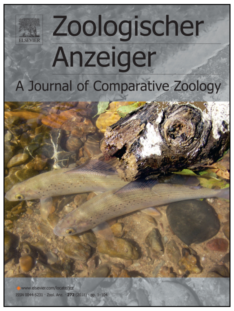

Comparison of skull growth in two ecosystem modifiers: Beavers *Castor canadensis* (Rodentia: Castoridae) and muskrats *Ondatra zibethicus* (Rodentia: Cricetidae)

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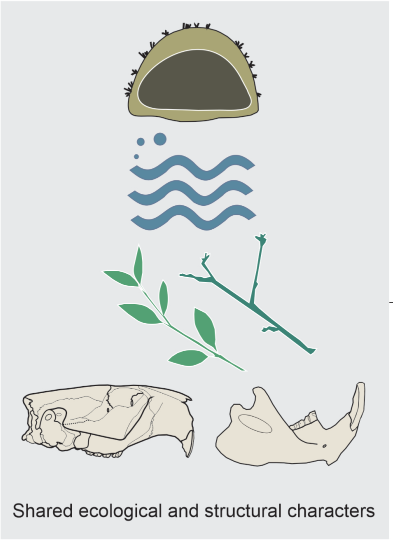
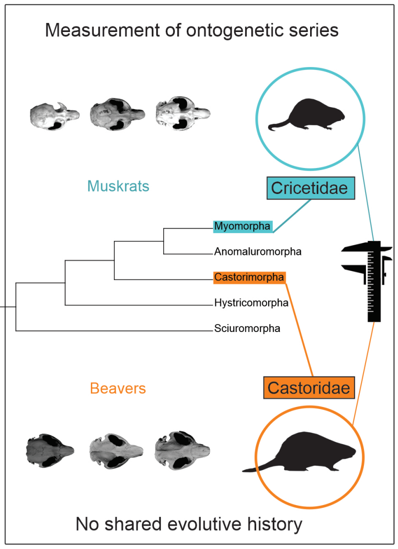

Shared ecological and structural characters



No shared evolutive history

Variable	Growth trend
BB	- -
BBU	= -
BO	- +
BP	= =
CL	= =
DL	+ +
HBU	+ -
HC	= -
HD	- -
HO	= -
IB	= -
LBU	- -
LD	= -
LN	+ +
LO	- +
LR	- -
RB	+ =
RH	+ -
UR	- -
ZB	+ +

No shared ontogenetic pattern

Comparison of skull growth in two ecosystem modifiers: beavers *Castor canadensis* (Rodentia: Castoridae) and muskrats *Ondatra zibethicus* (Rodentia: Cricetidae)

Running Header: Skull growth in beavers and muskrats

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Abstract

Beavers and muskrats are semi-aquatic, generalist herbivorous rodents regarded as invasive in southern South America, with high impacts on the ecosystem. They share some morphological characters of the skull, but different body sizes and phylogenetic history, showing evident shape differences in young and adult skulls during the development in both species. Considering their similar ecological specializations, skull shape could be achieved through different or similar patterns of allometric growth during ontogeny. We analyzed quantitatively the ontogenetic series including 94 specimens of beavers and muskrats and performed multivariate and bivariate analyses considering 20 linear measurements. Our main results from the different approaches suggest high differences in the ontogenetic trajectories of beavers and muskrats, implying disparity in the muscular, functional, and structural conditions of the skull of both species. These differences reflect that although skulls might undergo similar mechanical stress, it is possible to reach a cranial morphology compatible with the similar behavioral and ecological specializations between both species from patterns of skull development that are markedly different.

Keywords:

Development-Cranial Ontogeny-Invasive Mammals-Ecosystem engineer

1. Introduction

Rodents are among the most speciose mammalian order (over 2600 species), accounting for more than 40% of all living taxa (Samuels, 2009; Lacher et al., 2016; Mammal Diversity Database, 2022). The group has spread over all continents and most islands, occupying almost all terrestrial ecosystems, except Antarctica (Fabre et al., 2012). They show a wide range of locomotory specializations (e.g., cursorial, scansorial, saltatorial, gliding, aquatic, fossorial), and their feeding strategies are diverse, including herbivorous, frugivorous, granivorous, insectivorous, vermivorous, and omnivorous species (Maestri et al., 2017; Verde Arregoitia and D'Elía, 2021). In the order Rodentia, the skull morphology is relatively conservative compared with other mammalian orders, because all rodents are characterized by a set of functional features specialized for gnawing (a single pair of ever-growing chisel-like upper and lower incisors, elongated rostrum, diastema separating incisors from cheek-teeth, and large masseter muscles) (Samuels, 2009; Druzinsky, 2015; Potapova, 2020). However, some muscular characteristics (related to the disposition of the masseter muscle and development of temporal muscle) showed consistent differences in the group, with the muscular arrangement being the most important basis for classifying suborders in living and fossil rodents (Simpson, 1945; Cox and Jeffery, 2015). Within the order Rodentia, beavers (*Castor canadensis*) belong to the family Castoridae (suborder Castorimorpha); they are semi-aquatic rodents and generalist herbivores of large size (16000-31000 g; Baker and Hill, 2003). Muskrats (*Ondatra zibethicus*) do not share the phylogenetic history with beavers, since they belong to the family Cricetidae (suborder Myomorpha), and the adult size is smaller, ranging from 700 to 1800 g (Pardiñas et al., 2017). The substantial difference in body size is present from birth (340-630 g in beavers, 20 g in muskrats; Jenkins and Busher,1979; Willner et al., 1980), and although both species exhibit shape and size differences in the skull, they also share important morphological traits in adults, such as broad and short braincase, rostrum comparatively broader than other rodents, nasals expanded in its anterior portion, expanded zygomatic arches, mastoid process laterally projected, globose tympanic bulla, upper tooth row projected ventrally respect to the zygomatic arch in lateral view, and external auditory meatus projected laterally (Figs. 1 and 2). Both species also share the habitat, as they are semi-aquatic mammalian herbivores, exhibiting considerable niche overlap (Higgins and Mitsch, 2001; Mott et al., 2013), and being frequently observed using lodges together (Mott et al., 2013). Besides, both sympatric species use vegetation as construction material for lodges (Jenkins and Busher, 1979; Willner et al., 1980). Beavers and muskrats are recognized as invasive mammals in southern South America (Argentina and Chile; Cassola, 2016); they were introduced in Tierra del Fuego to develop a fur industry in 1946 and 1948, respectively (Skyriene and Paulauskas, 2012; Castello, 2013; Anderson et al., 2019; Deferrari et al., 2019; Anderson, 2023; Deferrari, 2023). Due to their strong impact on the environment (including Patagonian landscapes), such as alteration of plant abundance, community composition, invertebrate diversity, and potential nutrient cycling (Van der Valk and Davis, 1978; Wainscott et al., 1990; Connors et al., 2000; de Szalay and Cassidy, 2001; Cassola, 2016; Anderson et al., 2019; Deferrari et al., 2019), these species were termed ecosystem engineers (Wright et al., 2002; Müller-Schwarze, 2011), although Bomske and Ahlers (2021) recently discussed the literature that supports muskrats as ecosystem engineers, concluding that is necessary long-term research pointed to uncovering the impacts of muskrats on ecosystems. Beyond these considerations, beavers and muskrats have convergent characteristics for aquatic life, e.g., they can remain underwater for up to 15-20 min and have a valvular mouth that closes behind the incisors to gnaw while submerged (Irving and Orr, 1935; Errington, 1961; Godin, 1977). In addition, their unrooted incisor teeth are well suited for gnawing as well as transporting materials through an aquatic environment (Godin, 1977), which is a highly specialized behavior.

Previous studies about ontogeny in beavers and muskrats have focused on body mass growth (Errington, 1939; Aleksiuk and Frohlinger, 1971; Simpson and Boutin, 1993), fetal body length (Bergerud and Miller, 1977), behavior (Patenaude, 1984; DeStefano et al., 2006; Mott et al., 2011), reproductive conditions (Bond, 1956), diving and thermoregulatory abilities (MacArthur and Humphries, 1999; MacArthur et al., 2001), and age or sex estimation (Baumgartner and Bellrose, 1943; Robertson and Shadle, 1954; Van Nostrand and Stephenson, 1964; Hartman, 1992; Otgonbaatar and Shar, 2019). However, the postnatal development of the skull has not been quantified in these specialized rodents to date. A large part of the morphological diversity of the mammal skull is the result of changes in ontogenetic trajectories, which are likely to vary with ecology and phylogeny (Zelditch and Carmichael, 1989; Klingenberg, 1996, 1998; Meiri et al., 2005; Segura et al., 2021b; Flores et al., 2022). Besides, mammal skull morphology is also thought to respond to biological pressures such as size variation (Klingenberg, 1998; Morales and Giannini, 2010) or mechanical limitations (e.g., Marcy et al., 2016). Evaluating the processes of morphological change during ontogeny in two species that share habits and morphological characters, it is possible to detect how selection has altered growth patterns, affecting adult morphology (Creighton and Strauss, 1986). Similarities in ontogenetic trends are also thought to be the effect of selection pressures acting to maintain an adult cranial morphology and function (Morris et al., 2019).

