



# Skull Ontogeny of the Hyraxes *Procavia capensis* and *Dendrohyrax arboreus* (Procaviidae: Hyracoidea)

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## Abstract

Extant hyraxes are small, rabbit-sized, herbivorous paenungulates, with a notable feeding mechanism: they crop with the molars instead of the incisors, unlike most modern hoofed mammals. We investigated the postnatal development of the skull, and their functional correlates, in two extant representative forms of hyraxes, the terrestrial grazer *Procavia capensis* and the arboreal browser *Dendrohyrax arboreus*. We measured 18 linear variables representing fundamental descriptive and functional aspects of the skull, and estimated allometric equations on the basis of bivariate and multivariate analyses of an ontogenetic series of 32 specimens of *P. capensis* and 27 specimens of *D. arboreus*. Results showed that the ontogenetic trajectories of both species are similar in overall shape and size, but differ in localized regions of the skull associated with the masticatory apparatus. Examples include both differences in degree of allometry (upper postcanine row more positively allometric in *Procavia*) as well as opposing trends (positive allometry of diastema length in *Dendrohyrax* versus negative allometry in *Procavia*). In the mandible, the height of mandible and the length of the lower postcanine row showed significant differences. These changes could be associated with the acquisition of contrasting herbivorous specialization along the browsing-grazing gradient as exemplified in hyraxes.

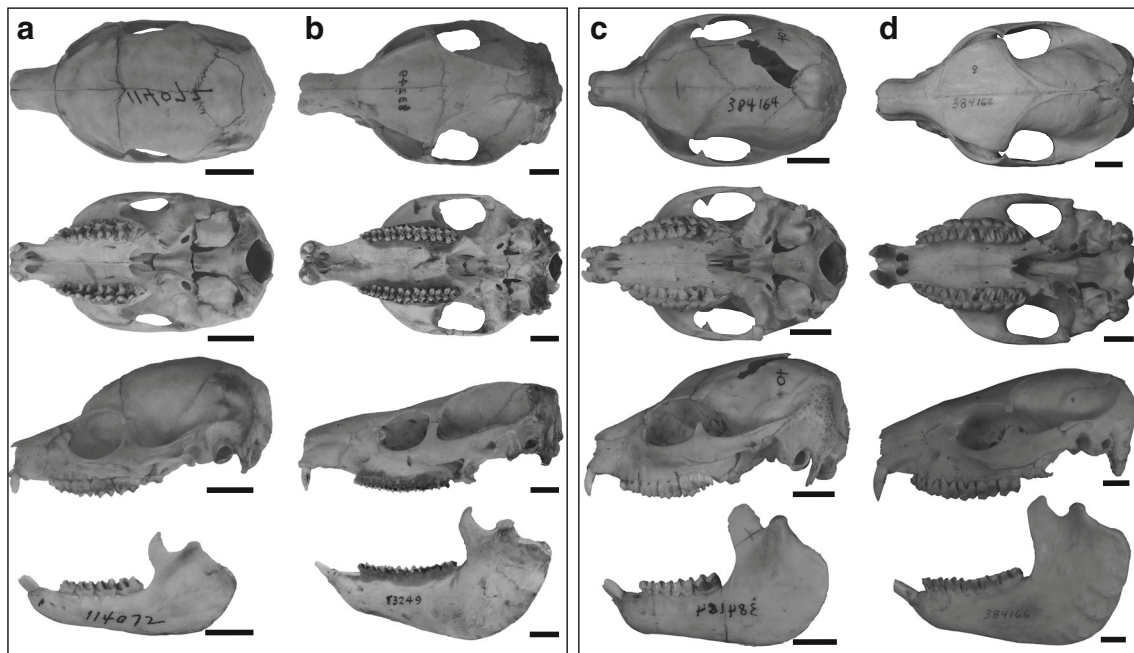
**Keywords** Allometry · Browsing-grazing gradient · *Dendrohyrax* · Hyrax · Ontogeny · *Procavia*

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## Introduction

The Hyracoidea are small-sized herbivores that originated in the Afro-Arabian landmass during the Eocene (Barrow et al. 2010) as part of the diversification of Paenungulata, a group of afrotherian hoofed mammals that also include proboscideans and sirenians (Tethytheria; Simpson 1945; Seiffert 2007; Asher and Helgen 2010). Extant hyraxes are restricted to tropical and subtropical habitats in continental Africa and the Middle East, across a wide range of elevations from 400 m below sea level near the shores of the Dead Sea, to 3500 m above sea level in East Africa (Shoshani 1992). However, this order was more diverse in the past, with 17 extinct genera (Rasmussen and Gutierrez 2010). Recent species are united in a single family, Procaviidae, with three extant genera, *Procavia*, *Heterohyrax*, and *Dendrohyrax* (Hoeck 2011). The three hyrax genera are quite similar and share many morphological character states, but nonetheless they can be differentiated by anatomical, physiological, and behavioral characters (Hoeck 1975; Corbert 1979; Shoshani 1992, 2001; Eley 1994).



**Fig. 1** Skull (dorsal, ventral, lateral) and mandible (lateral) of: *Dendrohyrax arboreus*, (a), infant (AMNH 114072); (b), adult (AMNH 83249); *Procavia capensis*; (c), infant (USNM 384164); (d), senile adult (USNM 384166). Scale bar: 10 mm

Hyraxes lack sexual size dimorphism (Hoeck 2011). The incisors are hypertrophied and resemble tusks (Fig. 1); unsuitable for food processing, incisors are not used in the ingestion of plants that compose their diets (Sale 1966). Thus, hyraxes exhibit a rather unconventional mode of food intake using the molar teeth; for browsing they turn the head sideways (at 90° to the body) and use the molar teeth to bite off the shoot or leaf and take it in through the side of the mouth (Sale 1966). Hyraxes lack permanent canine teeth and exhibit a large diastema between incisors and premolars (like many ungulates), more pronounced in the upper than in the lower jaw (Eley 1994); the upper diastema is longer in *D. arboreus* (~17 mm) than in the similar sized *P. capensis* (~9 mm) (Fig. 1b, d; Thomas 1892). *Procavia* and *Heterohyrax* have a short muzzle and a high and broad cranium with an incomplete postorbital bar, while *Dendrohyrax* have a large muzzle and a narrow and flattened cranium, with a depression above the orbit and a complete postorbital bar (Fig. 1; Shoshani 1992). Hyraxes are agile climbers: *Procavia* (rock hyrax) and *Heterohyrax* (bush hyrax) occupy rocky outcrops (kopjes) and are gregarious and diurnal, while *Dendrohyrax* species (tree hyraxes) are arboreal, usually solitary, and nocturnal (Eley 1994; Hoeck 2011). All species are herbivores with a diet consisting mostly of leaves, twigs, grasses, fruit, and some insects. Although they do not ruminate, the digestive system is complex, with three separate areas of microbial fermentation for food, similar to that of ruminant ungulates (see Hoeck 2011). *Procavia capensis* and *D. arboreus* exhibit both similarities and differences in their biology, which are summarized in Table 1.

