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(Serpentes: Dipsadidae) as a model of snake
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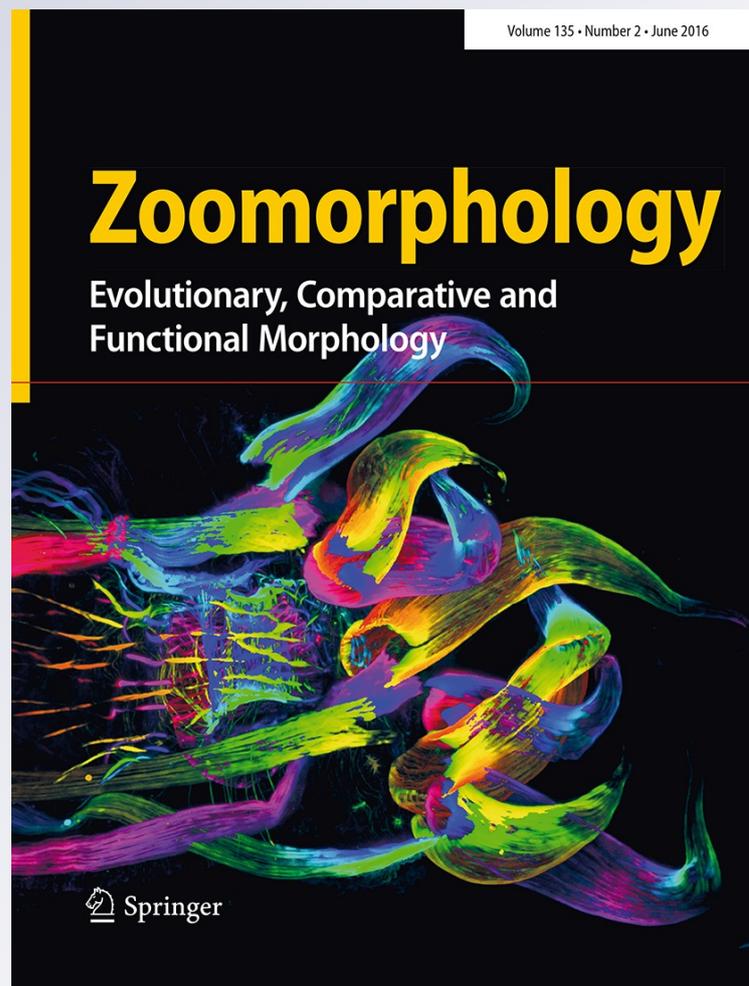
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The skull of *Hydrodynastes gigas* (Duméril, Bibron & Duméril, 1854) (Serpentes: Dipsadidae) as a model of snake ontogenetic allometry inferred by geometric morphometrics

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Abstract Allometric growth is one of the dominant factors of morphological variation, although this issue is still poorly explored. Using geometric morphometrics, we evaluated and described the ontogenetic allometry in the skull of the snake *Hydrodynastes gigas*. Furthermore, we described the skull morphology of the species and compared it with its congener, *H. bicinctus*. We found that 46.91 % of shape variation was explained by allometry: smaller centroid sizes were mostly correlated to short postorbital process, medial region of frontals elongated, shortened nasals and elongated parietal, and shortened/oblique supratemporals in relation to the anteroposterior axis of the skull; larger centroid sizes point mainly to postorbital process elongated, elongated nasals and shortened parietals, posterior region of parietal strongly tapered, and elongated/parallel supratemporals in relation to the anteroposterior axis of the skull. In general aspect, the skull of *H. gigas* differs from the skull of *H. bicinctus* by being less dorsoventrally compressed. Comparisons between our results and the results of other studies which considered allometry in specific bones of snakes' skull showed some common patterns, although we found a different correlation between parietal and skull length. These results reinforce the importance of further studies to evaluate the existence

of recurrent patterns of allometric growth in the skull of other representatives of this group of snakes. Moreover, the analyses presented herein revealed a significant ontogenetic allometry in the skull of *H. gigas* and represent the first approach of geometric morphometrics with this goal for snakes.