In this context, we analyzed and compared quantitatively the postnatal skull growth pattern in two well-represented samples of Patagonian populations of beavers and muskrats. The objective of this report was to test the hypothesis that both species will be similar in their ontogenetic trajectories and allometric trends, considering the several common morphological traits of the skull, and that they are presumably under strong functional pressures provided by the similar ecological niche they share (both are herbivores, semi-aquatic, and lodges builder rodents). We expect ontogenetic trajectories and allometric trends of both species, will integrate a related morphological space, aligned (as a continuum) in a single intra- and interspecific growth program. That growth program responds to comparable functional pressure imposed by the ecology (habitat, diet, and behavior). Alternatively, despite the similar ecological specializations of both species, skull shape in adults could be achieved through different pathways during development (i.e., different growth patterns), considering their different sizes and phylogenetic legacy.

2. Materials and methods

2.1. Sample

We analyzed ontogenetic series including 94 specimens of beavers (N=55) and muskrats (N=39) (Figs. 1 and 2). All the specimens were originally collected in Tierra del Fuego, Argentina. The material studied is deposited in the mammal collection of CADIC (Centro Austral de Investigaciones Científicas, Ushuaia, Tierra del Fuego, Argentina; see Appendix A). For both species, we obtained a continuum from young to adult specimens, with a range of a cranial size (geometric mean) of 27.29-41.36 for beavers and 12.09-17.85 for muskrats (Figs. 1 and 2). We considered the geometric mean as the independent variable because it is a better predictor of the size of an individual than the commonly used total length of the skull, which is not always isometric (e.g., Flores et al., 2010). The geometric mean is a size variable derived from the N^{th} root of the product of N measurements; consequently, it has the same dimensionality as skull measurements (Mosimann, 1970). We performed this analysis in Past 3.20 (Hammer et al., 2001).

For practical purposes, we used the following age stages: kit (only in beavers), young, subadult, and adult (described in Appendix B). In beavers, no differences in external and cranial measurements between adult males and females have been reported (Osborn, 1953; Bond, 1956). In muskrats, lack of sexual dimorphism in external or cranial measurements was reported by some authors (Willner et al., 1980), whereas others reported a strong pattern of sexual size dimorphism (Hood, 2000). In our sample, both males and females of each species exhibited the same ontogenetic trajectory (i.e., non-significant slope or intercept differences in bivariate plots, see Fig. 3). For this reason, we were confident to pool males and females of all ages in a single sample.

2.2. Skull Measurements

We took 20 linear measurements with a digital caliper (to the nearest 0.01 mm) to depict the three dimensions of the skull structures (Fig. 4). We chose the skull measurements to cover different functional aspects and demands of the whole skull (e.g., Baverstock et al., 2013; Ginot et al., 2018).

2.3. Study of Growth

Our study of skull growth includes two complementary approaches: bivariate and multivariate allometries of log-transformed skull measurements, which were applied separately in both species. We used both approaches because bivariate allometry is suitable for statistical comparison of slopes and intercepts for two regressions (e.g., two species), whereas in multivariate allometry size is considered as a latent variable affecting all measured variables simultaneously, although it is less suitable for statistical comparisons of rate values, beyond the allometric trend (see Flores et al., 2015).

2.4. Multivariate analysis of allometry

To identify the major components of variation and visualize shape changes in a multivariate morphospace, we performed a principal component analysis (PCA) on each species across ontogeny and another PCA that combined both species. In such analyzes we used the Jolliffe cut-off value as an indication of how many principal components should be considered significant (Jolliffe, 1986); components with eigenvalues smaller than the Jolliffe cut-off may be considered non-significant.

The method for investigating allometry in a multivariate context was based on Jolicoeur (1963), in which the data sets are log-transformed and subjected to PCA. The first principal component (PC1) is then regarded as a size axis, and the allometric coefficient for each original variable is estimated by the PC1 loading for that variable. We obtained the first eigenvector from the PCA for each species (performed on a variance-covariance matrix). For each variable, allometry is the statistical deviation of its corresponding eigenvector element from a hypothetical isometric value, which is expected to be equal for all elements if the global growth pattern is isometric (size invariant). The isometric value is calculated as $1/p^{0.5}$, with p being equal to the number of variables (0.224 for the present study), and the statistical deviation from isometry was estimated using the jackknife application developed by Giannini et al. (2004). This technique generates confidence intervals (CI) for each element derived from the first eigenvector. The CI may be inclusive of the isometric value 0.224 and therefore statistically indistinguishable from isometry, or it may exclude such value and therefore be considered significantly allometric. The observed element will be considered positively and negatively allometric if it is >0.224 and <0.224, respectively. For the multivariate statistical analyses, we used the R script available from Giannini et al. (2010) and Flores et al. (2018).

2.5. Bivariate analysis of allometry

We analyzed the relationship of each variable with the overall size of the skull using linear (log10) transformation of the power equation of allometry: $log\ y = log\ b_0 + b_1\ log\ x + log\ e$, where y is a skull variable, b_0 is the y-intercept, b_1 is the slope of the regression or coefficient of allometry, x is the variable considered as the independent term, and e is the error term (Alexander, 1985). We tested deviations from isometry by means of two-tailed *t*-tests and interpreted the allometric coefficient as isometric when it was not possible to distinguish it statistically from unity. Thus, we considered negative allometry if b_1<1.0 and positive allometry if b_1>1.0. We used reduced major axis regression (RMA) and a likelihood ratio test for the common RMA slope, following Warton et al. (2006). Thus, if the species shared a common slope, we compared the significance of the common normalization constant (*y*-intercepts) using the Wald test (Warton et al., 2006). We performed all regression coefficients, statistical parameters, and tests using the SMATR package of R (Warton and Weber, 2002).

3. Results

3.1. Analyses of skull variation

In the multivariate analysis of the ontogeny of beavers, including kits, PC1, and PC2 explained 79.28 % and 5.97% of the total variation, respectively (Fig. 5; Jolliffe cut-off value=0.0023). PC1 showed the ontogenetic trajectory progressively arranged with the onset (i.e., kits) separated from the remaining specimens, located on the negative end of

PC1 and on the positive side of PC2 (Fig. 5). Juvenile specimens were distributed mainly on the negative side of PC1, although some specimens of this age were positioned on the positive side, relatively overlapping with subadults. In turn, all subadults were located on the positive side of PC1, and on both sides of PC2. Finally, the older adult specimens were located on the positive end of PC1, and mostly on the positive side of PC2, although very few marginal specimens were on the negative side of PC2, with very little overlap with subadult specimens. The variable with the highest loadings on PC1 was diastema length (DL), followed by length of nasals (LN) and height of the coronoid process (HC), whereas the variables with lowest loadings on this component were breadth of the palate (BP) and of the braincase (BB) (Fig. 6A). To explore the morphometric variation without extreme age stages, we plotted a multivariate space excluding the kits, obtaining a notably lower variability compared to the analysis with the complete sample (Supplementary Material Fig. S1). In the PCA without kits, PC1 explained only 59.70% and PC2 accounted for 9.71% (Jolliffe cut-off value=0.0017). The ontogeny arranged on PC1 was related to size, with juvenile and adult specimens successively placed (Supplementary Material Fig. S1), although the dispersion was larger than in the analysis including kits. The variable with highest loadings was rostral height (RH), followed by diastema length (DL), length of nasals (LN), and rostral breadth (RB). The variables with lowest loadings were breadth of the braincase (BB) and length of the orbit (LO) (see Supplementary Material Fig. S2).