Most authors refer to the dietary habits of extant hyraxes as either grazers or browsers, including the use of mixed-feeders categories, which is also true, for most herbivorous mammals

**Table 1** A comparison of *Procavia capensis* and *Dendrohyrax arboreus* showing important biological events and a summary of ecological features in both species

	<i>Procavia capensis</i>	<i>Dendrohyrax arboreus</i>
Gestation period (months)	Six to seven	Seven to eight
Young in litters	One to four	One to two
Average birth weight	195 g	200 g
Weaning (months)	One to five	Three to seven
Sexual maturity (months)	16–17	20–30
Replacement of the milk dentition by permanent dentition	After the eruption of M1	After the eruption of M2
Average adult weights	4.3 kg	1.7–4.5 kg
Total length of adults	305 to 550 mm	320 to 600 mm
Habits	Diurnal, gregarious, and live in crevices and cavities in the rocks	Nocturnal, solitary, and arboreal
Diet	Grazer	Browser/Folivore
Hypsodonty index (HI)	1.69 (hypsodont)	1.127 (brachydont)

Biological events and a summary of ecological features in both species were extracted from the literature (Churcher 1956; Sale 1960; Millar 2015; Olds and Shoshani 1982; Rudnai 1984; Janis 1988; Gaylard and Kerley 1997; Hoeck 2011; Milner and Gaylard 2013)

(e.g., Janis 1990; Mendoza and Palmqvist 2008; Cassini 2013 and references therein). Bargo and Vizcaíno (2008) remarked upon the ambiguous nature of the terms browsing and grazing, because the terms have been used to refer both to the mode of food acquisition (i.e., selectivity) and to the type of food ingested (i.e., botanical connotation). Following Janis (2008), we adopt the latter concept in our work. As such, browsers and grazers differ in many traits including behavior, physiology, and morphology (Clauss et al. 2008). In particular, several authors agree that grazing ungulates tend to have higher hypsodonty index (i.e., relative crown height), wider muzzle and palate, and longer molar versus premolar tooth rows than browsers do (see also Table 1 in Mendoza 2005 and Tables 3.4 and 3.5 in Clauss et al. 2008). Hypsodonty has evolved numerous times in mammals and probably represents a fairly simple developmental change, involving delaying the closure of the tooth roots (Janis 1988) or any of a series of heterochronic changes from crown to root (Koenigswald 2011). Hypsodonty is present for instance in tusks, as in hyraxes (Koenigswald 2011), but it is more often referred to cheek teeth and it has been associated with grass consumption (Williams and Kay 2001) and foraging in open habitats (Mendoza and Palmqvist 2008). Compared with artiodactyls and perissodactyls, the rock hyrax *P. capensis* has a low hypsodonty index (HI  $\sim$  1.69; Janis 1988) but higher than the value we calculated for *D. arboreus* (mean HI = 1.13; sd. = 0.0305;  $n = 3$ ). Mendoza et al. (2002) related this lower HI to the lower metabolic rate and the consequently lower than expected daily intake for an ungulate of its size. Thus, hyraxes are shown to vary along the brachyodont-hypsodont gradient, with *Dendrohyrax* being typically brachyodont and *Procavia* exhibiting a tendency to hypsodonty.

The Hyracoidea have received much attention in ecological, systematic, molecular, and behavioral research (e.g., Roche 1975; Prinsloo and Robinson 1992; Shoshani 1992, 2001; Eley 1994; Milner and Harris 1999; Visser 2013). Anatomy of fossil and extant forms has also been intensely investigated (e.g., Thomas 1892; Beddard 1909; Churcher 1956; Bothma 1967; Klein and Cruz-Urbe 1996; Pickford 1996, 2005; Barrow et al. 2010). However, the paucity in developmental data precludes in-depth evolutionary comparisons with paenungulates and other hoofed mammals. An account of the morphological changes with functional significance during any period of development is lacking for procaviids as a group.

Here, we contribute a quantitative study of postnatal skull ontogeny in two contrasting hyrax species in a comparative framework, the terrestrial, predominantly grazing rock hyrax *P. capensis*, and the arboreal, browsing tree hyrax *D. arboreus*. Cranial ontogeny is highly relevant to understanding the relationship between function and trophic ecology; here, we describe the ontogenetic basis of cranial differences between two species

that constitute one important example of the key browsing-grazing functional gradient in the evolution of ungulates.

## Material and Methods

### Study Specimens

We analyzed postnatal ontogenetic series of 32 specimens (with 18 females and nine males) of *Procavia capensis*, and 27 specimens (with 14 females and seven males) of *D. arboreus*. Specimens (listed in Table 2) are housed in the Mammal collections of the Field Museum of Natural History (FMNH, Chicago, USA), National Museum of Natural History, Smithsonian Institution (USNM, Washington, D.C., USA), and the American Museum of Natural History (AMNH, New York, USA).

We assigned relative individual dental age stages or IDAS, following Anders et al. (2011). Our sample covered all stages in the ontogenetic series of both species, infant, juveniles, adults, late adults, and seniles (IDAS 1 to 5, respectively; Table 2). This methodology has the advantage to be generalized and useful for both fossil and extant placental mammals, providing a wide comparative basis for ontogenetic studies. Thus, we provide this classification as informative and for future comparative purposes. The *Dendrohyrax* sample was composed of nine infants (IDAS 1), of which the smallest specimen was 51.37 mm in condyle-basal length (FMNH 17505, Table 2); eight juveniles (IDAS 2), five adults (IDAS 3), three late adults (IDAS 4), and two senile specimens (IDAS 5), of which the largest specimen was 94.12 mm in condyle-basal length (FMNH 17508, Table 2). The *Procavia* sample consisted of six infants, of which the smallest specimen was 44.77 mm in condyle-basal length (USNM 468208, Table 2), 13 juveniles, five adults, four late adults, and four senile specimens, of which the largest specimen was 92.41 mm in condyle-basal length (FMNH 47371, Table 2).

### Study of Growth and Measurements

Allometry refers broadly to how specific traits grow at a given rate as compared with the body growing as a whole. In morphometric studies, the term refers to the association between size and shape variation (Huxley 1932; Mosimann 1970; Gould 1977; Mitteroecker et al. 2013). Ontogenetic allometry (or growth allometry) deals with covariation among characters (modifications in structures) as the animal grows (Klingenberg and Zimmermann 1992; Klingenberg 1996). In addition, allometry explicitly considers timing of changes as the rate of development (i.e., the rate of change in shape) and the rate of growth (i.e., the rate of change in size) throughout the lifetime (Piras et al. 2011 and references therein). Allometry of size

**Table 2** Specimens of *Dendrohyrax arboreus* (Da) and *Procapra capensis* (Pc) examined in this study

Sp	Collection no	GM	CBL (mm)	UPL (mm)	IDAS
Da	AMNH_83253	1.224356	72.40444	18.850079	1
Da	AMNH_53806	1.381578	58.69590	14.725033	1
Da	AMNH_53812	1.407957	58.96972	14.319810	1
Da	AMNH_114072	1.206464	54.35871	12.735153	1
Da	AMNH_53843	1.218867	58.60775	15.817291	1
Da	FMNH_17510	1.441130	63.52615	17.396224	1
Da	FMNH_17505	1.445619	51.36765	13.640310	1
Da	FMNH_17494	1.298199	55.56975	13.621244	1
Da	FMNH_17493	1.461177	62.18063	19.590177	1
Da	AMNH_27843	1.403725	81.86932	28.933648	2
Da	AMNH_83246	1.323533	85.81100	28.323730	2
Da	AMNH_83255	1.454487	83.34641	29.088464	2
Da	AMNH_36002	1.454954	78.86153	27.034116	2
Da	AMNH_114074	1.228562	84.84017	26.089282	2
Da	FMNH_17488	1.349173	61.74773	19.412846	2
Da	FMNH_17487	1.388704	72.84018	24.667854	2
Da	FMNH_17490	1.452255	81.08039	24.493272	2
Da	AMNH_83259	1.442198	88.87053	32.268987	3
Da	AMNH_83249	1.408280	91.80944	32.573740	3
Da	FMNH_17489	1.189256	91.31508	32.695721	3
Da	FMNH_17495	1.155545	86.46957	31.136886	3
Da	FMNH_17501	1.254746	89.99838	32.333643	3
Da	AMNH_27842	1.390141	86.78767	31.927719	4
Da	AMNH_83247	1.425349	94.12369	34.829659	4
Da	FMNH_86883	1.398646	84.40435	31.359931	4
Da	AMNH_55878	1.428433	86.63987	33.033740	5
Da	FMNH_17508	1.268158	93.91804	32.878844	5
Pc	FMNH_104811	1.362514	75.56154	21.658478	1
Pc	FMNH_17474	1.266852	59.74735	19.053934	1
Pc	USNM_382483	1.190703	48.04444	12.094127	1
Pc	USNM_384164	1.269688	59.69291	15.762406	1
Pc	USNM_468209	1.134452	45.71178	9.074377	1
Pc	USNM_468208	1.115143	44.77520	9.712188	1
Pc	FMNH_17502	1.352880	66.46954	25.793027	2
Pc	FMNH_17503	1.305403	60.74681	22.266077	2
Pc	FMNH_34195	1.376341	79.42163	25.432480	2
Pc	FMNH_86880	1.447313	85.15284	37.711571	2
Pc	FMNH_86881	1.414036	85.14788	32.160999	2
Pc	FMNH_44876	1.351250	72.16070	27.843618	2
Pc	FMNH_17471	1.321585	74.33789	24.580701	2
Pc	FMNH_17484	1.297250	61.75655	17.927977	2
Pc	FMNH_108214	1.365420	77.67550	22.133737	2
Pc	FMNH_135738	1.433286	84.35117	27.201979	2
Pc	FMNH_81519	1.357369	75.83241	30.943757	2
Pc	USNM_384169	1.333141	68.48341	19.599351	2
Pc	USNM_384170	1.348894	69.93338	17.477701	2
Pc	FMNH_73066	1.463820	90.26247	39.203466	3
Pc	FMNH_73025	1.441447	85.69152	36.321193	3