Keywords Morphology · Osteology · Ontogeny · Xenodontinae

Introduction

The term allometry is defined as the dependence of shape on size, and it tends to be one of the dominant factors of morphological variation (Klingenberg 2010). Allometric analyses address variation at several levels, corresponding to the different biological origins of variation and covariation among traits (Klingenberg 1998). Three types of allometry can be distinguished (Cock 1966; Klingenberg 1998): ontogenetic allometry—growth is the source of morphological variation; static allometry—reflects covariation of traits among individuals at a particular ontogenetic stage and within a single population; and evolutionary allometry—addresses the variation among phylogenetic lineages considering a similar ontogenetic stage. Allometric growth can exert considerable impact on the morphology of vertebrates (e.g., *fishes*—Meyer 1990; Monteiro et al. 2005; *amphibians*—Ponssa and Vera Candiotti 2012; *reptiles*—Rossman 1980; Blanco et al. 2015; *birds*—Zeffer et al. 2003; *mammals*—Cardini and O'Higgins 2005; Prevosti et al. 2012; Knigge et al. 2015), but this issue is still poorly explored. Moreover, allometry can be studied through geometric morphometrics (GM), a method that offers precise and accurate description of morphological

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shape and also meets the equally important purpose of visualization, interpretation, and communication of results (Zelditch et al. 2004).

Studies on ontogenetic allometry of snakes have employed conventional morphometric methods and focused on morphometric variation associated with ontogenetic changes in diet which, in turn, are related to changes in the feeding apparatus as well as quadrate and supratemporal bones (Rossman 1980; Vincent et al. 2004; Schuett et al. 2005; Natusch and Lyons 2012; López et al. 2013; Hampton 2014). Conventional morphometrics has some methodological limitations that can be overcome with GM. The effect of size in shape has a central importance in understanding the evolution of all living beings, and therefore, size requires a mathematical definition—in GM, this definition is given by the centroid size, where the centroid corresponds to the location of the center of the form, while the centroid size corresponds to a specific measure, independent of shape, based on the distance between each landmark and the centroid (see Zelditch et al. 2004 for more information). A similar problem deals with the definition of operational homology, which is surpassed by the use of landmarks in GM, where homology represents the correspondence between landmarks (Monteiro and Reis 1999). Finally, the measures of conventional morphometrics do not accurately describe the geometry of biological shape, only distances—in GM, shape is described through Cartesian coordinates, and it is independent of size (Monteiro and Reis 1999). The use of GM in studies of snakes is very recent (Manier 2004; Kaliontzopoulou 2011; Sarris et al. 2012; Mangiacotti et al. 2014; Ruane 2015), and approaches exploring skull shape variation are even more scarce (Gentilli et al. 2009).

Hydrodynastes gigas (Duméril et al., 1854) is a large semiaquatic snake which feeds mainly on amphibians and fishes, but is considered an aquatic generalist, occasionally showing necrophagic behavior (Dowling and Gibson 1970; Strussman and Sazima 1990; Sazima and Strussman 1990; Franco et al. 2007; Knox and Jackson 2010), and having no evidences of ontogenetic changes in diet. Considering data on the skull morphology of *H. gigas*, Duméril et al. (1854) showed a plate with the ventral view of the skull. The illustration, however, may not faithfully represent the skull shape of the species, since it shows a shortened maxilla, with only seven prediastemal teeth, while *H. gigas* has 15–17 maxillary teeth (Franco et al. 2007). Jan and Sordelli (1876) illustrated the maxilla of the species, but unfortunately the quality of the image precludes the visualization of any structure.