In the multivariate analysis of the ontogenetic series of muskrats (Fig. 7), PC1 and PC2 explained 83.96% and 3.55 % of the total variation, respectively (Jolliffe cut-off value=0.0018). The morphospace showed information related to size. Smaller juveniles had negative scores, adults had positive scores, and subadult specimens occupied an intermediate position, showing specimens on both sides of PC1. At all age stages, the specimen distribution on PC2 was on the positive and negative sides (Fig. 7). The variable with the highest loading on PC1 was length of orbit (LO), followed by breadth of occipital plate (BO) and diastema length (DL) (Fig. 6B). The variable with lowest loading was breadth of the braincase (BB), followed by length of the bulla (LBu) and length of the lower tooth row (LR) (Fig. 6B).

In the combined morphospace of beavers and muskrats (taking into account kit beavers; Fig. 8), PC1 explained 98.85% of the total variation (Jolliffe cut-off value=0.0045) and showed both species completely separated. This PC is clearly related to size and exhibited the largest species (beavers) to the positive values and the smaller species (muskrats) to the negative values of this axis. However, kit specimens of beavers were placed on the negative side of this component, occupying lower values (Fig. 8). PC2 summarized only 0.35% of the total variation and seemed to be related to ontogenetic trajectories since it is observed that the position of the trajectories is mostly aligned with this axis, with the juveniles being placed on the positive values, and subadult and adult specimens being mostly placed on negative values in both species (Fig. 8). PC1 of the combined analysis without the inclusion of kits is shown in Supplementary Material Fig. S3, in which the spatial distribution of the ontogenetic trajectories of both species is similar to that obtained considering the kits but with a lower dispersion of beavers (i.e., when removing kits, the trajectory did not show specimens positioned on the negative score of PC1). Because size is an important factor of variation when we analyzed both species together (i.e., PC1 explains 98.85% of the total variation, see above), we also explored a multivariate space standardizing the data set. We divided each measure by the geometric mean (a linear estimator of size; Mosimann, 1970), obtaining also a clear separation of both species on PC1 and ontogenetic trajectories aligned to PC2

(Supplementary Material Fig. S4). However, PC1 accumulated only 62.7% and PC2 16.1% of the total variation, respectively (Jolliffe cut-off value=0.023).

3.2. Multivariate allometric trends

The multivariate allometric trends are provided by analyses with 95% of confidence intervals and showed notably different patterns in both species (Table 1). Beavers showed all trends with almost similar percentages, with 35% of the variables showing isometric growth, 35% being negatively allometric, and the remaining 30% being positively allometric. On the other hand, muskrats resulted less isometric in their growth, with only 15% of the variables being isometric and the remaining variables being allometric (60% negative and 25% positive).

Variables associated with the neurocranium and the feeding apparatus (splanchnocranium) showed negative and positive allometry, respectively (Table 1). Despite the profound differences in the allometric trends, we found that beavers and muskrats shared negative allometry in two variables related to neurocranium (BB and LBU). Additionally, in beavers, the neurocranial variables BO and LO showed negative allometry, whereas in muskrats, all neurocranial variables exhibited negative allometry, except for BO and LO, which showed positive allometry (Table 1). The splachnocranial variables with positive trends for both species were DL, LN, and ZB. In beavers, the rostral variables RB and RH were also positively allometric, whereas in muskrats, there were no additional variables related to feeding apparatus with positive allometry. In the mandible, LR showed negative allometry in both species, as observed in the upper toothrow (UR). There are no mandibular variables that show positive allometry, and the differences between species are restricted to HC and LD, with isometry in beavers and negative allometry in muskrats (Table 1). In only four variables (BO, HBU, LO, RH) the allometric trends showed completely opposite signs, reflecting strong morphological differences in occipital and rostral regions between both species.

3.3. Comparative allometry of bivariate results

The ontogenetic trajectories in both species (Supplementary Material Table S5) differ in all parameters of the linear regression (i.e., slope or intercept, Table 2). We detected statistically similar slope values in 50% of the variables (10 characters), in measurements of both neuro- and splanchnocranium (Fig. 3, Table 2). In the remaining 10 variables, beavers showed higher slope values in 8 characters, in variables related to neurocranium (HBU, HO, IB, LBU) and splanchnocranium (HC, RB, RH, UR), and only two variables (both neurocranial, BO, LO) showed a higher slope in muskrats. For the 10 variables in which the slope values were statistically similar, the intercept values showed significant differences, with muskrats exhibiting higher values of intercept in seven regressions related to length or to splachnocranial region (CL, DL, LD, LN, ZB, BP), and only one neurocranial variable (BBu). On the other hand, regressions also showed that the intercept of beavers was higher than that of muskrats in only three cases (BB, HD, LR). Additionally, muskrats showed enantiometry (i.e., reduction of the absolute size during growth *sensu* Huxley and Teissier, 1936) in one variable, interorbital breadth (IB) (Table 2).

4. Discussion

4.1. Ontogenetic pattern of the skull in beavers and muskrats

Muskrats and beavers are herbivorous, semi-aquatic species that use dentition and masticatory muscles to feed and construct burrows with vegetation, producing profound modifications of the landscape (Baker and Hill, 2003; Pardiñas et al., 2017; but see Bomske and Ahlers, 2021). Such characteristics represent a specialized lifestyle (a similar ecological niche), generating a potential convergent pattern of growth, acting as driver of cranial morphology (Harmon et al., 2005). In fact, both species share several morphological traits in the neuro and splachnochanium (see above). We expected that the studied species will share a similar growth allometry pattern, reflecting the selective forces such as ecology and behavior. However, despite the possibly similar mechanical stress undergone by skulls, both species may have overlapped some aspects of their ecology occupying different places of a multivariate morphospace, without overlapping their developmental trajectories (Fig. 8, Supplementary Material Fig. S4). Our main results suggest profound differences in the ontogenetic pattern of the skull between beavers and muskrats, which is likely the result of the phylogenetic distance and differences in size (Figs. 3 and 8, Tables 1 and 2). These results were a possibility since closely related species are often more similar than more distant ones, which is generally associated with evolutionary conservation (Üzüm et al., 2015; Tavares et al. 2016). Previous works in skull variation of rodents showed similar results (e.g., Caumul and Polly, 2005; Barčiová and Macholán, 2006; Barčiová, 2009; Pérez et al., 2009; Tavares et al., 2016). In beavers and muskrats, there was no clear association between the ecosystem engineer condition and skull growth pattern. The selective forces acting in the skull of two syntopic ecosystem engineers do not drive convergent allometric growth, despite the shared morphological traits. The differences in trends are spread throughout the skull (Table 1), affecting both the neurocranial region, such as the occiput and sense organs (bullae and orbits) and the splanchnocranium, where strong differences in the development pattern were observed (both in rostral and mandibular areas). Considering the shared specialized lifestyle, a conservative pattern of growth might be expected in the splanchnocranium, as well as a shared negative allometry in the neurocranial growth, which is considered as a generalized trend in mammals (Emerson and Bramble, 1993). The observed differences in the ontogeny of beavers and muskrats (despite their ecological parallelism) are both related to heterochronic events in shared characters, as well as in morphological differences patent in the adult skull. For example, allometric trends of the breadth of the occipital plate (BO, negative in beavers, positive in muskrats) reflect early development of the mastoid process and lambdoid crest in beavers (Fig. 1), which occurs later in muskrats (Fig. 2). Besides, the growth trends of the rostral height (RH, positive in beavers, negative in muskrats) reflect the elevation of the orbit in a more dorsal position on lateral view in beavers (Fig. 1), which is probably related to more developed swimming habit in beavers than muskrats. However, although most juvenile stages lack this character, the ability to move in an aquatic environment is present in beavers from an early age, being these very precocial for this behavior (Mott et al., 2011; Rosell and Campbell-Palmer, 2022). In mammals, the negative allometry of the braincase (exhibited herein by both species, Table 1) is related to the early morphogenesis of the nervous system, which induces the early development of the membranous bone of the braincase (Emerson and Bramble, 1993; Smith, 1997). The morphogenesis of the nervous system and the development of the membranous bone occur throughout the fetal and embryonic periods, and tend to decrease during the postnatal period (Wilson, 2011), being the negative allometry of the neurocranium plesiomorphic in several groups of mammals (e.g., marsupials, Flores et al., 2018, 2022; primates, Flores and Casinos, 2011; rodents, Segura et al., 2021a; carnivores, Segura et al., 2021b).