**Table 2** (continued)

Sp	Collection no	GM	CBL (mm)	UPL (mm)	IDAS
Pc	FMNH_57427	1.440565	88.13949	38.964514	3
Pc	USNM_350109	1.380199	76.08116	35.581761	3
Pc	USNM_350106	1.429498	87.76672	36.503898	3
Pc	FMNH_17486	1.464812	86.46278	35.940850	4
Pc	FMNH_47372	1.475555	90.77844	37.351801	4
Pc	FMNH_47377	1.430381	87.13721	37.570651	4
Pc	USNM_122543	1.439286	87.38684	35.074653	4
Pc	FMNH_73057	1.418278	82.24368	36.803748	5
Pc	FMNH_47371	1.459798	92.40727	37.436652	5
Pc	FMNH_60412	1.404867	80.05380	37.069300	5
Pc	USNM_384166	1.463793	92.39808	39.675781	5

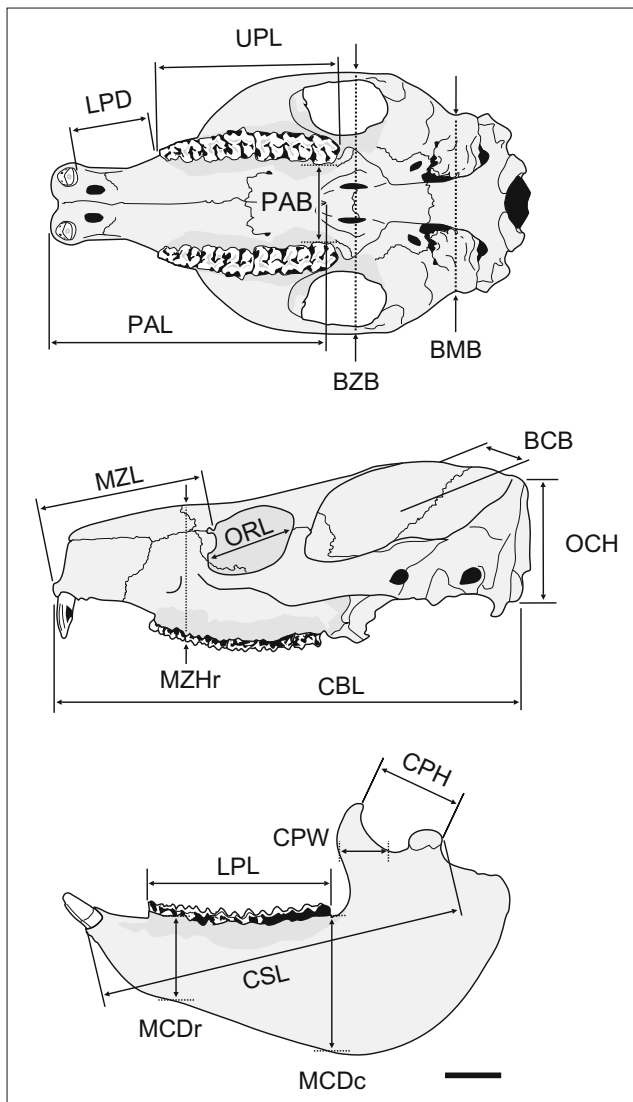
*Abbreviations:* *Sp*, species; *GM*, geometric mean; *CBL*, condyle-basal length; *UPL*, upper postcanine tooth row length; *IDAS*, individual age stages

compares shape changes against overall size along a growth series (i.e., rate of development versus rate of growth) wherein the time frame is implicit. Consequently, the association between size and shape across different age stages can be used as an estimate of a population's ontogenetic trajectory, especially when the calendar ages are not known (Mitteroecker et al. 2013). In our study, we use a Mixed Cross-Sectional Data (sensu Cock 1966) collected in different specimens in several known relative age stages (i.e., IDAS, Table 2). For the allometric analysis, we used 18 skull linear measurements (Fig. 2; Table 3) including length, breadth, and height of neurocranial and splanchnocranial components describing overall skull structure and general functional attributes. The craniomandibular dimensions analyzed herein partially overlap with those considered in other morphometric studies of mammalian skulls (e.g., Abdala et al. 2001; Giannini et al. 2004, 2010; Cassini et al. 2012, 2015; Flores et al. 2013; Tarnawski et al. 2014a, b, 2015). We pooled males and females of all ages in a single sample given the lack of sexual size dimorphism in hyraxes (Hoeck 2011), and then analyzed the data in both bivariate regression and multivariate allometry frameworks. Both methodologies fall in the concept of allometry of size in which developmental time is implicit in the growth series, and ontogenetic changes are compared against a change in size (see Abdala et al. 2001). The regression approach is suitable for statistical comparison of slopes, intercepts, and shifts of regressions between both species, whereas the multivariate approach focuses on allometric coefficients all simultaneously affected by size as a latent variable (see below).

### Bivariate Analyses

The ontogenetic trajectories were obtained by bivariate linear regressions after log transformation (log10) of the





**Fig. 2** Skull and mandible measurements used in this study. Variable abbreviations as in Table 3

measurements (Weston 2003). In the comparisons of ontogenetic trajectories, there are different growth patterns in a common size-shape space, where size is a proxy of time (see Reilly et al. 1997; Abdala et al. 2001; Piras et al. 2011; Sheets and Zelditch 2013). The trajectory itself may differ in direction (slope), position ( $y$ -intercept), and in length (shift). There are three basic types of evolutionary change (Weston 2003; Tarnawski et al. 2014a, b): 1. ontogenetic scaling: trajectories overlap so direction and position are the same and trajectories differ in their offset; 2. lateral shift: in which the trajectories share direction but the position is different (parallel trajectories with different intercept), indicative of change in the onset (i.e., juveniles of one group resembles an older or younger age-class of the other group); and 3. directional change, in which trajectories are different in the direction and position as reflected in the slope, indicative of novel modes of postnatal

growth (e.g., convergent to the same offset shape or divergent from the same onset shape).