This paper aims to apply for the first time GM methods to describe the ontogenetic allometry in the skull of a snake, *H. gigas*. Furthermore, detailed information on skull morphology with accurate descriptions of the different bones that constitute this complex structure is scarce, and there is no

specious family of snakes for which a thorough survey of skull form has been performed (see Cundall and Irish 2008: 594). Moreover, many osteological characters have been used to infer phylogenetic relationships in snakes emphasizing differences in the form, position, and proportion of skull bones (e.g. Kluge 1993; Lee and Scanlon 2002; Lee et al. 2007; Fenwick et al. 2009; Carrasco et al. 2012). However, none of these studies focused on the intraspecific variation in these characters, either considering ontogenetic changes or variations in individuals of the same age class. Therefore, the present study also intends to provide a detailed description of the skull of *H. gigas* in order to properly interpret the ontogenetic changes in this taxon, and to compare these results with data from other congener, *H. bicinctus* (Hermann, 1804), with the purpose of evaluating the main differences and similarities of the skull morphology of these two closely related evolutionary lineages.

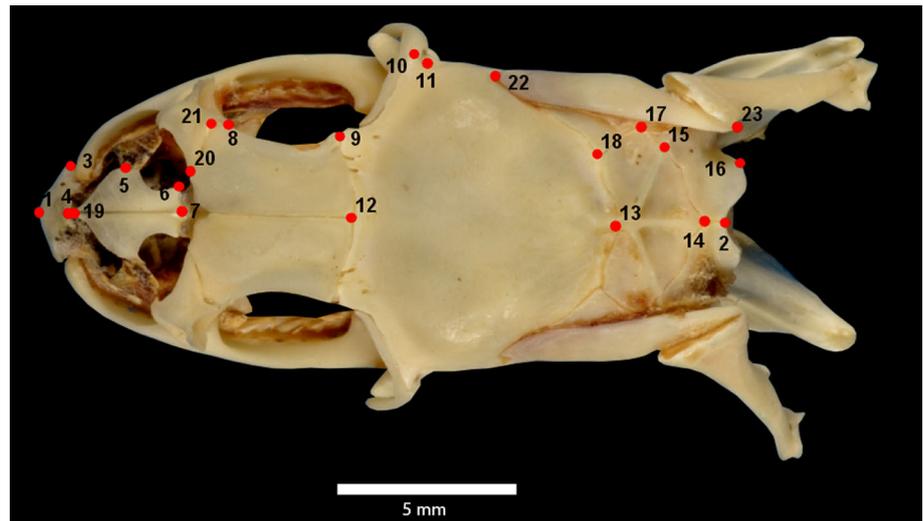
Materials and methods

We analyzed sixteen skulls of *H. gigas* in a range of sizes according to their total length (TL) measured from tip of snout to the most posteromedial point of the exoccipitals (Table 1). Since there is a positive correlation between skull length and snout vent length in snakes during ontogeny (Natusch and Lyons 2012; López et al. 2013; Hampton 2014), and considering that we have a large range of sizes (Table 1), we assumed different sizes to represent different stages of development. Osteological material is deposited in the collection of Fundación Miguel Lillo,

Table 1 Total length of the skull of 16 analyzed individuals of *Hydrodynastes gigas*

Individual	Total length of skull (mm)
FML 1214	18
FML 1718	19
FML 1719/2-1	20.9
FML 1719/2-2	19.5
FML 1721	18.9
FML 1742/2	18.2
FML 1742/3	17.5
FML 1742/4	18.6
FML 1742/5	18.7
FML 1742/6	19.1
FML 1742/7	14.1
FML 1743	19
FML 1744	20.1
FML 1746	41.7
FML 1848	33.5
FML 1853	24.6

Fig. 1 Landmarks digitalized for the GM analysis of ontogenetic allometry in the skulls of *Hydrodynastes gigas* (FML 1744)