4.2. Growth and muscle arrangement

The space generated between the lateral wall of the braincase (reflected by the trend of the breadth of the braincase and interorbital breadth) and the zygomatic arches (reflected by the trend of the zygomatic breadth; Figs. 1 and 2; Table 1), allows the accommodation of part of the massive masticatory muscles (e.g., temporalis, masseter, and zygomatico-mandibularis muscles; Turnbull, 1970; Cox et al., 2011, 2012; Cox and Jeffery, 2015). In this trade-off for space, the larger masticatory muscles reduce the space available to orbits, which grow with negative allometry in beavers but positive in muskrats (Table 1 and 2). Muskrats exhibit a myomorph condition of muscle arrangement, showing isometry of the braincase and an enantiometric condition (i.e., reduction of absolute size during growth) in the interorbital breadth (Figs. 2 and 3; Table 2). It determines a pattern of growth deeply different than that of beavers, in which the braincase shows negative allometry and the interorbital breadth is isometric (Figs. 1 and 3; Table 1). The dominance of the masseter muscle in rodents allows the propalinal movements used to crush the food with the cheek teeth (Turnbull, 1970), and increases the bite force in both the molars and incisors (Maynard-Smith and Savage, 1959; Greaves, 1991). On the other hand, the temporal muscle may increase the mechanical advantage at the incisor level, which is especially important if the incisors are used to process harder material (Turnbull, 1970). Besides, a large temporal muscle helps to resist dislocating forces encountered when hard vegetation is bitten (Ball and Roth, 1995; Satoh, 1997; Michaux et al., 2007). In beavers, the masseter muscle accounts for more than 60% of the masticatory muscular mass, and the temporalis comprises 26.8 % (Cox and Baverstock, 2016). Both muscle masses together promote a bite force of approximately 80 kg, which is much larger than that predicted from body mass (Cox and Baverstock, 2016), and probably necessary for their described lifestyle. However, in beavers, the deep masseter is relatively smaller (Cox and Baverstock, 2016), whereas in muskrats the deep masseter and superficial masseter are equally important in size (Cox and Jeffery, 2015). Despite these differences in muscular arrangement and growth pattern, both species produce an effective and efficient bite, which permitted them to become highly successful exploiting or modifying aquatic environments and their associated vegetation.

4.3. Growth of the feeding apparatus and diet

The mechanical effort required for herbivory, which is the dietary type of feeding of beavers and muskrats, was linked to the development of a massive skull necessary to support large masticatory muscles (Michaux et al., 2007; Wilson and Sánchez-Villagra, 2010). But also, was related to the need to withstand the stress resulting from specific activities like food processing, considering the repeated chewing of fibrous vegetal material and the biting of hard food (e.g., trunks, branches), and burrows building (Samuels, 2009).

The elongation of the rostrum, mediated by the positive allometry of the diastema and nasals (Figs. 1 and 2, Table 1), is a trend shared by both species and by other rodents (e.g., Segura et al., 2021a). Such extension, which is not accompanied by the condyle basal length (which scales isometrically), allows a functional separation between incisors and molars (Druzinsky, 2015). Such separation has not been found in other mammals (e.g., didelphids, carnivores, primates; Giannini et al., 2010; Flores and Casinos, 2011; Segura and Prevosti, 2012; Segura, 2014; Tarnawski et al., 2014; Flores et al., 2018), except for the wild boar *Sus scrofa scrofa* (Sánchez-Villagra et al., 2017) and some diprotodontians (Flores et al., 2022). A proportionally wider rostrum, has typically been found in rodents and other herbivorous mammals, such as ungulates (Janis and Ehrhardt, 1988; Samuels, 2009). Besides, the growth rate of the rostrum in beavers (i.e., rostral height and breadth) was higher than that of the rest of the skull (Fig. 3), following the general growth of the large alveoli that house incisor teeth, as reported previously in other rodents (Wilson and Sánchez-Villagra, 2010; Segura et al., 2021a). Regarding the early dental eruption during ontogeny, a character shared with most members of Rodentia (Jekl, 2009; Tuttle and Buttler, 2020), both species exhibit negative allometry of toothrows, although the growth rate of the upper row is greater in beavers (Fig. 3; Table 2). This difference could be a consequence of the different dental formulas in both rodents, since beavers have four post-canine dental elements, although in proportion they are less anteroposteriorly lengthened than the three elements of muskrats (Figs. 1 and 2).

Although several factors, such as allometry (static and ontogenetic), ecological component (e.g., diet), and the evolutionary history, have been previously reported as pressures acting on skull shape in rodents (e.g., Caumul and Polly, 2005; Barčiová and Macholán, 2006; Barčiová, 2009; Pérez et al., 2009; Samuels, 2009; Tavares et al., 2016; Segura et al., 2021a; Barbero et al., 2023), these are not independent, and could constrain (or stimulate) different phenotypes (Michaux et al., 2007). Besides, the important size differences between species could also play a significant role in the structural formation of the skull because the multivariate growth trajectory in beavers are larger than in muskrats (i.e., beavers with more size variation during postnatal development); however, the direction of the multivariate ontogenetic trajectories is comparable but positioned in very different places on PC1 (Fig. 8; Supplementary Material Fig. S4). Moreover, beavers have a longer gestation period than muskrats (see

Table 3), and a larger size variation during postnatal ontogeny. The shorter multivariate growth trajectory and the mostly negative allometry of growth in muskrats (Table 1) suggest a precocial condition in which they reach a skull configuration comparable to that of adults from early age stages (Table 3). However, it could be an artifact caused by the representativeness of the muskrat's sample, where the kits were absent. In fact, the exploratory multivariate analysis excluding the kits of beavers (Supplementary Material Fig. S3) showed similar lengths in growth vectors of both species. It is also possible that the skull phenotype across development resembles phylogenetic differences since both species belong to different families. The ontogenetic trajectory divergence could also be related to the diet, because although both species are herbivorous, muskrats mainly feed on the roots of water plants, leaves, grasses, twigs, and bark of smaller trees (bushes) than beavers (Pietsch, 1982; Stefen et al., 2011); therefore, the functional commitment could be different. Further research could aim to establish and compare the quantitative postnatal pattern of growth in North American populations of beavers and muskrats, (which have been separated from the southern populations under study for more than seven decades), where both species evolved by exploiting other resources and under different selection pressures, as well as to know the growth trajectories of same species living alone.

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Declaration of Competing Interest

The authors declare that no competing financial or personal interests could inappropriately influence this work.

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Legends

Table 1. Results of the multivariate analysis of skull allometry in beavers (B) and muskrats (M). The observed departure is the difference between the observed allometric coefficient of a variable (i.e., the corresponding element of the first eigenvector per variable), and the expected coefficient (i.e., the value under the assumption of isometry, 0.224 for all variables). The remaining columns show jackknife results calculated with trimmed (m = 1) sets of pseudovalues (see section multivariate analysis of allometry for details). The resampled allometric coefficient is the value generated by first-order jackknife resampling. Bias is the difference between the resampled and observed coefficients. The jackknifed 95% confidence interval (CI) is provided, and the growth trend indicates the allometric variables are those whose CIs exclude the expected value under the assumption of isometry (0.224). "=" isometry; "+" positive allometry, "-" negative allometry.

Table 2. Test for common slopes and common intercepts for the ontogenetic trajectories of beavers (B) and muskrats (M). b_{1com}, common slope from reduced major axis analysis; $Log(b_0)_{com}$, common intercept from reduced major axis analysis; Lr, likelihood ratio (Warton et al., 2006); W, Wald statistic (Warton et al., 2006); P_{b1}, P-value of Lr parameter; $P_{(logb0)}$, P-value of W parameter.

Table 3. Biological information about beavers (*Castor canadensis*) and muskrats (*Ondatra zibethicus*) compiled from published literature (Jenkins and Busher, 1979; Willner et al., 1980; Baker and Hill, 2003; Pardiñas et al., 2017).

Fig. 1. Three ontogenetic stages (A, young; B, subadult; C, adult) illustrating dorsal, lateral, and ventral views of the skull, and lateral view of the mandible of beavers. Scale bar: 10 mm.

Fig. 2. Three ontogenetic stages (A, young; B, subadult; C, adult) illustrating dorsal, lateral, and ventral views of the skull, and lateral view of the mandible of muskrats. Scale bar: 10 mm.

Fig. 3. Plots of bivariate regressions for all variables (Log base10) versus geometric mean. In orange, beavers; in green, muskrats. Abbreviations as in Fig. 4.

