity is likely due to evolutionary convergence. Notably, the omnivorous *Stenocephalemys*, which lacks significant differences in traits reflecting feeding ecology (e.g. UMR and LMR, see Fig. 6), is more closely related to the herbivorous pair *Arvicanthis* and *Otomys* than to the omnivorous *Lophuromys*. Regarding *Lophuromys*, the two studied species differ in the proportion of animal matter in their diet. While *L. flavopunctatus* is omnivorous/insectivorous, *L. melanonyx* is a true herbivore (Yalden & Largen 1992). Consequently, *L. melanonyx* has a broader skull and higher values of AD (the cross-sectional area at the diastema; a predictor of bite force – Freeman & Lemen (2008)) compared to *L. flavopunctatus*. These results support the general trend that specialised herbivores, primarily consuming vegetative plant parts, tend to have a broader skull and higher bite force (e.g. Samuels 2009, Verde Arregoitia et al. 2017).

Our data exemplify phylogenetic niche conservatism. The genus *Otomys* and the tribe Arvicanthini shared a common ancestor around nine million years ago, according to Mikula et al. (2021). The *Otomys* lineage appears to have been herbivorous since then, supported by fossil evidence demonstrating the gradual evolution of its distinctive laminated molars (Pocock 1976, Denys 1989) adapted to chewing grassy food. This conclusion is evidenced by a higher complexity of the occlusal surface (Evans et al. 2007, Tiphaine et al. 2013) and a specialised digestive tract for herbivory in extant species (Bronner et al. 1988). Given the dietary diversity within the tribe

Arvicanthini, herbivory emerges as a less common trait, suggesting both retention of an ancestral state and convergence.

Multivariate analysis revealed a second prominent pattern, highlighting interspecific differentiation within the genera *Stenocephalemys* and *Lophuromys*. This pattern indicates specialization for life in different habitats spanning different elevational zones within the Afroalpine ecosystem (see Mizerovská et al. 2020, 2023). The species of the genus *Stenocephalemys* best exemplified this differentiation. *Stenocephalemys albipes* is a forest-dwelling species with a relatively small skull and small orbits separated by a wide interorbital constriction. On the opposite end of the spectrum is *S. albocaudatus*, an Afroalpine specialist with a relatively larger skull and orbits and a narrower interorbital constriction. The other species fall between these two extremes. Those inhabiting ericaceous bushy vegetation consistently display a slightly more 'forest-like' morphology than their Afroalpine counterparts, as reflected in a relatively wider interorbital constriction. East of the rift, *S. griseicauda* aligns more closely with *S. albipes* than *S. albocaudatus*, and on the western side, the same relationship is observed between *S. sokolovi* and *S. zimai* (or again, in the specific case of the Guassa plateau, with *S. albocaudatus*). Similarly, the two species of *Lophuromys* show differentiation along the same line as the five species of *Stenocephalemys*. The highland specialist *L. melanonyx* from Bale Mts. shifts towards the high-elevation side of the gradient, primarily owing to its narrower interorbital constriction, and only marginally overlaps with *L. flavopunctatus* (see Fig. 3). This suggests that the latter species is primarily adapted to life in more forested habitats at relatively lower elevations.

The variations in size and shape associated with this elevational trend corroborate the findings of a geometric morphometric study that included a wider range of species from the genera *Stenocephalemys*, *Lophuromys*, and *Arvicanthis* across different elevational zones (Mizerovská et al. 2023). Likewise, Peterhans et al. (1998) observed a narrow-headed (i.e. stenocephalic) rodent guild inhabiting high-altitude open moorland in the Rwenzori Mountains in Uganda. This guild comprised vole-like herbivorous rodents such as *O. typus dartmouthi*, *O. denti denti*, and *Dasymys montanus*. The stenocephalic phenotype, characterised by large orbits and a relatively narrow interorbital constriction facilitating the shift of eyes to the top of the head, is recognised as an adaptation to life in open Afroalpine habitats. In such environments, rodents benefit from improved and faster detection of aerial predators (Peterhans et al. 1998, Beolchini & Corti 2004, Mizerovská et al. 2023). The influence of altitude on shaping mammalian morphology has also been demonstrated in mammals from Tibet. High-altitude populations of several rodent species showed a larger and broader skull and a larger bulla compared to populations from lower altitudes (Feijo et al. 2019). In this context, it is important to emphasise that the observed morphological changes in size predominantly indicate the influence of altitude. Relatively larger body size is advantageous in mitigating the increased thermoregulatory demands associated with colder temperatures at high-altitude environments. Conversely, morphological changes in shape, such as enlarged orbits and a narrower interorbital constriction, primarily represent adaptations to life in open habitats. These specific morphological changes are considered adaptations that enhance the ability to thrive in open environments.