Tucumán, Argentina (FML). The analyzed material included dried and cleared and stained skulls. We photographed the dorsal view of the skulls of *H. gigas* for GM analysis of allometry using a camera Nikon D200, with macro-lens 60 mm, and digitalized the landmarks with the software TpsDig version 2.16 (Rohlf 2010) on the right half of each skull image. We selected landmarks based on their ability to represent geometric form (Larson 2002). We performed an analysis of allometry considering the dorsal view of skull, using 16 specimens and 23 landmarks of types 1, 2, and 3 (sensu Bookstein 1991) (Fig. 1; Table 2). We used the software TPSUtil 1.4 (Rohlf 2008) to compile and convert image files to be analyzed, and employed the software MorphoJ 1.01b (Klingenberg 2008) to superimpose landmark configurations through generalized procrustes analysis (Rohlf and Slice 1990), generate a covariance matrix, and also to evaluate ontogenetic allometry through a regression analysis with procrustes coordinates on centroid size. Whereas the null hypothesis considers that the skull shape is developed isometrically, a significant result indicates that shape changes according to a predictive model related to increase in size.

We also compared the morphology of the skulls of *H. gigas* and *H. bicinctus*, the latter based on data from Murta-Fonseca et al. (2015). Only the distinguishable features between these taxa are presented herein. We followed Cundall and Irish (2008) for skull terminology.

Results

Ontogenetic trajectories

We examined skulls with TL ranging from 14.1 to 41.7 mm (*mean* = 21.3; *median* = 19; *SD* = 6.84;

Table 2 Description of landmarks used in the GM analysis of allometry in the skull of *Hydrodynastes gigas*

Number of landmark	Location of landmark
1	Anteromost point of the premaxilla
2	Most posteromedial point of the exoccipital
3	Lateralmost point of the premaxilla
4	Rearmost point of the premaxilla
5	Lateralmost point of the nasal
6	Most posterolateral point of the nasal
7	Most posteromedial point of the nasal
8	Lateralmost point of prefrontal–frontal joint
9	Lateralmost point of frontal–parietal joint
10	Lateralmost point of postorbital process
11	Base of postorbital process
12	Most medial point of frontal–parietal joint
13	Rearmost point of parietal
14	Rearmost point of supraoccipital
15	Lateralmost point of transversal crest of supraoccipital
16	Most posterolateral point of exoccipital
17	Lateralmost point of supraoccipital
18	Lateralmost point of parietal–supraoccipital joint
19	Anteromost point of nasal
20	Most medial point of the prefrontal–frontal joint
21	Distal point of vertex process of frontal
22	Anteromost point of supratemporal
23	Rearmost point of supratemporal

$n = 16$) (Table 1). We rejected the null hypothesis of isometric growth since the result of regression analysis was significant ($p < 0.05$). We found that 46.91 % of shape variation was explained by allometry ($p < 0.01$) (Fig. 2).

Fig. 2 Ontogenetic allometry of the skull of *Hydrodynastes gigas* in dorsal view. Shapes on the bottom show the predicted ontogenetic changes: Gray shows the average configuration of skulls, and black shows configuration on centroid size = 2 (left), centroid size = 5 (middle), and centroid size = 8 (right), which covers the whole size range studied