Fig. 4. Measurements for dorsal, ventral, lateral views of the skull, and mandible. Abbreviations: BB, breadth of the braincase; BBU, breadth of the bulla; BO, breadth of the occipital plate; BP, breadth of the palate; CL, condyle-basal length; DL, diastema length; HBU, height of the bulla; HC, height of the coronoid process; HD, height of the dentary; HO, height of occipital plate; IB, interorbitary breadth; LBU, length of the bulla; LD, length of the dentary; LN, length of the nasals; LO, length of the orbit; LR, length of lower tooth row; RB, rostral breadth; RH, rostral height; UR, length of upper tooth row; ZB, zygomatic breadth.

Fig. 5. Plot of the Principal Component Analysis (first and second components) for beavers, including kit specimens. Light circles, kit specimens; dark circles, young specimens; light squares, subadult specimens; dark squares, adult specimens.

Fig. 6. Variable loadings on the first principal component of beavers (A) and muskrats (B). Abbreviations as in Fig. 4.

Fig. 7. Plot of the Principal Component Analysis (first and second components) for the ontogenetic sample of muskrats. Dark circles, young specimens; light squares, subadult specimens; dark squares, adult specimens.

Fig. 8. Plot of the principal component analysis (first and second components) for the combined ontogenetic samples of beavers and muskrats. Orange squares, beavers; green circles, muskrats.

Appendix A. List of specimens used in this study.

Appendix B. Definition of age stages of beavers and muskrats depicted by morphological characters.

Supplementary Material

Supplementary Material Fig. S1. Plot of the principal components analysis (first and second components) for ontogenetic sample of beavers, without the inclusion of kit specimens. Orange dark circles, young specimens; light squares, subadult specimens; dark squares, adult specimens.

Supplementary Material Fig. S2. Variable loadings on the first principal component of beavers, not including kit specimens. Abbreviations as in Fig. 4.

Supplementary Material Fig. S3. Plot of the principal component analysis (first and second components) for the combined ontogenetic samples of beavers and muskrats, without the inclusion of kits of beavers. Orange squares, beavers; green circles, muskrats.

Supplementary Material Fig. S4. Plot of the principal components analysis (first and second components) for the combined ontogenetic samples standardized with the geometric mean of beavers and muskrats, without the inclusion of kits of beavers. Orange squares, beavers; green circles, muskrats.

Supplementary Material Table S5. Summary of regressions of the cranial measurements on the geometric mean of beavers and muskrats. Abbreviations: n, sample size; R^2, adjusted coefficient of determination; log b_0, y-intercept; b_1, coefficient of allometry (Reduced Major Axis). Abbreviations of measurements as in Fig. 4.

Appendix A

List of specimens used in this study

Beavers (*Castor canadensis*) N=55 PCC (Proyecto Castor Canadensis):

Females: 305; 307; 356; 360; 542; 554; 555; 566; 570; 572; 573; 577; 664; 672; 675; 679; 681; 682; 701; 708; 718; 719; 720.

Males: 306; 313; 314; 359; 551; 560; 563; 564; 565; 575; 663; 669; 674; 676; 683; 684; 691; 693; 695; 699; 710; 714; 716; 717; 775; 776; 777; 784.

Unsexed: 308; 544; 576; 673.

Muskrats (*Ondatra zibethicus*) N=39 POZ (Proyecto Ondatra Zibethicus):

Females: 35; 40; 166; 184.

Males: 19; 22; 25; 26; 43; 57; 137; 147; 157; 163; 227.

Unsexed: 21; 23; 36; 38; 42; 49; 50; 52; 56; 96; 108; 110; 145; 146; 153; 160; 164; 165; 185; 187; 188; 189; 208; 210.

Appendix B

Definition of age stages of beavers (*Castor canadensis*) and muskrats (*Ondatra zibethicus*) depicted by morphological characters

Castor canadensis

Kit. Unfused spheno-occipitalis synchondrosis. Fourth element in process of eruption. Wide external auditory meatus, at the same level in the horizontal plane as the zygomatic arch.

Young. Unfused spheno-occipitalis synchondrosis. Fourth element erupted. Wide external auditory meatus still positioned at the same level in the horizontal plane as the zygomatic arch.

Subadult. Unfused spheno-occipitalis synchondrosis. Fourth element erupted. Narrow external auditory meatus positioned in the horizontal plane between the zygomatic arch and the suture squamosa.

Adult. Partially fused spheno-occipitalis synchondrosis. Fourth element erupted. Narrow external auditory meatus positioned in the horizontal plane above the zygomatic arch at the level of the suture squamosa.

Ondatra zibethicus

Young. Unfused spheno-occipitalis synchondrosis. No lambdoid crest. Foramen magnum in a ventral and posterior position. Occipital condyles at the same level as the occipital plane in lateral view. Interparietal bone visible in dorsal view. Skull length less than 50 mm (Otgonbaatar and Shar, 2019).

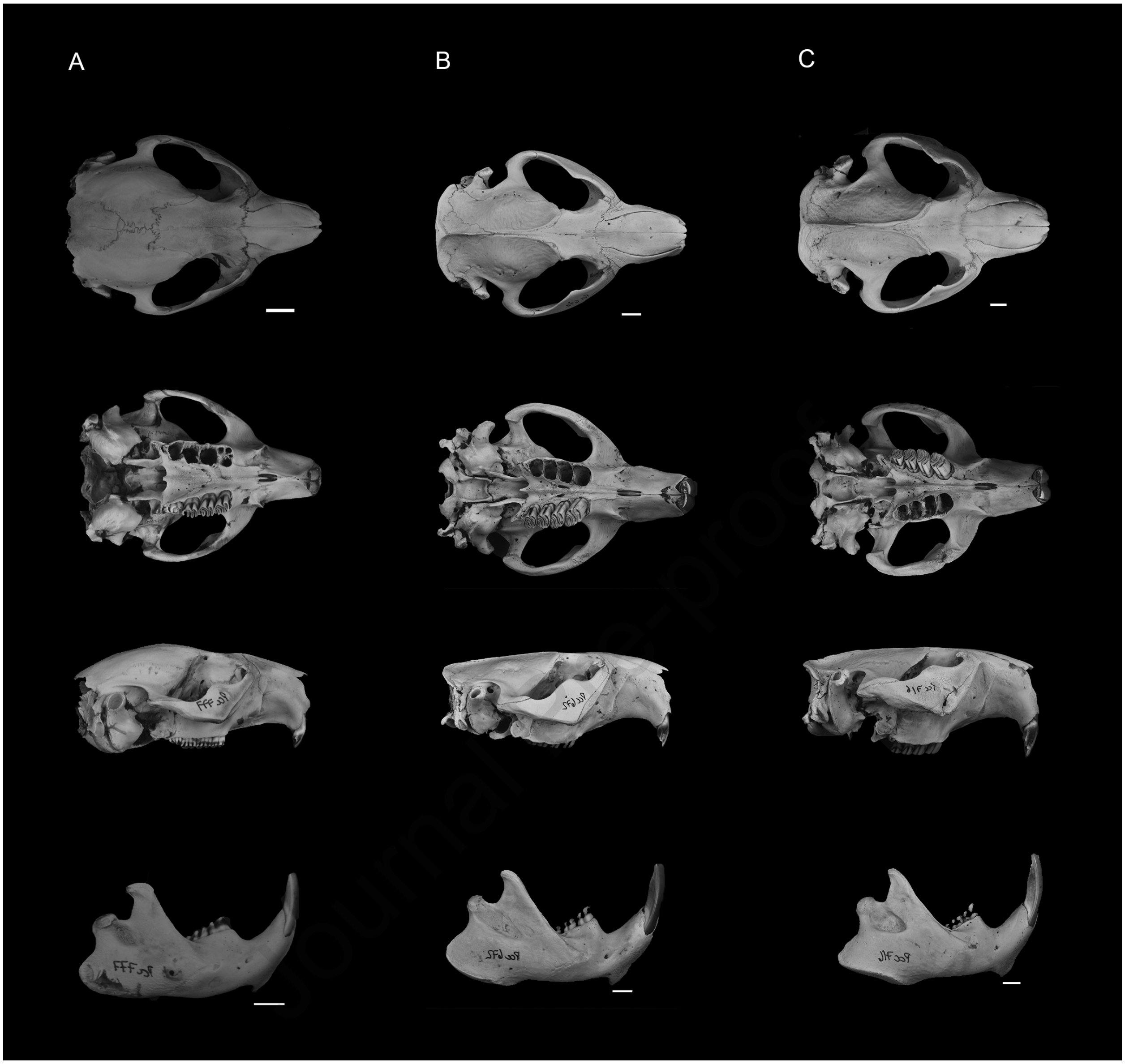
Subadult. Unfused spheno-occipitalis synchondrosis. Lambdoid crest barely marked. Foramen magnum in a ventral and posterior position. Occipital condyles at the same level as the occipital plane in lateral view. Interparietal bone visible in dorsal view. Skull length less than 60 mm (Otgonbaatar and Shar, 2019).

