



## Original investigation

On the growth of the largest living rodent: Postnatal skull and dental shape changes in capybara species (*Hydrochoerus* spp.)

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## ABSTRACT

We report on intraspecific and interspecific morphological variation in the cranium, mandible and teeth along the ontogenetic trajectories of the two species of the largest living rodent, the capybara. A three dimensional geometric morphometrics approach was used to compare 171 *Hydrochoerus hydrochaeris* and 44 *Hydrochoerus isthmius* specimens ranging from newborn to adult. The specimens were assigned to seven different age classes according to cranial suture closure. The species can be differentiated in the morphospace occupation. They differ in the angle between the braincase and rostrum—*H. hydrochaeris* displays a straight transition whereas the snout of *H. isthmius* is inclined ventrally. The males in both species are bigger than the females, but no shape differences were detected. The youngest two age classes (up to 0.5 months and 0.5–10 months; before reaching sexual maturity) can be morphologically differentiated from the older age classes. Shape changes during growth are similar in both species: with increasing age, the round neurocranium flattens and the proportionally short snout elongates. Moreover, both species follow similar ontogenetic trajectories. *H. hydrochaeris* and *H. isthmius* can be differentiated by size and shape; the shape differences may indicate differences in diet and habitat. This study illustrates the relevance of an ontogenetic perspective to characterize species and examine the bases of disparity in adults. Furthermore, variation recorded in dental features serves to evaluate taxonomic and evolutionary aspects in fossil capybaras.

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## Introduction

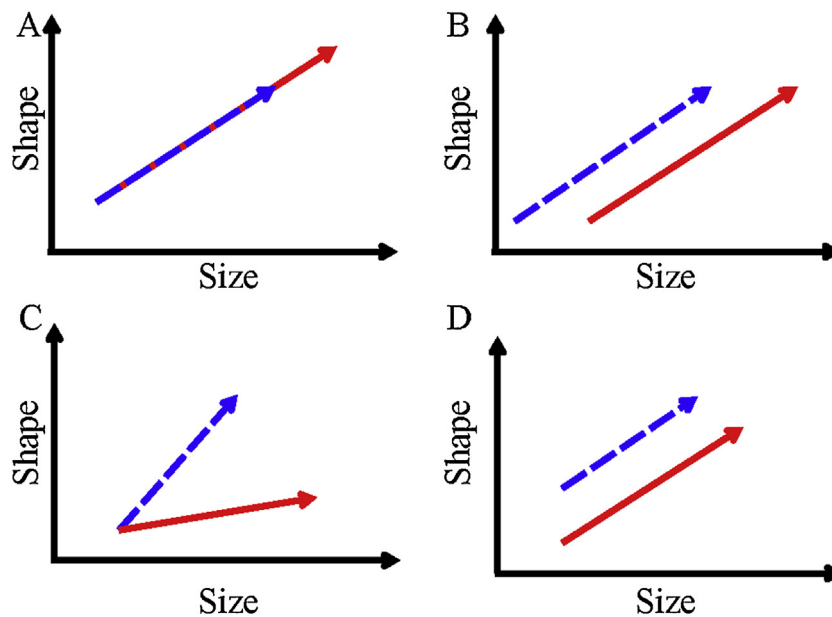
Comparing the patterns of change in ontogeny and postnatal growth among species serves to understand how morphological disparity has arisen in evolution (Wilson and Werneburg, 2014). Skulls are excellent markers of such changes (e.g., Flores et al., 2010; Hautier et al., 2012; Herrel et al., 2012; Hughes et al., 1978), given their complexity, and also teeth, given their common occurrence in the fossil record (e.g., Deschamps et al., 2007, 2013; Vucetich et al., 2005, 2014, 2015a). Caviomorph rodents offer an excellent case study, as the radiation of these hystricognath rodents includes much diversity in form and species (Álvarez et al., 2015; Vassallo and Antenucci, 2015; Weisbecker and Schmid 2008). To understand the evolution of form, methods have been developed to study changes in shape and size (Lawing and Polly, 2010; Mitteroecker et al., 2013). The variation in size is particularly significant in caviomorphs, as best exemplified by the capybara (*Hydrochoerus*), the largest living rodent, with fossils documenting even larger

forms and a wide temporal and geographic distribution for the clade (Vucetich et al., 2015b; Pérez et al. in press), as in the closely related *Neocherus* (Hulbert, 2001). And yet, we know little about growth in the capybara, and how the differences between the two extant species of the genus, a taxonomic distinction resting on few characters, rise in the ontogeny of their skulls and teeth. In this contribution, we investigate the skull shape and size changes of capybaras and their dental variation during postnatal growth. Furthermore, we study skull shape and size variation in relationship with sexual dimorphism in each species, and with geographic distribution in *Hydrochoerus hydrochaeris*.