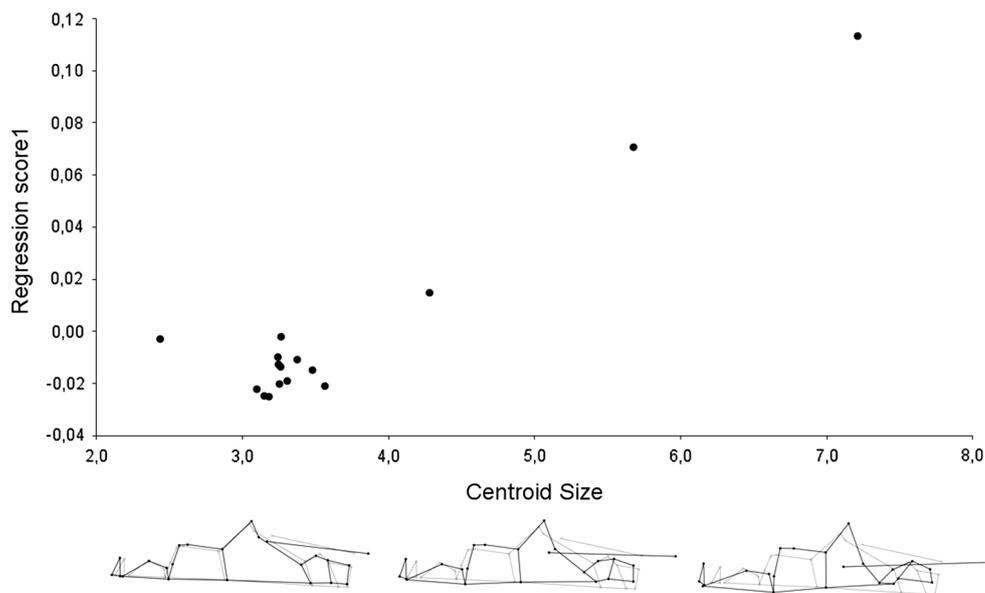
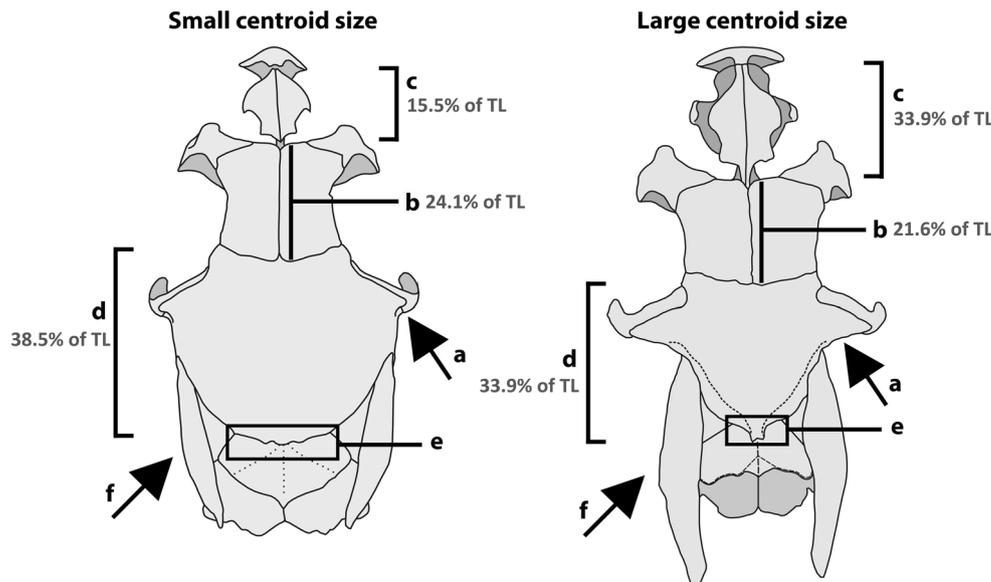


Fig. 3 Differences between skulls of *Hydrodynastes gigas* of small (FML1742-03; TL = 17.5 mm) and large centroid sizes (CS) (FML1746; TL = 41.7 mm). **a** Size of postorbital process. **b** Relative size of medial region of frontals. **c** Relative size of nasals. **d** Relative size of parietal. **e** Contact between parietal and supraoccipital and shape of posterior region of parietal. **f** Position and relative size of supratemporals. Percentages express the size of a feature relative to total length of the skull. TL total length



Smaller centroid sizes were correlated to short postorbital process, medial region of frontals elongated, shortened nasals and elongated parietal, pronounced contact between parietal and supraoccipital, posterior region of parietal slightly tapered, and shortened and oblique supratemporals in relation to the anteroposterior axis of the skull (Figs. 2, 3). Larger centroid sizes, on the opposite, point to postorbital process elongated, medial region of frontals shortened, frontoparietal suture straight, elongated nasals and shortened parietal, posterior region of parietal strongly tapered, and elongated and parallel supratemporals in relation to the anteroposterior axis of the skull (Figs. 2, 3).