In bivariate analysis, the scaling of any measurement can be affected strongly by the choice and scaling of the independent variable (Smith 1981; Wayne 1986). Several researchers have taken the total skull length (TSL), or a correlated measurement such as the condyle-basal length (CBL), as a proxy of overall size and as an independent variable (e.g., Abdala et al. 2001; Flores et al. 2003; Weston 2003; Giannini et al. 2004; Cassini et al. 2012; Kruska and Steffen 2013), because they demonstrated that it was isometric. However, this was not the case in all mammalian groups (see Tarnawski et al. 2014a, b, 2015). In hyraxes, CBL exhibited negative allometric growth (see below). To avoid the bias of such trends, we used the geometric mean of all cranial and mandibular measurements as the proxy of size and so the independent variable (Mosimann 1970; Tarnawski et al. 2015 and references therein). To examine the allometric changes of each variable to overall size (geometric mean), we used the log transformation of the power growth function,  $y = b_0 \cdot x^{b_1} \cdot e$ , to obtain the equation of allometry:  $\log(y) = \log(b_0) + b_1 \log(x) + \log(e)$ , where  $y$  is the focus variable,  $\log(b_0)$  is the  $y$ -intercept,  $x$  is the geometric mean,  $b_1$  is the slope of the line or coefficient of allometry, and  $e$  is the error term (see Alexander 1985; Giannini et al. 2004). We use the standardized major axis (SMA) regression to determine an axis or line of best fit because is more appropriate than the ordinary least squared regression (OLS) for dealing with allometric approaches (for extensive overviews on the subject, see Warton et al. 2012). Following Mitteroecker et al. (2013), in the classic concept of allometry a trait is considered as “negatively” or “positively” allometric if it increases less or more in size than other traits, or overall size, do(es). The relationship between the two variables is isometric when the slope is equal to one (a value expected under geometric similarity between two variables with the same dimensionality; Peters 1993). As a first step, we performed  $F$ -tests to assess the significance of the deviations from isometry in the allometry coefficients under the null hypothesis  $b_1 = 1.0$  (Warton and Weber 2002). Consequently, if  $b_1 < 1.0$  the case was one of “negative” allometry, and of “positive” allometry if  $b_1 > 1.0$  (Emerson and Bramble 1993). Testing for a common interspecific coefficient of allometry between *P. capensis* and *D. arboreus* for a given variable was the second step in the analysis. We used the likelihood ratio test to find a common SMA slope following Warton et al. (2006). If both species shared a common coefficient of allometry, the significance of a common constant of normalization ( $y$ -intercepts) was compared using the Wald statistic (Warton et al. 2006). Finally, if both slopes and  $y$ -intercepts were shared, the data points were scattered around a common axis with no difference in elevation. The Wald statistic was to test the hypothesis that there might be an ontogenetic shift along the axis, as in Warton et al. (2006). All coefficients, statistical

**Table 3** Abbreviations of the linear skull measurements

Acronym	Measurement	Definition
BCB	Braincase breadth	Greatest breadth of the braincase.
BMB	Bimeatal breadth	Between the lateral most edges of the auditory meatus.
BZB	Bizygomatic breadth	Between the lateral most edges of the zygomatic arches.
CBL	Condyle-basal length	From the rostral most end of the premaxilla to the caudal most end of the occipital condyle on the sagittal plane.
CPH	Coronoid process height	From the dorsal most end (at the midpoint) of the coronoid process to the caudal most point of the condylar process.
CPW	Coronoid process width	From the ventral most point of the notch between the coronoid and condylar processes to the anterior most point in a straight line perpendicular of the coronoid length axis.
CSL	Condyle - symphysis length	From the rostral most end of the mandibular symphysis to the caudal most part of the condylar process.
LPD	Diastema length	From the distal alveolar edge of I1 to mesial alveolar edge of the first cheek tooth (P1).
LPL	Lower postcanine tooth row length	From the mesial alveolar edge of the first cheek tooth (P1) to the distal alveolar edge of the last cheek tooth.
MCDc	Mandibular corpus depth in last functional tooth	From the caudal edge of the alveolus of the last functional tooth to the ventral most point of the mandible, perpendicular to the alveolar line.
MCDr	Mandibular corpus depth in pm1	From the caudal edge of the alveolus of the 1st functional tooth to the ventral most point of the mandible, perpendicular to the alveolar line.
MZHR	Muzzle height	From the caudal border of the alveolus of the 2nd functional tooth to the dorsal most point of the cranium (perpendicular to the alveolar row).
MZL	Muzzle length	From the apex of the premaxilla to the anterior margin of the orbit.
OCH	Occipital plate height	From the base of the foramen magnum to the apex of the occipital ridge.
ORL	Orbital length	Greatest orbit length from the more rostral end of the orbital edge to postorbital process of the jugal bone.
PAB	Palate breadth	At the level of distal alveolar edge of the last cheek tooth.
PAL	Palate length	From the rostral most end of the premaxilla to the caudomedial end of the palatine (torus palatinus).
UPL	Upper postcanine tooth row length	From the mesial alveolar edge of the first cheek tooth (P1) to the distal alveolar edge of the last cheek tooth.

parameter estimations, and tests were performed using `smatr` 3.4–3 package in R (Warton et al. 2012).

### Multivariate Analysis

We used a multivariate approach to allometry based on the generalized allometry equation proposed by Jolicoeur (1963). In contrast with bivariate analyses, multivariate allometry considers size as a latent variable affecting all original variables simultaneously (see also Giannini et al. 2004). The various allometric relationships of all variables with the latent size can be expressed in the first eigenvector of a principal components analysis (PCA). This eigenvector is extracted from a variance-covariance matrix of log-transformed variables and is scaled to unity. In this approach, allometry is a deviation with respect to a hypothetical isometric eigenvector, which represents pure size change. All eigenvector elements are the same and represent the expected isometric value; it is calculated as the squared root of  $1/p$  with  $p$  equal to the number of variables. The hypothetical isometric vector equals 0.236 for 18 skull variables. To estimate

the statistical deviation from isometry of our variable set, we used the application of jackknife developed by Giannini et al. (2004) and applied in several studies (see Flores et al. 2015 and references therein). This technique generates confidence intervals for each of the empirically derived first-eigenvector elements (Giannini et al. 2010). If the confidence interval for a given variable includes the isometric value (here 0.236), the variable is statistically indistinguishable from isometry. Alternatively, the interval may exclude the isometric value, being “positive” if the observed element is  $>0.236$ , or “negative” otherwise. Statistical departures from isometry were estimated using a jackknife procedure (Quenouille 1956; Manly 1997), removing one specimen at a time. Here, we report results from untrimmed (full set of jackknife pseudovalues used) and trimmed analyses (with the  $m$  smallest pseudovalues removed in the calculations, with  $m = 1$ ), and report 95% confidence interval for each allometry coefficient (for details see Giannini et al. 2004). The multivariate statistical analysis (PCA + jackknife resampling; Giannini et al. 2010) was programmed in an R script (R Development Core Team 2004) and is available from the authors.

Several approaches were used to explore and compare ontogenetic and multivariate allometric trends in different groups (e.g., ordinations such as PCA or between-group PCA: Mitteroecker and Bookstein 2011; plot growth trajectories and allometric vectors on PCA: Coquerelle et al. 2011; compare multiple allometric vectors by PCA: Mitteroecker et al. 2013). In our study we used the angle between the first eigenvectors obtained for each species in this section to compare the ontogenetic trajectories, by means of this R command:  $\text{angle} = \text{acos}(\text{sum}(a*b)/(\text{sqrt}(\text{sum}(a*a))*\text{sqrt}(\text{sum}(b*b))))$ , where  $a$  is the first eigenvectors of *P. capensis*, and  $b$  is the first eigenvectors of *D. arboreus*. In addition, we performed a permutation test to assess the significance of directional difference between vectors under the null hypothesis that the angle value is smaller than obtained by chance. All data generated during our analyses in the current study are available from the corresponding author on reasonable request.

## Data Availability

All data generated during our analyses in the current study are available from the corresponding author on reasonable request.

## Results

### Bivariate Analysis

#### Allometry in *Dendrohyrax arboreus*

All regression coefficients were significant (Table 4) except those of y-intercepts of length of palate (PAL), the breadth of palate (PAB), and the height of coronoid process (CPH) (Table 4). Regressions resulted in high determination coefficients values for almost all variables (i.e., 0.75 or higher) except for breadth of braincase (BCB) and (CPH). The observed allometric trends were isometric in five from 18 variables (i.e., 27.8%; PAB, BZB, CSL, CPH, and CPW). In the remaining measurements, positive allometry was detected in seven variables (i.e., 38.9%; PAL, MZL, LPD, UPL, LPL, MCDr, and MCDc), while allometric negative coefficients were found in six variables (i.e., 33.3%; CBL, OCH, MZHr, ORL, BCB, and BMB).