Adult. Fused spheno-occipitalis synchondrosis. Lambdoid crest notably marked. Foramen magnum in a posterior position. Occipital condyles exceed the level of the occipital plane in lateral view. Interparietal bone is barely visible in the dorsal view. Skull length greater than 60 mm (Otgonbaatar and Shar, 2019).

Variable	Species	Observed departure	Resampled Allometric coefficient	Bias	95% CI	Growth trend
BB	B	-0.218	0.005	0.005	-0.039-0.050	-
	M	-0.140	0.084	0.001	0.058-0.110	-
BBU	B	-0.022	0.202	-0.008	0.130-0.273	=
	M	-0.089	0.135	0.007	0.114-0.156	-
BO	B	-0.177	0.046	0.001	0.005-0.087	-
	M	0.17	0.394	-0.007	0.341-0.446	+
BP	B	0.065	0.289	-0.014	0.139-0.438	=
	M	0.017	0.24	-0.002	0.213-0.267	=
CL	B	0.001	0.225	-0.003	0.197-0.253	=
	M	0.012	0.236	0.000	0.221-0.251	=
DL	B	0.111	0.335	-0.008	0.306-0.364	+
	M	0.087	0.311	0.001	0.295-0.326	+
HBU	B	0.071	0.294	-0.010	0.265-0.324	+
	M	-0.123	0.1	0.005	0.074-0.126	-
HC	B	0.002	0.226	0.002	0.191-0.261	=
	M	-0.033	0.19	-0.001	0.158-0.223	-
HD	B	-0.050	0.174	0.000	0.139-0.209	-
	M	-0.042	0.182	-0.002	0.149-0.215	-
HO	B	0.023	0.246	-0.017	0.216-0.277	=
	M	-0.025	0.198	-0.002	0.182-0.214	-
IB	B	-0.020	0.204	-0.001	0.165-0.243	=
	M	-0.208	0.016	-0.002	-0.022-0.054	-
LBU	B	-0.048	0.176	0.006	0.134-0.217	-
	M	-0.137	0.087	0.004	0.065-0.108	-
LD	B	0.034	0.258	0.002	0.217-0.299	=
	M	-0.021	0.202	0.004	0.193-0.211	-
LN	B	0.090	0.314	-0.006	0.264-0.364	+
	M	0.073	0.297	-0.001	0.277-0.316	+
LO	B	-0.181	0.043	0.017	-0.010-0.096	-
	M	0.244	0.468	-0.026	0.441-0.494	+
LR	B	-0.068	0.156	0.001	0.124-0.188	-
	M	-0.12	0.103	-0.002	0.084-0.122	-
RB	B	0.045	0.268	0.006	0.229-0.308	+
	M	-0.007	0.217	0.001	0.203-0.231	=
RH	B	0.127	0.350	-0.002	0.307-0.394	+
	M	-0.042	0.182	0.015	0.155-0.209	-
UR	B	-0.102	0.122	0.011	0.087-0.157	-
	M	-0.091	0.133	-0.002	0.115-0.151	-
ZB	B	0.027	0.251	-0.008	0.233-0.269	+
	M	0.04	0.263	-0.001	0.243-0.284	+

	Common slope			Common intercept		
Variable	Lr_{b1}	P_{b1}	b_{1com}	W $_{(logbo)}$	$P_{(logbo)}$	Log ($_{b0}$)$_{com}$
BB	0.4740	0.4911	0.6361	32.2682	1.342E-08	B> M
BBU	3.1941	0.0739	0.9979	33.0430	9.014E-09	M> B
BO	47.2230	6.334E-12	M> B			
BP	2.1912	0.1387	1.2542	9.3897	0.0021	M> B
CL	0.0825	0.7738	1.2042	183.1422	0	M> B
DL	1.3244	0.2497	1.5431	402.7185	0	M> B
HBU	16.3582	5.242E-05	B> M			
HC	16.2398	5.580E-05	B> M			
HD	0.0638	0.8004	1.0446	5.1689	0.0229	B> M
HO	11.0493	0.0008	B> M			
IB	8.5504	0.0034	B> M			
LBU	5.8967	0.0151	B> M			
LD	1.7640	0.1841	1.1124	36.9583	1.206E-09	M> B
LN	0.0361	0.8491	1.5265	80.4787	0	M> B
LO	56.1904	6.572E-14	M> B			
LR	3.2845	0.0699	0.7181	24.3552	8.010E-07	B> M
RB	11.7812	0.0005	B> M			
RH	4.6860	0.0304	B> M			
UR	7.4995	0.0061	B> M			
ZB	0.4149	0.5194	1.3083	57.5306	3.330E-14	M> B

Species	Gestation period	Litter size	Birth weight	Adult weight	Weaning	Sexual maturity	Life span	Social system
Castor canadensis	107 days	3-4	340-630 g	16000-31000 g	3 months	1.5 years	10 years	monogamy
Ondatra zibethicus	25-30 days	4-8	20 g	700-1800 g	1 month	1 year	3-4 years	monogamy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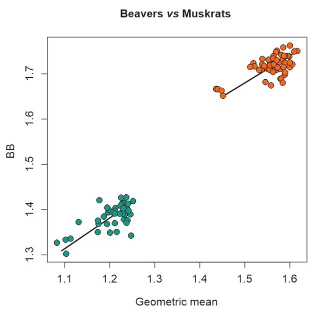
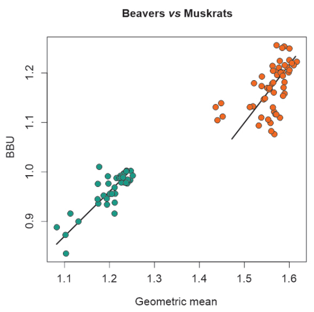


Beavers *vs* Muskrats



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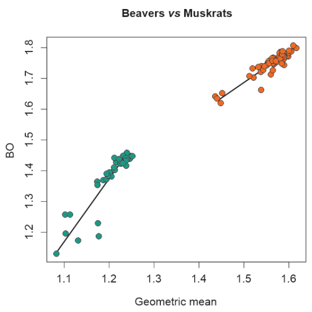

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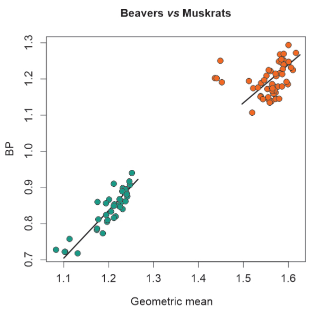

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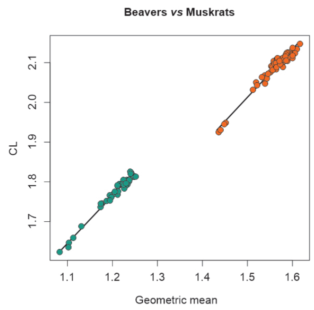

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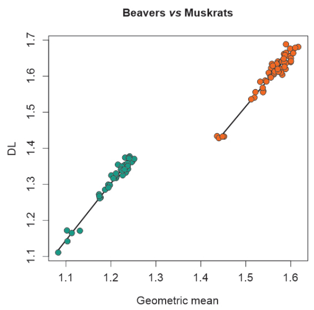

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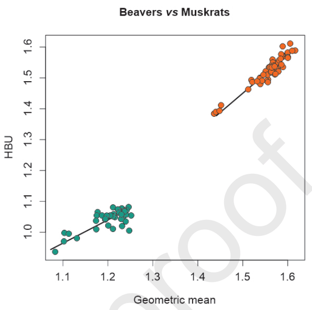

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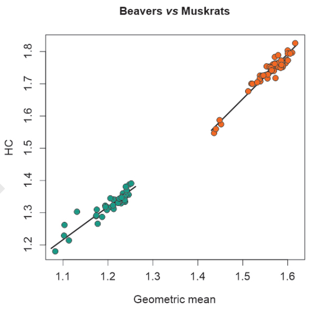