The two capybara species are currently recognized based on karyotypic differences (*H. hydrochaeris*  $2n = 66$ ; *Hydrochoerus isthmius*  $2n = 64$ ), body size differences (mean body weight 48 kg and 20 kg, respectively) and morphological features (see Moreira et al., 2013). Mones and Ojasti (1986) mentioned *H. isthmius* having wider frontals, a proportionally longer lower diastema and shorter and thicker pterygoid processes than the larger species. Additionally, they noted that there are no body size differences between the sexes, but that the body size in *H. hydrochaeris* increases with increasing latitude. The two species do not overlap in their geographic distribution. *H. hydrochaeris* shows a wide distribution

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**Fig. 1.** The four hypotheses how size and shape differences between *H. hydrochaeris* (red, solid) and *H. isthmus* (blue, dashed) could be established. Modified from Sheets and Zelditch (2013). (A) Both species have overlapping trajectories with a common starting point of shape, size, and direction but with an unequal magnitude of net ontogenetic change, resulting in a species-specific shape and size. (B) Both species have parallel trajectories with the same magnitude of net ontogenetic change and same starting point of shape but with different starting size, resulting in a similar shape but different size. (C) The two species display directionally different ontogenetic trajectories of equal or unequal magnitude resulting in species-specific shape and size. (D) Both species have parallel trajectories with the same starting size but different starting shape and unequal magnitude of net ontogenetic change, resulting in species-specific shape and size. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

in the tropical regions of South America (Venezuela, Colombia, Ecuador, Peru, Suriname, Guyana, French Guiana, Bolivia, Brazil, Paraguay, Argentina and Uruguay). *H. isthmus*, called the lesser capybara, is found in Panama, north-western Colombia and north-western Venezuela (Moreira et al., 2013).

To characterize the two extant capybara species and provide a framework of comparison for extinct ones, skull growth will be compared. We hypothesize that skull form differences between *H. hydrochaeris* and *H. isthmus* are established in growth according to one of the following patterns (Sheets and Zelditch, 2013; Fig. 1):

- A.) Both species have overlapping trajectories with a common starting point of shape, size, and direction but with an unequal magnitude of net ontogenetic change, resulting in a species-specific shape and size (Fig. 1A).
- B.) Both species have parallel trajectories with the same magnitude of net ontogenetic change and same starting point of shape but with different starting size, resulting in a similar shape but different size (Fig. 1B).
- C.) The two species display directionally different ontogenetic trajectories of equal or unequal magnitude resulting in species-specific shape and size (Fig. 1C).
- D.) Both species have parallel trajectories with the same starting size but different starting shape and unequal magnitude of net ontogenetic change, resulting in species-specific shape and size (Fig. 1D).

When considering growth, it is worth examining life history variables of the species in question. *H. hydrochaeris* newborns weigh ~1500 g, whereas *H. isthmus* newborns weigh ~1100 g. Gestation lengths of *H. hydrochaeris* and *H. isthmus*, are reportedly 150.6 and 108 days respectively (Moreira et al., 2013), although this difference seems unlikely based on what is known for other closely related mammalian species (Clausen et al., 2014); Trapido (1949) had reported 119–126 days of gestation period for *H. hydrochaeris* and 104–111 for *H. isthmus*. In *H. hydrochaeris* the young are weaned

when they are about 60 days old and reach sexual maturity between 6–12 months (Moreira et al., 2013; and references therein).

## Materials and methods

### Data sampling

In total, 215 crania and 225 mandibles of 237 capybara specimens as well as numerous teeth (connected and isolated) of 183 of these specimens were examined. If detailed location information was available, we assigned each specimen of *H. hydrochaeris* to the geographical regions defined by Morrone (2014). Table 1 summarizes the geographic distribution of the samples. We noted the sex of the investigated specimens only if there was information available in the collections examined, as the two sexes cannot be differentiated by skeletal characters of the skulls (Mones and Ojasti, 1986; Moreira et al., 2013). The studied skulls are from the collection of the Zoologisches Museum in Zürich (ZM), the Naturhistorisches Museum in Basel (BA), the Zoologische Staatssammlung in München (ZSM), the Muséum National d'Histoire Naturelle in Paris (MNHN), the American Natural History Museum in New York (AMNH), the Smithsonian Institution National Museum in Washington (SI) and the Florida Museum of Natural History in Gainesville (UF). Additionally, measurements from 69 teeth of the fossil capybara *Neochoeerus* sp. in the collection of the American Natural History Museum in New York (AMNH), the Smithsonian Institution National Museum in Washington (SI) and the Florida Museum of Natural History in Gainesville (UF) were taken.

### Age classes

We categorized the specimens into seven age classes (AC) according to cranial suture closure following Ojasti (2011) (Fig. 2). Capybaras are born with all their permanent teeth erupted, so no eruption pattern is detectable in the postnatal series we examined.

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