#### Allometry in *Procavia capensis*

Bivariate regressions coefficients were significant except those of y-intercepts of length of palate (PAL) and meatal breadth (BMB) (Table 4). Regressions resulted in high determination coefficients values for almost all variables (i.e., 0.75 or higher) except for breadth of braincase (BCB), breadth of palate (PAB), length of diastemata (LPD), and meatal breadth (BMB). The observed allometric trends were isometry in six from 18 variables (i.e., 33.3%; e.g., CBL, PAB, BMB, BZB, CSL, and CPW). In the remaining measurements, positive allometry was detected in eight variables

(i.e., 44.4%; PAL, MZL, LPD, UPL, LPL, MCDr, MCDc, and CPH), while negative coefficients were found in four variables (i.e., 22.2%; OCH, MZHr, ORL, and BCB).

### Interspecific Comparisons

In both species, the condyle-basal length (CBL), length of palate (PAL), and length of rostrum (MZL) showed the higher determination coefficient ( $R^2$ ) among variables, and so the highest correlation with size (Table 4). Although we detected common allometric trends in the SMA analyses (i.e., the same allometric sign in 15 of 18 variables, 83.3%), the statistical analyses show that both species shared a common slope in only nine of the 18 variables (i.e., 50%; PAL, MZL, OCH, LPD, BZB, CSL, LPL, CPH, and CPW; Table 5).

Comparison of growth trajectories showed three patterns of developmental changes, or their lack thereof, illustrated with examples in Fig. 3. Two patterns corresponded with trajectories with the same slope (Fig. 3a, b), and one with trajectories with different slopes (Fig. 3c). The first pattern (Fig. 3a) occurred only in three of the total variables and shows differences neither in slope, intercept, or shift (BZB, CSL, and CPH). The second pattern has the same slope but different intercept (i.e., parallel trajectories; Fig. 3b), and occurred in six variables. In three (PAL, MZL, and LPD) of these six variables, *Dendrohyrax* showed greater intercept values than *Procavia* whereas the reverse was true in OCH, LPL, and CPW. The third pattern corresponded with significant differences in slopes (Fig. 3c), and occurred in seven variables, in which, we observed convergent trajectories (TBL, PAB, BCB, MCDr, and MCDc) and divergent trajectories (UPL and ORL).

### Multivariate Analyses

The results of multivariate analysis of allometry are shown in Table 6. Fig. 4 shows the distribution of confidence intervals of each species with respect to the expected isometric value (0.236). *Procavia capensis* and *D. arboreus* shared fourteen allometric trends (77.7%). Of the common set, seven variables (CBL, OCH, MZH, ORL, BCB, BMB, and BZB) were negatively allometric; six (PAL, MZL, UPL, LPL, MCDr, and MCDc) were positive and only one (HCP) was isometric (Table 6). The remaining four variables (LPD, PAB, CSL, and CPW) differed between species (Table 6). In *D. arboreus*, PAB, CSL, and CPW showed negative allometry (isometric in *P. capensis*) and LPD positive allometry (negative in *P. capensis*; Table 6). Still, in PAB, CSL, and CPW, the confidence intervals (ci) overlapped between the species (Fig. 4). The angular comparison yielded an  $8.95^\circ$  angle between the first eigenvectors obtained for each species. The permutation test showed that both ontogenetic trajectories were significantly different ( $P$ -value = 0.0011 with 10,000 random permutations).

It is noteworthy that ten of 18 variables showed the same trend in bivariate and multivariate analyses. The remaining

**Table 4** Results of Bivariate Analysis of Cranial Allometry in *Procavia capensis* (Pc; N=32) and *Dendrohyrax arboreus* (Da; N=27)

Var	Sp	Regression		Intercept			Slope			Trend
		$R^2$	$F_{(1, n-2)}$	$\text{Log}(b_0)$	$t_{(n-2)}$	$p\text{-value}_{b_0}$	$b_1$	$F_{\text{iso}(1, n-2)}$	$p\text{-value}_{b_1}$	
Cranium										
CBL	Pc	0.965	832.539	0.581	13.210***	4.88E-14	0.943	2.962	0.096	iso
	Da	0.989	2218.052	0.700	28.176***	1.84E-20	0.869	44.729***	5.22E-07	–
PAL	Pc	0.969	933.635	0.042	0.844	0.406	1.130	14.410**	6.67E-04	+
	Da	0.990	2375.427	0.030	0.941	0.355	1.154	49.491***	2.25E-07	+
PAB	Pc	0.503	30.329	–0.706	–3.101**	4.18E-03	1.290	4.007	0.054	iso
	Da	0.754	76.431	–0.168	–1.374	0.182	0.909	0.930	0.344	iso
MZL	Pc	0.960	721.606	–0.234	–3.862**	5.58E-04	1.210	27.684***	1.11E-05	+
	Da	0.982	1384.257	–0.227	–5.139***	2.60E-05	1.221	56.818***	6.83E-08	+
OCH	Pc	0.745	87.808	0.724	10.381***	1.90E-11	0.552	46.648***	1.41E-07	–
	Da	0.813	108.480	0.596	8.366***	1.03E-08	0.607	36.014***	2.88E-06	–
LPD	Pc	0.596	44.183	–0.909	–4.280**	1.76E-04	1.334	6.335*	0.017	+
	Da	0.901	228.516	–1.012	–7.851***	3.30E-08	1.514	46.159***	4.03E-07	+
UPL	Pc	0.901	273.249	–1.224	–8.048***	5.53E-09	1.933	151.906***	2.85E-13	+
	Da	0.949	462.234	–0.665	–7.175***	1.61E-07	1.508	87.088***	1.27E-09	+
MZHr	Pc	0.801	120.985	0.435	5.630***	3.93E-06	0.693	21.314***	6.86E-05	–
	Da	0.741	71.527	0.670	9.337***	1.26E-09	0.520	47.500***	3.18E-07	–
ORL	Pc	0.953	614.139	0.210	5.087***	1.82E-05	0.766	46.955***	1.32E-07	–
	Da	0.893	209.020	0.434	8.256***	1.32E-08	0.593	70.023***	1.03E-08	–
BCB	Pc	0.409	20.728	0.747	7.509***	2.27E-08	0.517	25.479***	2.04E-05	–
	Da	0.413	17.560	1.027	15.300***	3.35E-14	0.323	81.914***	2.31E-09	–
BMB	Pc	0.689	66.379	0.171	1.286	0.208	0.949	0.260	0.614	iso
	Da	0.878	180.751	0.641	11.428***	2.03E-11	0.593	61.413***	3.42E-08	–
BZB	Pc	0.847	165.833	0.285	2.959**	0.006	0.985	0.046	0.832	iso
	Da	0.938	378.464	0.386	6.231***	1.62E-06	0.918	2.978	0.097	iso
Mandible										
CSL	Pc	0.969	937.707	0.417	9.592***	1.20E-10	0.987	0.154	0.697	iso
	Da	0.967	728.561	0.499	10.869***	5.81E-11	0.930	4.032	5.56E-02	iso
LPL	Pc	0.864	190.541	–0.531	–3.957**	4.29E-04	1.454	32.341***	3.35E-06	+
	Da	0.960	594.685	–0.795	–9.093***	2.11E-09	1.607	150.107***	4.60E-12	+
MCDr	Pc	0.910	303.236	–0.786	–7.628***	1.66E-08	1.373	34.657***	1.91E-06	+
	Da	0.968	754.044	–1.133	–14.552***	1.04E-13	1.604	187.183***	4.11E-13	+
MCDc	Pc	0.905	285.445	–0.722	–6.489***	3.58E-07	1.442	44.155***	2.33E-07	+
	Da	0.974	925.007	–1.549	–17.264***	2.11E-15	2.040	570.775***	0.0E+00	+
CPH	Pc	0.777	104.392	–0.660	–4.300**	1.67E-04	1.298	9.344**	0.005	+
	Da	0.631	42.817	–0.372	–2.047	0.051	1.104	0.671	0.421	iso
CPW	Pc	0.869	199.522	–0.447	–4.710***	5.27E-05	1.050	0.538	0.469	iso
	Da	0.815	110.221	–0.455	–3.836**	7.53E-04	1.017	0.040	0.843	iso

Variable abbreviations as in Table 3. Parameters:  $R^2$ , coefficient of determination; F, F-test for regression;  $\text{Log}(b_0)$ , intercept from standardized major axis; t, Student's t-value from a null intercept test;  $b_1$ , slope from standardized major axis; F iso-test, from no deviation of expected isometric value test; Trend is the allometric trend of each variable. iso, isometry; (–), negative allometry; (+), positive allometry. Var, variables; Sp, species. Symbols: \*\*\* p-value <0.001; \*\* p-value <0.01 and \* p-value <0.05

variables showed partially similar trends between methods (i.e., in one of the two species; CBL, PAB, LPD, BMB, CSL, CPH, and CPW) or different trends (i.e., in both species; BZB).