Skull morphology

The skull of *H. gigas* differs from the skull of *H. bicinctus* (character states in parentheses) by being less dorsoventrally compressed (Fig. 4).

Premaxilla triangular in frontal view with slender transverse process slightly oblique dorsally and posteriorly slanted in ventral view (vs. transverse process slightly oblique ventrally and straight in ventral view). *Septomaxilla* with anterior edge slightly bifurcated (vs. anterior edge simple) and anterolateral process oblique dorsally and posteriorly slanted (vs. anterolateral process with rounded

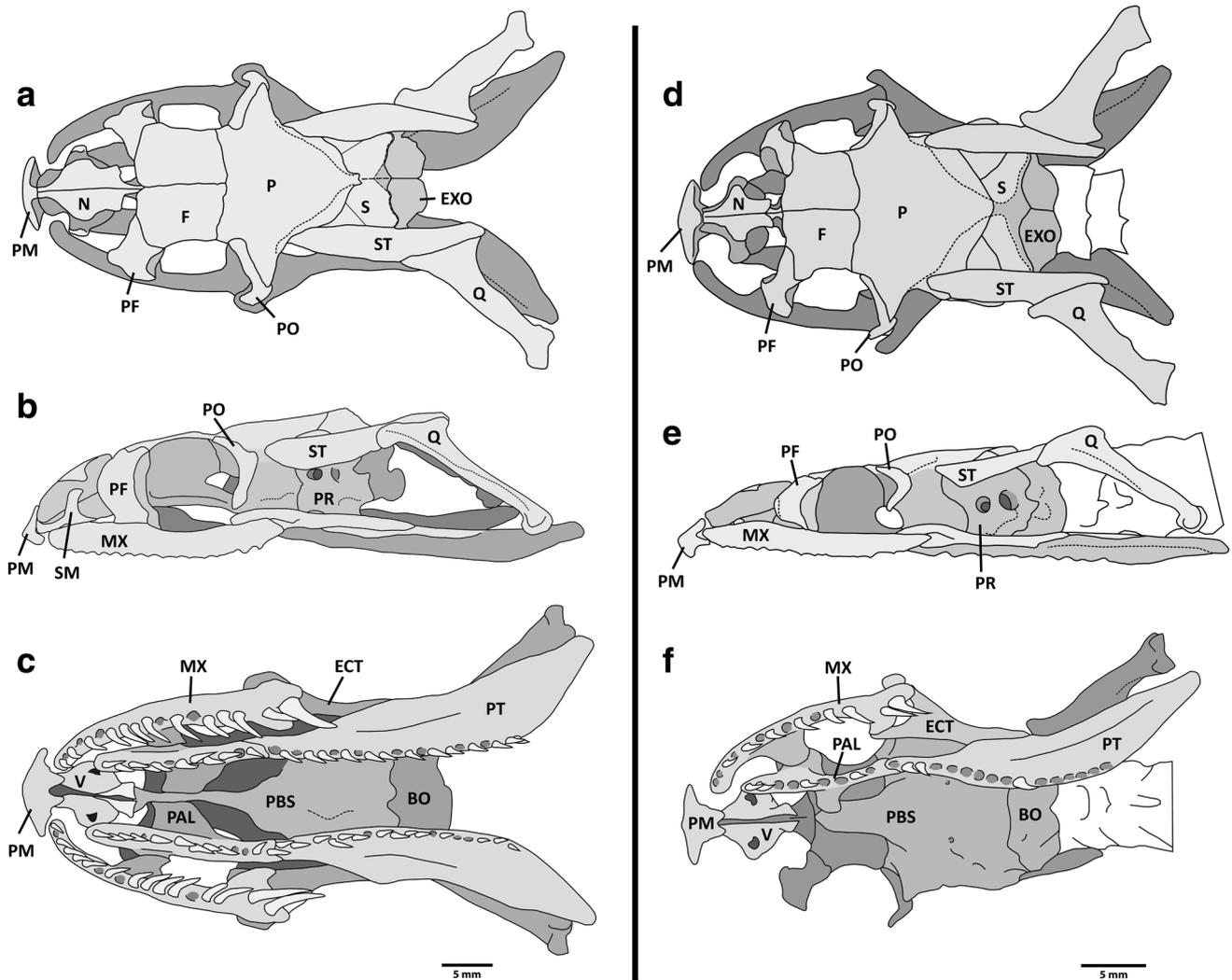


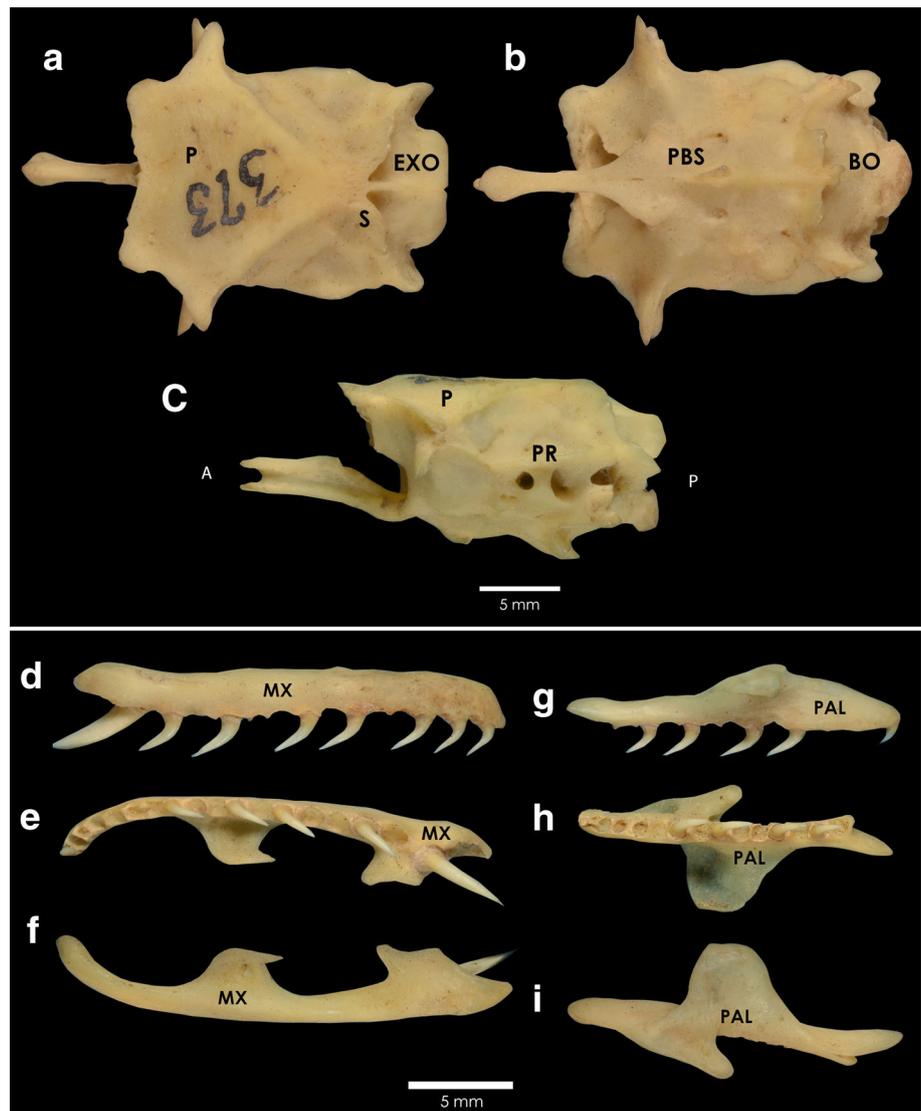
Fig. 4 Comparison between the skulls of *Hydrodynastes gigas* (FML 1746; left) and *H. bicinctus* (MNRJ 4767; right). Dorsal (a, d), lateral (b, e), and ventral (c, f) views. BO basioccipital, ECT ectopterygoid, EXO exoccipital, F frontals, MX maxilla, N nasals, P parietals, PAL