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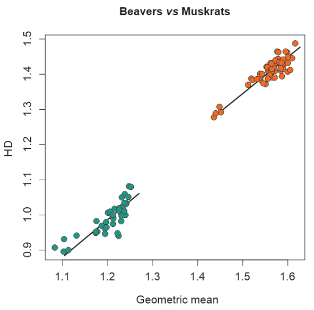

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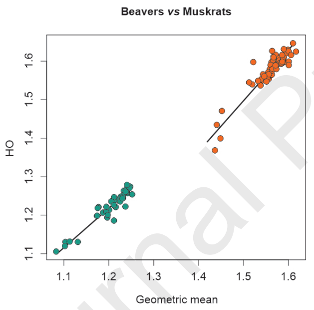

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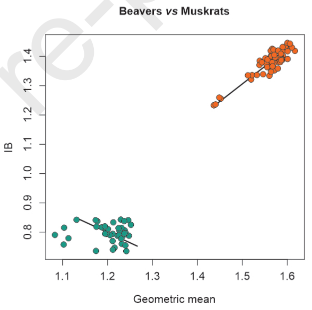

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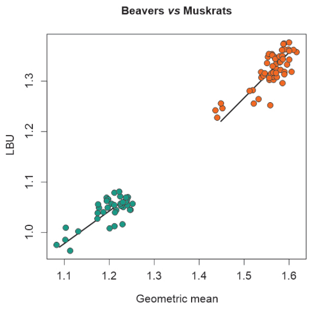

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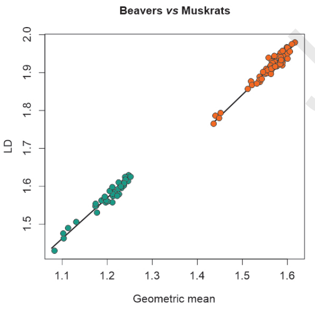

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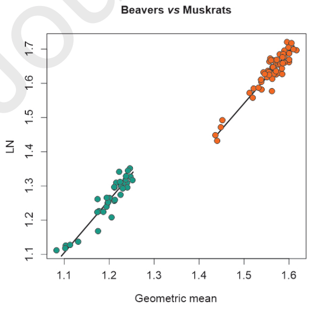

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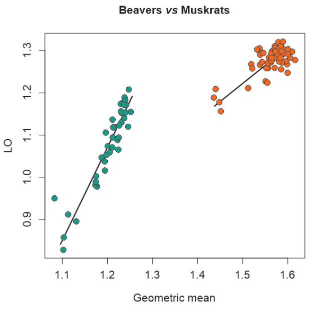

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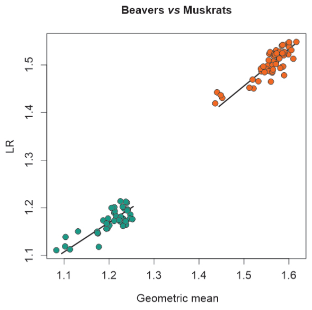

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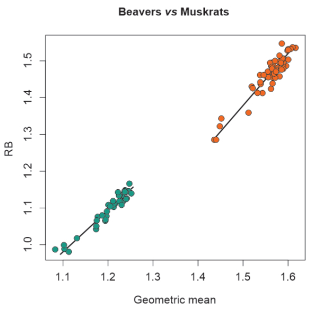

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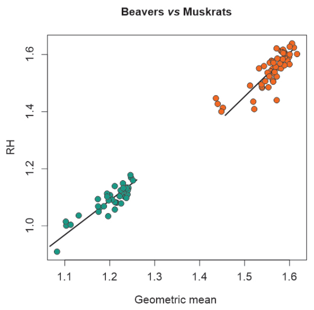

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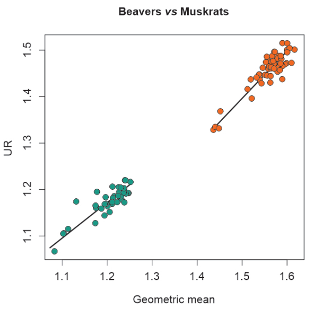

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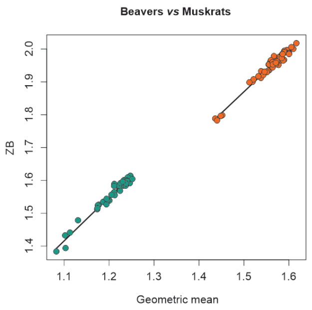