## Discussion

Analyses of allometry in the hyraxes *P. capensis* (terrestrial, grazer, tendency to hypsodonty) and *D. arboreus* (arboreal,



**Table 5** Test for common slope, common intercept and shift in the allometric trajectories for *Procavia capensis* (Pc) and *Dendrohyrax arboreus* (Da)

Var	Lr	p-value(Lr)	Common Slope (b <sub>1</sub> )	Growth trend	W(b <sub>0</sub> )	p-value(W <sub>b0</sub> )	Common Intercept (b <sub>0</sub> )	W(shift)	p-value (W <sub>shift</sub> )
<b>Cranium</b>									
CBL	3.968	0.046	<b>Pc &gt; Da</b>						
PAL	0.300	0.584		+	25.867	<0.0001	<b>Da &gt; Pc</b>		
PAB	4.430	0.035	<b>Pc &gt; Da</b>						
MZL	0.036	0.849		+	17.328	<0.0001	<b>Da &gt; Pc</b>		
OCH	0.555	0.456		-	54.210	<0.0001	<b>Pc &gt; Da</b>		
LPD	0.895	0.344		+	58.784	<0.0001	<b>Da &gt; Pc</b>		
UPL	10.281	0.001	<b>Pc &gt; Da</b>						
MZHr	4.560	0.033	<b>Pc &gt; Da</b>						
ORL	9.808	0.0017	<b>Pc &gt; Da</b>						
BCB	4.895	0.027	<b>Pc &gt; Da</b>						
BMB	12.836	<0.001	<b>Pc &gt; Da</b>						
BZB	0.640	0.424		iso	1.320	0.251	0.359	0.176	0.675
<b>Mandible</b>									
CSL	1.499	0.221		iso	0.398	0.528	0.455	0.305	0.581
LPL	1.575	0.209		+	23.474	<0.0001	<b>Pc &gt; Da</b>		
MCDr	5.251	0.022	<b>Da &gt; Pc</b>						
MCDc	21.947	<0.0001	<b>Da &gt; Pc</b>						
CPH	1.142	0.285		+	1.945	0.163	-0.545	0.048	0.826
CPW	0.081	0.775		iso	22.416	<0.0001	<b>Pc &gt; Da</b>		

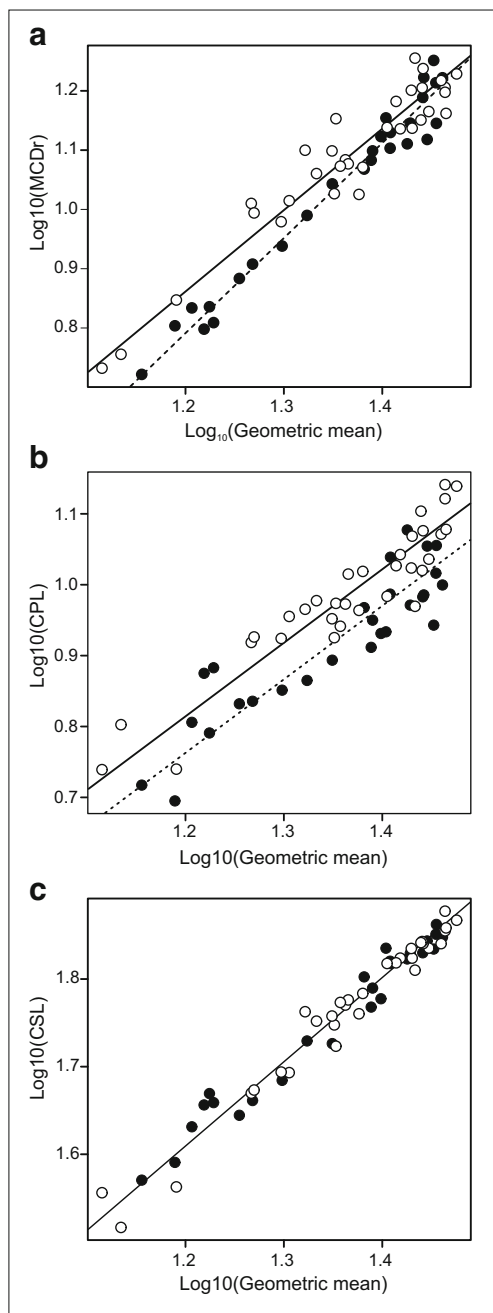
Variable abbreviations as in Table 3. Parameters: Lr, likelihood ratio (Warton et al. 2006) for common slope test; b<sub>1</sub>, common slope from standardized major axis; W(b<sub>0</sub>), Wald statistic (Warton et al. 2006) for common intercept test; b<sub>0</sub>, common intercept from standardized major axis; W(shift), Wald statistic (Warton et al. 2006) for common growth extension. Growth trend is the allometric trend of the common slope for each variable. iso, isometry; -, negative allometry; +, positive allometry; Var, variables. In bold resulted when both species of hyrax differ in slope or intercept

browser, brachyodont) indicated common growth trends in three-quarters of the cranial variables investigated. Multivariate ontogenetic trajectories were statistically different between species, but the relatively small angle of 8.95° between them suggested that both allometric vectors were not quite divergent.

Hyraxes are morphologically similar to each other, but differ in ecologically important features (see Table 1). Conservation of a majority of allometric patterns in *Procavia* and *Dendrohyrax* suggests that they simply follow the same growth processes as their common ancestor, but with some significant particularities in each species. The bivariate analysis showed that adults of both species converged to approximately the same total skull length. However, functionally important trends have been recovered in both bivariate and multivariate analyses and relate to differences in life style, specifically the grazing versus browsing habit. We interpret these trends as follows.

Both species of hyrax shared negative growth trends in zygomatic breadth (BZB) and braincase variables (BCB, BMB, and OCH), as observed in other ungulates (e.g., cervids, Cassini et al. 2015; tapirs, Moyano and Giannini 2017). Churcher (1956) described the adult cranium of *Dendrohyrax* as narrow and less globular, and Thomas

(1892) described the adult skull of *Procavia* as broad. Our study showed that the breadth of braincase is the most negative allometric of all variables in both species, but more so in *Dendrohyrax* (Fig. 4), which explains its adult shape. The meatal breadth suggests a relatively narrower skull in adults than in juveniles of both species. The height of occipital plate showed a higher intercept in *Procavia*; i.e., this character is juvenilized with respect to *Dendrohyrax* (*Procavia* with a taller occipital plate than *Dendrohyrax*). In the orbital region, the results of bivariate and multivariate analyses are the same (Tables 4 and 6). Zygomatic breadth of both species had the same slope and intercept, in both cases presenting slightly negative allometry. The same trend was reported in the extinct notoungulate *Nesodon*, the pampas deer *Ozotoceros bezoarticus*, and one species of *Tapirus* (Cassini et al. 2012, 2015; Moyano and Giannini 2017). Zygomatic breadth showed positive allometry in mammals with large temporalis muscles; space for the temporalis is created by the combination of the negative allometry of braincase breadth and the positive allometry of zygomatic breadth (e.g., as in *Didelphis albiventris*, an omnivorous didelphid: Abdala et al. 2001; *Adinotherium ovinum*, a herbivore notoungulate: Cassini et al. 2012; *Lycalopex culpaeus*, a carnivoran: Segura and Prevosti 2012). In hyraxes, as in most modern ungulates



**Fig. 3** Bivariate plots of three skull measurements against geometric mean. **a**, same slope and intercepts; **b**), same slope and different intercepts; and **c**), different slopes between the growth trajectories. Open symbols and continuous are *Procavia capensis*, solid symbols and dashed line are *Dendrohyrax arboreus*. Variable abbreviations as in Table 3

(Greaves 2012 and references therein), the temporalis is relatively less important than the masseter, and this is reflected in the modest expansion of zygomatic breadth but great development of the angular process of the mandible (insertion of the masseter; see below).