When comparing high-altitude species within the genus *Stenocephalemys*, it is noteworthy that *S. albocaudatus* occupies a slightly different position in the defined morphospace than *S. zimai*, *S. griseicauda*, and even more so than *S. sokolovi*. This distinction results from its larger and wider average skull size (CBL and ZW) (see Figs. 3 and 4). Furthermore, *S. sokolovi* has a significantly wider interorbital constriction than all other Afroalpine species. These morphological differences may influence microhabitat selection within the Afroalpine rodent community. In areas where *S. albocaudatus* occurs sympatrically with either *S. griseicauda* (Arsi and Bale Mts.; in the latter, they occupy different elevational zones) or *S. sokolovi* (Guassa), the relatively robust skull and narrow interorbital constriction of *S. albocaudatus* suggest a superior adaptation to life in open Afroalpine habitats compared to its congeners. It is plausible that the larger size of *S. albocaudatus* confers a competitive advantage over the smaller *S. sokolovi* and *S. griseicauda*. This conclusion is supported by observations in areas where *S. sokolovi* occurs alone, such as in Borena Saynt National Park, where it is commonly found in the highest Afroalpine habitats (Mizerovská et al. 2020), whereas the opposite pattern is observed in Guassa (based on our observations). We hypothesize that the coexistence of *S. sokolovi* and *S. albocaudatus* in the Afroalpine ecosystem is primarily driven by niche partitioning resulting from interspecific competition, with *S. albocaudatus* being a superior competitor due to its larger size and morphological adaptations for life in open habitats. A more in-depth

study of the ecological requirements and morphology of these species is warranted to gain a comprehensive understanding of their coexistence dynamics.

Morphological variation in locomotion-related indices

The rodent species studied also showed differentiation in locomotion indexes derived from the lengths of long bones of the front and hind limbs. Despite the relatively low variability in the locomotion indices, indicating a generalised (also called ambulatory) murid phenotype with no apparent specialisation for a particular locomotory style (see Samuels & Van Valkenburgh 2008), finer-scale differences were discerned among the rodents studied. Parallel to the patterns observed in cranial traits, a notable observation is the marked morphological distinctiveness of *O. helleri*, highlighted by its isolated position within the morphospace examined. This distinctiveness primarily stems from its relatively higher IMI compared to all other species examined (see Fig. 7). A relatively higher IMI suggests that rodents tend to use forelimbs and hindlimbs equally (Samuels & Van Valkenburgh 2008), indicating a limb configuration adapted to quadrupedal terrestrial locomotion (Howel 1965). Indeed, *Otomys* species are recognised as quadrupedal, employing a diagonal sequence of alternating limb movements during locomotion, as exemplified by *O. irroratus* (Davis 1972). In addition, they have been observed to run rapidly with the body held flat and close to the ground, probably an adaptation for rapid movement along vegetation runways (Davis 1972). Comparable IMI values to *Otomys* (IMI = 0.769 ± 0.01) were found in the California vole *Microtus californicus* (IMI = 0.786, Samuels & Van Valkenburgh 2008), whose locomotor mode resembles that of *Otomys*. Interestingly, recent research has shown that the quadrupedal running locomotion in *O. helleri* coincides with an enlarged spleen, leading to the hypothesis that this adaptation may be advantageous during endurance running. The enlarged spleen in *O. helleri* could release more red blood (Lövy et al. 2023) cells for aerobic physiology, suggesting a potential advantage during rapid movements, especially when disturbed during foraging and relocation within a territory (Lövy et al. 2023). Our results and field observations support this scenario and suggest that *O. helleri* relies on fast quadrupedal running, which may be advantageous in response to disturbances during foraging and territorial movements.

The remaining rodent species fell into two clusters (see Fig. 7). The first cluster consisted of *Stenocephalemys* species with relatively higher CI and BI. In contrast,

the second cluster included *A. abyssinicus* and three species of *Lophuromys*, which had relatively lower BI and CI values. Mode of locomotion is an important factor influencing a rodent's ability to coexist within communities, particularly in microhabitat occupancy and predation pressure (Taraborelli et al. 2003). For instance, saltatory bipedality is common in desert rodents, helping minimise predation risk when foraging in open habitats. This mode of locomotion offers advantages such as high speed, better manoeuvrability, and the ability to cover a more extensive home range in open habitats (e.g. Randall 1993, Kotler et al. 1994). Although bipedal rodents are not found in open Afroalpine habitats, our findings suggest that *Stenocephalemys* species are better adapted for jumping, as evidenced by their elongated tibiae (relatively high CI) and short humeri (relatively high BI) (see Table S5). These limb proportions are conducive to quadrupedal hopping. This locomotory pattern likely provides rapid acceleration and faster responses to predator attacks, similar to what has been observed in bipedal saltatory rodents (Taraborelli et al. 2003). Furthermore, locomotory pattern diversification, namely the differentiation between quadrupedal and bipedal rodents, may have played an essential role in shaping rodent communities in desert ecosystems (e.g. Moore et al. 2017). In contrast, *Arvicanthis* and *Lophuromys* rely more on quadrupedal running, although not to the extent of *O. helleri*, as described above. Rodents employing quadrupedal running to evade predators tend to live in areas with vegetation closer to their burrows than saltatory species (Schröpfer & Klenner-Fringes 1991). Indeed, *A. abyssinicus* is most abundant in the *Helichrysum-Festuca* habitat in the Simien Mountains and Guassa (M. Lövy, pers. observ.). This habitat provides enhanced protection against predation due to the up to 1 m high and wide canopy of *Helichrysum splendidum* (Wubie 2018).