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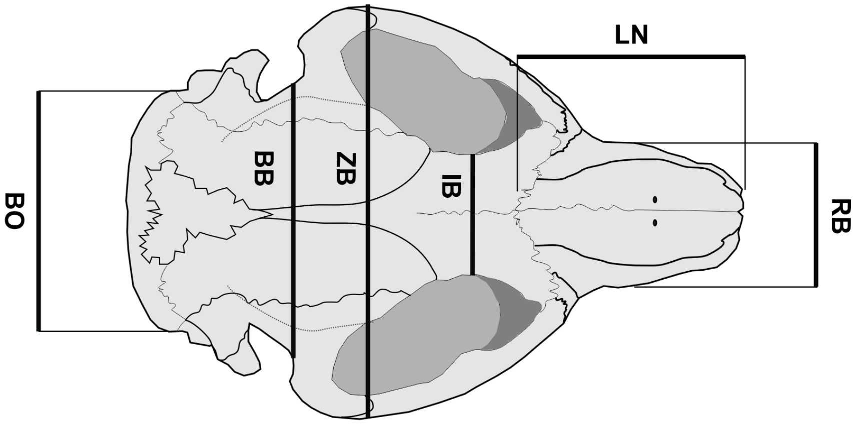
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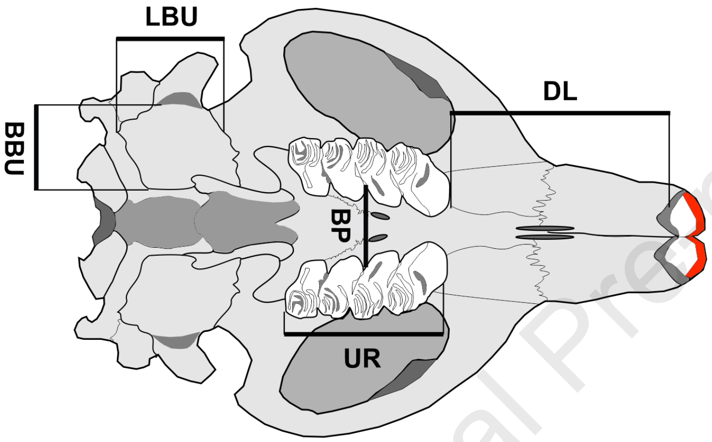
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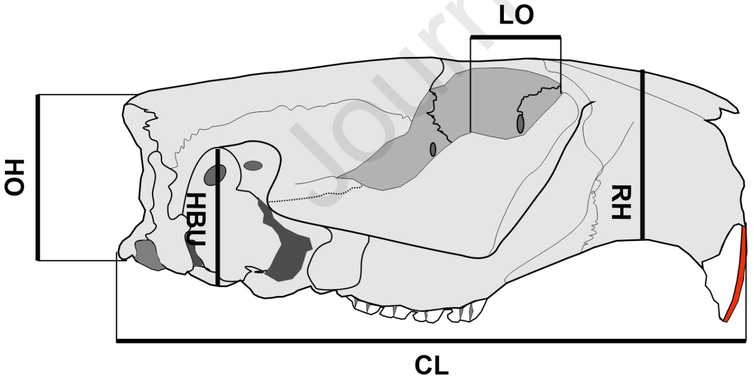
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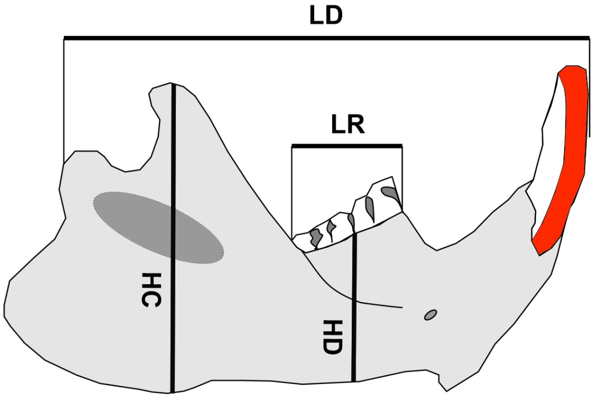
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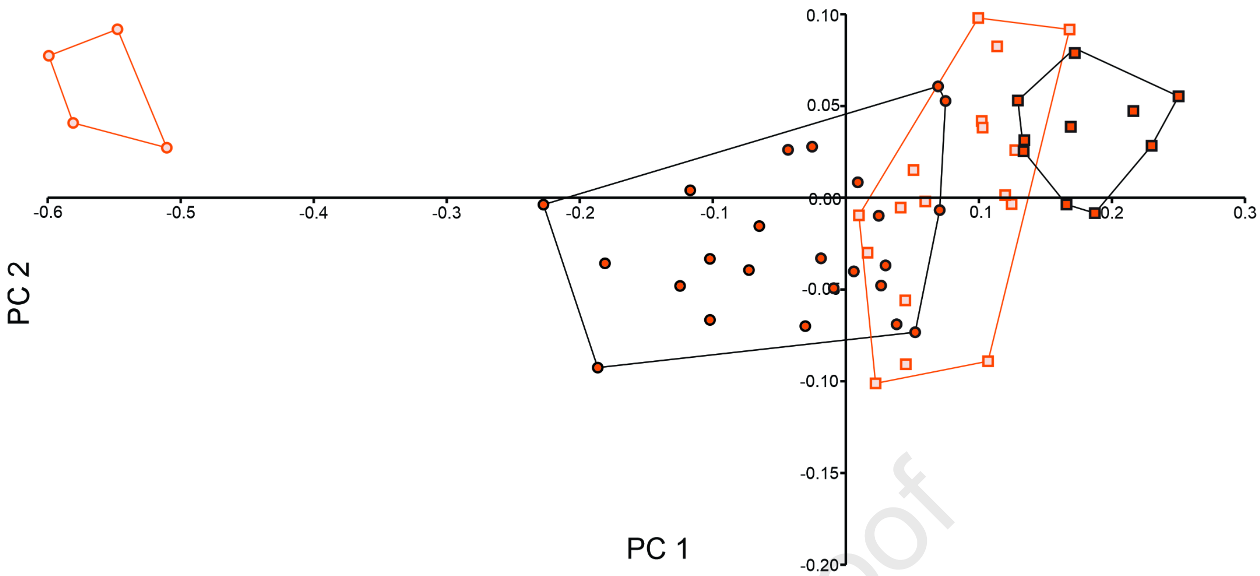
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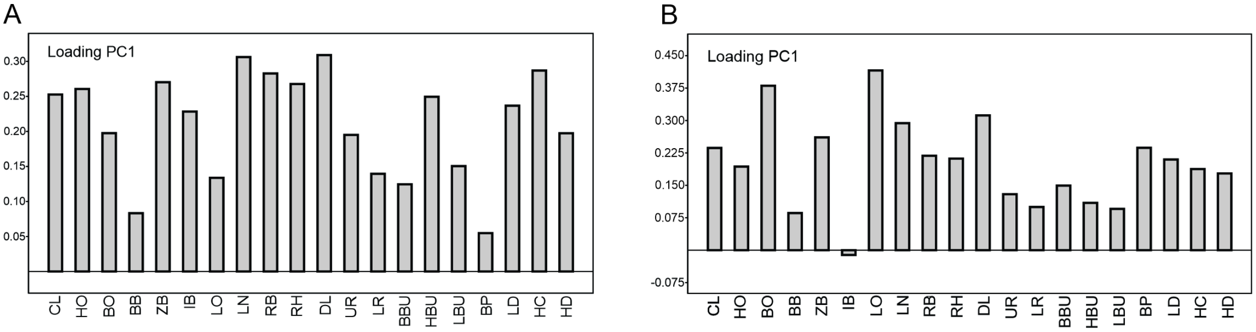
PC 2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Loading PC1
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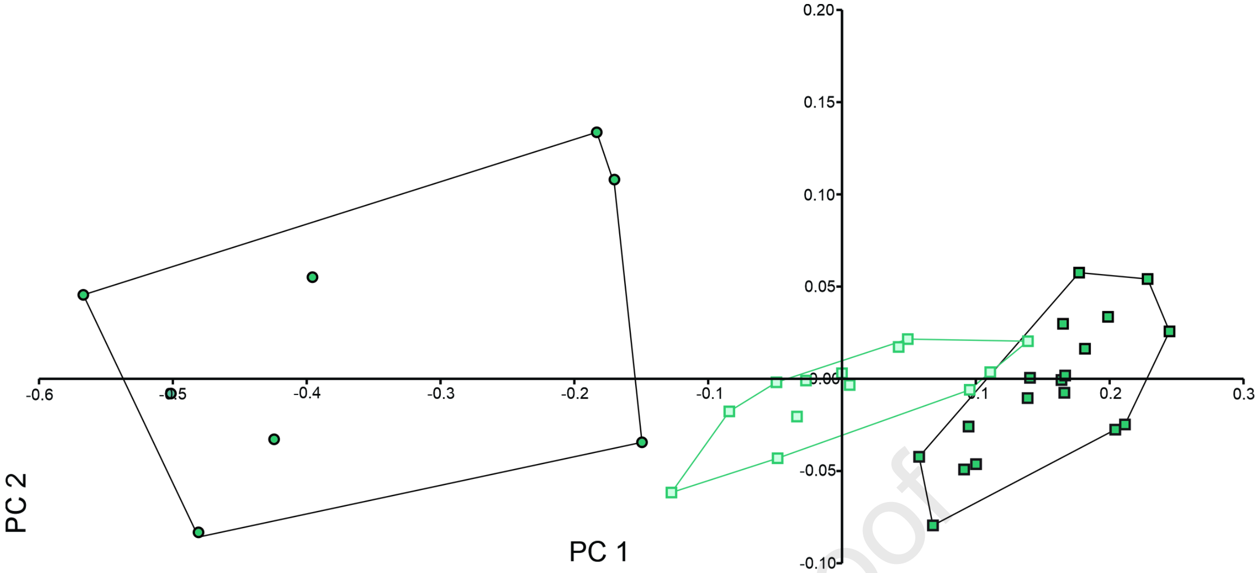

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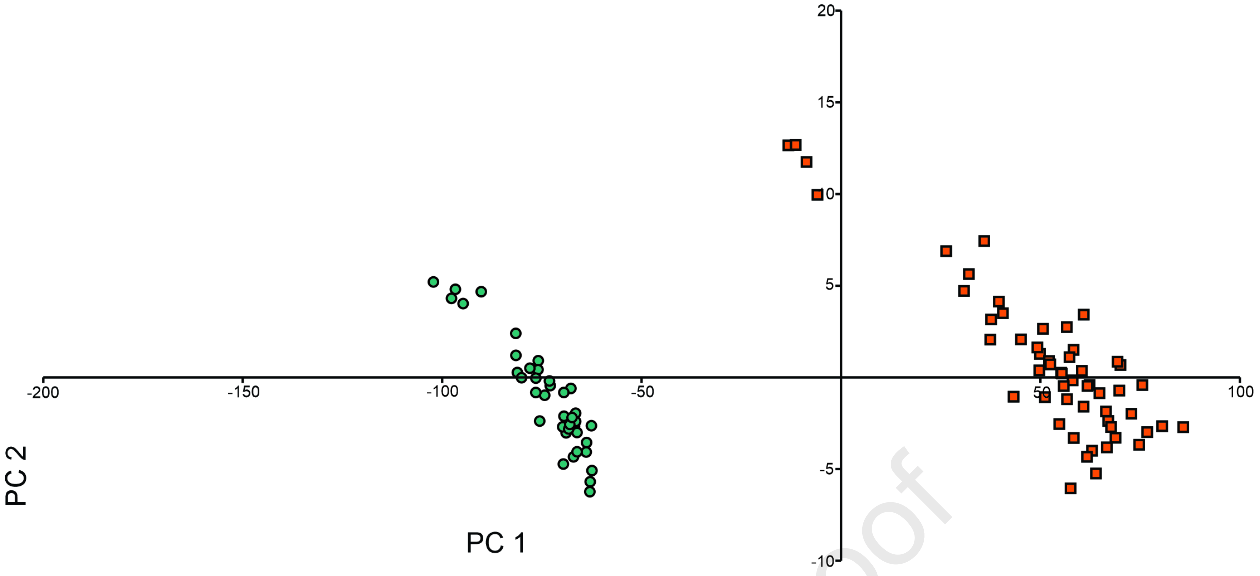
PC 1
PC 2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-150
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50
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PC 2
PC 1

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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