The allometric growth trends of muzzle variables (UPL, LPD, MZL, PAL, PAB, and MZHr) showed that hyraxes

developed a relatively long rostrum (with upper postcanine row and palate length showing positive allometry), which is also relatively low and narrow (with breadth of palate and height of muzzle showing negative allometry). Nonetheless, differences exist between *Dendrohyrax* and *Procavia*, and these are very important functionally. In *Procavia*, the upper postcanine row (UPL) grows much faster than in *Dendrohyrax*, which is reflected in the strongly negative growth of the upper diastema. That is, in *Procavia*, space for a considerably larger postcanine upper toothrow is gained during development at the expense of the diastema. This can be directly associated with the greater degree of hypsodonty and also to the grazing habit in *Procavia*; cheek teeth take an increased space in both the maxillary tuber and the mandible (see below) to house larger molars (Clauss et al. 2008). In addition, the cheek-teeth occlusal surface area (OSA), here only tangentially considered in the length of the postcanine toothrow (see also Appendix I in Vizcaíno et al. 2006), is larger in grazers than in browsers among ungulates, suggesting more extensive oral food processing (Vizcaíno et al. 2006 and references therein), which is also evident in hyraxes (Fig. 1). In ungulates, chewing area is also inversely related to the nutritional value of food (less quality in grazers; Jarman 1974; Shipley 1999; Vizcaíno et al. 2006). *Dendrohyrax* had a greater intercept of palate and rostrum length than *Procavia*, suggesting that the former began postnatal growth with a longer rostrum. Also, the muzzle in *Dendrohyrax* is relatively lower than that in *Procavia*, all of which is indicative of browsing habits (longer and finer rostrum used to more effectively select foliage, see above). Length of the orbit showed different modes of growth in the two hyraxes. The juveniles of *Dendrohyrax* begin the ontogeny with an orbit slightly larger than *Procavia* (intercept = 0.434 in *Dendrohyrax*, 0.210 in *Procavia*; Table 4), but greater growth rate in *Procavia* led to adults with greater value than in *Dendrohyrax*. Orbital growth differences in *Dendrohyrax* and *Procavia* could be related to the slight differences in the change of the orientation during the ontogeny; we observed that the orbits in *Dendrohyrax* are more vertically and laterally positioned in the newborn, and become more dorsally (horizontally) and anteriorly oriented in the adult (Fig. 1). These differences could be due to their differential use of substrate (Table 1). Several studies have related the anterior convergence of left and right orbits with the formation of a bony postorbital bar (present in *Dendrohyrax*, Fig. 1) for increased stereoscopic visual acuity and depth perception, which has been linked to arboreality and nocturnal vision (Watson et al. 2000; Finarelli and Goswami 2009 and references therein). Pilatti and Astúa (2016) described, for Didelphidae, that the elongation of rostrum implies orbits more dorsally positioned and a more convergent orientation in the cranium, whereas the widening implies more vertical position and a little divergent orbit orientation. We have not found significant differences in the length

**Table 6** Results by species of the multivariate analysis of cranial allometry in hyraxes

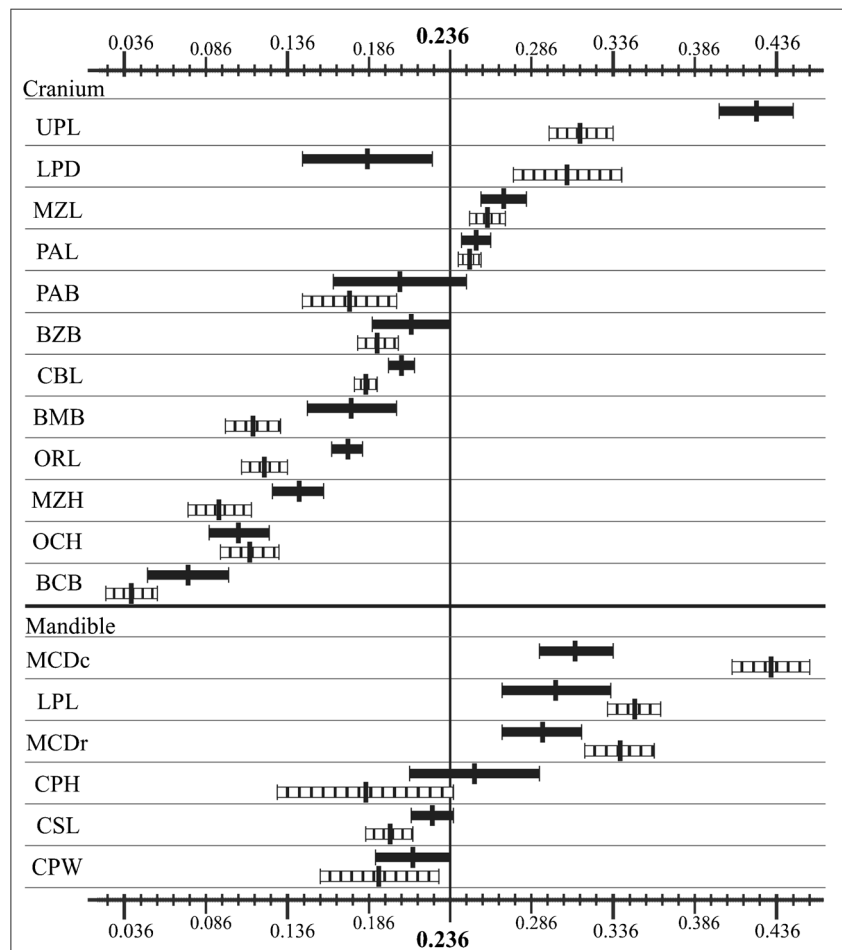
Var	sp	Untrimmed					Trimmed				
		Unbiased coeff.	Bias	95% C.I.	Departure	Growth trend	Unbiased coeff.	Bias	95% C.I.	Departure	Growth trend
<b>Cranium</b>											
CBL	Pc	0.206	2.83E-04	0.191–0.22	-0.03	-	0.206	1.56E-04	0.198–0.214	-0.03	-
	Da	0.185	-2.07E-04	0.177–0.193	-0.051	-	0.184	1.16E-04	0.177–0.191	-0.051	-
PAL	Pc	0.248	2.86E-04	0.231–0.264	0.012	iso	0.252	-1.89E-03	0.243–0.261	0.016	+
	Da	0.246	-9.77E-05	0.236–0.255	0.01	+	0.248	-1.27E-03	0.241–0.255	0.012	+
PAB	Pc	0.213	-3.83E-03	0.165–0.261	-0.023	iso	0.205	-9.63E-05	0.164–0.246	-0.031	iso
	Da	0.171	-9.78E-04	0.135–0.207	-0.065	-	0.174	-2.44E-03	0.145–0.203	-0.062	-
MZL	Pc	0.265	-4.78E-04	0.247–0.284	0.029	+	0.269	-2.37E-03	0.255–0.283	0.033	+
	Da	0.259	-1.31E-04	0.246–0.272	0.023	+	0.259	-3.94E-04	0.248–0.27	0.024	+
OCH	Pc	0.105	-1.57E-04	0.083–0.127	-0.131	-	0.106	-8.67E-04	0.088–0.125	-0.129	-
	Da	0.118	-1.06E-03	0.088–0.148	-0.118	-	0.113	1.36E-03	0.095–0.131	-0.123	-
LPD	Pc	0.241	-7.29E-03	0.156–0.326	0.005	iso	0.185	2.06E-02	0.145–0.225	-0.051	-
	Da	0.312	-1.93E-03	0.27–0.353	0.076	+	0.308	-9.37E-05	0.275–0.341	0.072	+
UPL	Pc	0.413	4.14E-04	0.378–0.449	0.177	+	0.424	-4.97E-03	0.401–0.446	0.188	+
	Da	0.316	-1.88E-05	0.287–0.345	0.08	+	0.316	-1.36E-04	0.297–0.336	0.08	+
MZHr	Pc	0.135	9.08E-04	0.113–0.157	-0.101	-	0.143	-2.79E-03	0.127–0.158	-0.093	-
	Da	0.095	4.29E-04	0.073–0.117	-0.141	-	0.094	8.25E-04	0.075–0.114	-0.141	-
ORL	Pc	0.165	6.49E-04	0.148–0.182	-0.071	-	0.173	-3.06E-03	0.163–0.182	-0.063	-
	Da	0.12	-2.35E-04	0.104–0.137	-0.115	-	0.122	-1.08E-03	0.108–0.136	-0.114	-
BCB	Pc	0.068	1.38E-03	0.035–0.1	-0.168	-	0.075	-2.32E-03	0.05–0.1	-0.16	-
	Da	0.045	-6.55E-04	0.023–0.067	-0.191	-	0.04	1.56E-03	0.025–0.056	-0.195	-
BMB	Pc	0.164	3.69E-03	0.12–0.208	-0.072	-	0.175	-1.89E-03	0.148–0.203	-0.061	-
	Da	0.119	-6.51E-04	0.097–0.141	-0.117	-	0.115	1.32E-03	0.098–0.132	-0.121	-
BZB	Pc	0.191	3.92E-03	0.153–0.229	-0.045	-	0.212	-6.29E-03	0.188–0.236	-0.024	-
	Da	0.191	-4.89E-04	0.176–0.206	-0.045	-	0.191	-6.58E-04	0.179–0.204	-0.044	-
<b>Mandible</b>											
CSL	Pc	0.216	-1.61E-05	0.19–0.243	-0.019	iso	0.225	-4.38E-03	0.212–0.238	-0.011	iso
	Da	0.196	-3.07E-04	0.177–0.214	-0.04	-	0.199	-1.91E-03	0.184–0.213	-0.037	-
LPL	Pc	0.306	-6.39E-04	0.257–0.354	0.07	+	0.301	1.46E-03	0.268–0.335	0.066	+
	Da	0.337	5.94E-04	0.308–0.366	0.101	+	0.349	-5.33E-03	0.333–0.365	0.113	+
MCDr	Pc	0.3	-3.88E-03	0.271–0.329	0.064	+	0.293	-2.38E-04	0.268–0.317	0.057	+
	Da	0.34	-6.78E-04	0.314–0.365	0.104	+	0.34	-7.03E-04	0.319–0.361	0.104	+
MCD-c	Pc	0.312	-2.04E-03	0.286–0.337	0.076	+	0.313	-2.93E-03	0.291–0.336	0.078	+
	Da	0.434	-5.75E-04	0.406–0.462	0.198	+	0.433	-6.66E-05	0.409–0.456	0.197	+
CPH	Pc	0.257	-2.33E-03	0.21–0.303	0.021	iso	0.251	4.78E-04	0.211–0.291	0.016	iso
	Da	0.189	-1.56E-03	0.121–0.257	-0.047	iso	0.184	1.04E-03	0.13–0.238	-0.052	iso
CPW	Pc	0.217	-3.30E-05	0.177–0.258	-0.018	iso	0.213	2.24E-03	0.19–0.236	-0.023	iso
	Da	0.197	-8.92E-04	0.148–0.246	-0.039	iso	0.192	0.001328	0.156–0.229	-0.043	-