At the interspecific level, differences in locomotory indices were generally less pronounced and, in many cases, not statistically significant within the genera *Stenocephalemys* and *Lophuromys* (see Table S7). This variation is likely due to the relatively small sample sizes for some species examined. Notably, *S. albipes* and *S. sokolovi* stand out from the other congeners by having a considerably longer tail relative to body length (see Table 1). Although this parameter was not analysed in the current study, as it does not pertain to the cranial, mandibular, or locomotory indices, a longer tail is indicative of enhanced climbing ability in these two species (see e.g. Verde Arregoitia et al. 2017). This ability was not explicitly revealed in our analyses. Enhanced climbing ability could be

advantageous for both *S. albipes*, a species adapted to forested environments, and *S. sokolovi*, which, despite inhabiting more open habitats at higher altitudes, shows a preference for areas with *Erica* shrubs (Mizerovská et al. 2020, M. Lövy, pers. observ. from Guassa). In the case of *Lophuromys*, *L. melanonyx* differed from the other two species by its higher IMI. Although we can only speculate at this point, it is conceivable that this difference reflects morphological adaptations associated with the predominant diurnal activity and foraging on vegetation, similar to the herbivorous *O. helleri*. However, more detailed research is needed to clarify this aspect.

Conclusions

It has been demonstrated that rodent assemblages in the Ethiopian Highlands exhibit functional diversification, primarily driven by differences in foraging habits and modes of locomotion. These findings confirm the results of previous studies conducted on rodent assemblages from high-elevation Afroalpine habitats in Uganda and Ethiopia. To advance research in this field, it is crucial to expand the range and number of rodent species studied in Africa and across other continents with similar environmental conditions. Investigating additional localities within the Eastern Afromontane Biodiversity Hotspot is crucial, as both its components – the Ethiopian Highlands and Albertine Rift Mountains – are recognized as significant centres of mammal endemism globally. To safeguard the unique biodiversity of this hotspot, especially its rich rodent communities, it is essential to have a deeper understanding of the dynamics that govern the coexistence of small mammals.

Author Contributions

M. Lövy: conceptualization, data analyses, writing – original draft, review and editing; R. Šumbera: conceptualization, review and editing; B. Konopová: data collection, review and editing; L. Svačinová: data collection, review and editing; J. Bryja: conceptualization, review and editing; Y. Meheretu: review and editing; O. Mikula: conceptualization, data analyses, review and editing.

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Supplementary online material

Table S1. Description of the studied morphological traits and locomotory indexes used in analyses and their definitions.

Table S2. Summary table of standardised skull characters measured for rodent species from the Ethiopian Highlands (for trait abbreviations, see Table S1).

Table S3. Summary table of standardised mandible and tooth characters measured for rodent species from the Ethiopian Highlands (for trait abbreviations, see Table S1).

Table S4. Summary table of standardised characters referring to bite force measured for rodent species from the Ethiopian Highlands (for trait abbreviations, see Table S1).

Table S5. Summary locomotory indices calculated from lengths of forelimbs and hindlimbs for rodent species from the Ethiopian Highlands (for trait abbreviations, see Table S1).

Table S6. Results of ANOVA tests analysing differences in cranial and mandibular traits with a priori set contrasts comparing sister branches of the phylogenetic tree containing the studied rodent species (for each trait, *P* overall and R2 values refer to the results of the main ANOVA test, other columns show *P*-values for each contrast; degrees of freedom were 8, 91).

Table S7. Results of ANOVA tests analysing differences in locomotory indices with a priori set contrasts comparing sister branches of the phylogenetic tree containing the studied rodent species (for each trait, *P* overall and R2 values refer to the results of the main ANOVA test; other columns show *P*-values for each contrast; degrees of freedom were 9, 106).

Fig. S1. Phylogenetic tree of the sampled species. The node labels show divergence times in million years (Ma) before present.

Fig. S2. Inter- and intraspecific variation in skull measurements shown by kernel density estimates (displayed as violin plots) or dots. The measurements are given in original units (mm) before size standardization.

Fig. S3. Inter- and intraspecific variation in auditory bulla measurements and molar row lengths shown by kernel density estimates (displayed as violin plots) or dots. The measurements are given in original units (mm) before size standardization.

Fig. S4. Inter- and intraspecific variation in mandible measurements shown by kernel density estimates (displayed as violin plots) or dots. The measurements are given in original units (mm) before size standardization.

Fig. S5. Differences in parameters related to bite force in the studied Afromontane rodents. Inter- and intraspecific variation in bite force parameters shown by kernel density estimates (displayed as violin plots) or dots. The measurements are given in original units (mm) before size standardization.

Fig. S6. Inter- and intraspecific variation in three locomotory indices shown by kernel density estimates (displayed as violin plots) or dots.

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