Variable abbreviations as in Table 3. Unbiased coefficient, is the value generated by first-order jackknife resampling; Bias, is the difference between the unbiased and observed coefficients. 95% C.I., the jackknifed 95% confidence interval (CI) is provided; allometric variables are those whose CIs exclude the expected value under isometry (0.236). Departure, represent the subtraction of expected value under isometry to the unbiased coefficient; Growth trend, is the allometric trend of each variable. iso, isometry; -, negative allometry; +, positive allometry. Var, variables; sp., species. Pc, *Procavia capensis*, Da, *Dendrohyrax arboreus*

of the muzzle to corroborate this hypothesis, but our data suggest an increase in the growth rate of palate breadth in

*Procavia*, which could be limiting a more vertical position (see Pilatti and Astúa 2016).

**Fig. 4** Distribution of confidence intervals for each species with respect to the isometric value (0.236). Solid lines are *Procavia capensis*; open lines are *Dendrohyrax arboreus*. Variable abbreviations as in Table 3



Regarding the mandible, three variables showed positive allometry. These were height of mandibular body (at first and last functional lower postcanine) and the length of postcanine row (MCDr, MCDc, LPL; Fig. 4). In all three cases, *Dendrohyrax* presented greater coefficients, and the mandible height at last molar in *Dendrohyrax* showed a higher rate of growth than in *Procavia* (unbiased coefficient = 0.433 in *Dendrohyrax* and 0.313 in *Procavia*, respectively; MCDc, Fig. 4 and Table 6). Janis (1983, 2008) observed that the jaws of hyraxes can be distinguished by the extreme deepening and posterior extension of the angle of the mandible, which corresponds with the enlarged masseteric-ptyergoid muscle complex commonly seen in herbivorous mammals (Greaves 2012 and references therein). In early age, the mandible of *Procavia* is more robust than that of *Dendrohyrax*, which can be related again with a tendency to hypsodonty in the young of *Procavia*, but the mandibular body in *Dendrohyrax* grew at a faster rate and so the trajectories converged in the adult of both species. Pickford (2005) observed that the mandibles of *Procavia* species are shallower relative to the level of the molar row, and the converse was true in *Dendrohyrax*. This can be corroborated in the relationship between MCDc and

LPL in the bivariate results (Fig. 3). Our study showed that the mandible in *Dendrohyrax* grew rapidly and was posteriorly taller than that of *Procavia*. This could not be related to the dentition type, but to the anatomy of the mandibular angle in *Dendrohyrax*, which seems to extend more anteroventrally than in *Procavia* and receive a greater share of insertion of superficial and deep masseter and medial pterygoid (Fig. 1; Janis 1983).

Cassini (2013) observed that the presence of high-crowned molars was related to mandibular shape. A similar relationship was observed in the anterior dentition. Hypsodont incisors present in *Procavia* resemble the condition seen in notoungulates (see tomography of *P. capensis* in Seiffert 2011), which requires a wide space in the anterior portion of the mandible to accommodate the hypsodont root (Cassini et al. 2017). In the lower dentition, the typotheres (Notoungulata: Typotheria) have procumbent incisors, inserted following the direction of the anterior face of the symphysis, and the root heights are about the same as those of the crown. The allometric growth of the anterior mandibular height in *Procavia* is positive but less so than in *Dendrohyrax* (Fig. 4; Table 6). This could be a consequence



of hypsodonty of milk incisors in *Procavia*; i.e., the space is already enlarged at the beginning of postnatal growth and so the rate of change is slower as compared with *Dendrohyrax*.

Hyraxes have a small coronoid process, which is considerably smaller than the coronoid process of most ungulates (Janis 1983), reflecting a lesser importance of the temporalis muscle in mastication as compared with the masseteric complex (see above). The temporalis muscle inserts onto the coronoid process; a relatively high and caudally curved coronoid process provides a large area for the insertion of the temporalis (Cassini and Vizcaíno 2012). A small process would result in longer fibers in the temporalis attachment, and hence it would permit a greater degree of stretch in this muscle (Janis 1983). The coronoid process is broader in *Procavia* than in *Dendrohyrax*, which functionally matches the presence of the sagittal crest in the former (absent in the latter).

## Conclusion

Our study on skull growth in hyraxes provides the developmental basis for the understanding of structural dissimilarities between closely related species, as well as the developmental basis of their divergent ecological role as grazing versus browsing mammalian herbivores. These small species in a rather isolated, low-diversity paenungulate clade evolved opposing trends along the grazing-browsing gradient, and we show how subtle developmental processes of the skull explain the acquisition of the adult functionality in the diverging ecologies of the adults. The trends we observed in hyraxes could reflect a more general, convergent pattern in the many ungulates lineages that evolved along the browsing-grazing continuum, and here we provided a comparative basis to that end with the lineage of hyraxes. Further studies in different lineages will certainly contribute to understanding the evolution of development in ungulates.

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