palatine, PBS parabasisphenoid; PF prefrontal, PM premaxilla, PO postorbital, PR prootic, PT pterygoid, Q quadrate, S supraoccipital, SM septomaxilla, ST supratemporal, V vomer

edge). *Nasal* with anterior edge much slender than posterior, nasals with pentagonal shape (vs. anterior edge slightly slender than posterior, nasals diamond shaped); mesolateral portion conspicuously ventrally directed (vs. not conspicuously ventrally directed); nasals contact ascending process of premaxilla (vs. do not contact ascending process of premaxilla). *Frontals* with squared shape in dorsal view (vs. trapezoidal shape in dorsal view); anterolateral and posterolateral portions approximately at the same level (vs. anterolateral portion laterally expanded relative to posterolateral portion); the presence of a small process in the vertex of the angle formed in the prefrontal–frontal joint—here referred as vertex process of frontal (vs. scaled prefrontal–frontal joint in *H. bicinctus*, not forming a vertex). Prefrontal–frontal joint oblique to mesolateral

axis of frontal in dorsal view (vs. parallel to mesolateral axis of frontal in dorsal view). *Prefrontal* in lateral view with anterior portion concave (vs. with acuminate projection); prefrontal is more elongated dorsoventrally in *H. gigas* than in *H. bicinctus*. *Parietal* (Fig. 5) with postorbital process even more conspicuous in adults of *H. gigas* than in *H. bicinctus*; two convergent well-developed dorsolateral crests, which are more developed in larger specimens, emerge at the level of postorbital process up to region of contact with supraoccipital, touching each other (vs. dorsolateral crests not in contact). *Postorbital* long (Fig. 4), nearly straight and ventrally directed, almost touching maxilla (vs. small, curved, oblique directed, not approaching maxilla). *Basioccipital* (Fig. 5) with three conspicuous dentigerous processes nearby the suture with

Fig. 5 Braincase of *Hydrodynastes gigas* (FML 2156) in dorsal (a), ventral (b), and lateral views (c). Maxilla in lateral (d), ventral (e), and dorsal views (f), and palatine in lateral (g), ventral (h), and dorsal views (i). *BO* basioccipital, *EXO* exoccipital, *MX* maxilla, *P* parietal, *PAL* palatine, *PBS* parabasisphenoid, *PR* prootic, *S* supraoccipital, *a* anterior, *p* posterior



parabasisphenoid, and lateral processes well developed, all of them more developed in larger specimens (vs. inconspicuous dentigerous and lateral processes); the absence of a longitudinal mesial crest (vs. the presence of a slight longitudinal mesial crest). *Parabasisphenoid complex* (Fig. 5) spear shaped, with anterior portion conspicuously tapered, from its edge to about the level of palatine-ptyergoid joint, where it turns broader with a longitudinal crest developed on posteromedial portion, which is more developed in larger individuals (vs. anterior portion not conspicuously tapered and the absence of longitudinal crest on posteromedial portion). Palatine process of *Maxilla* (Fig. 5) with broad base and slender edge, extending from eighth up to 13th teeth, with posteromedial edge acuminate (vs. palatine process with broad base and edge, extending from sixth up to ninth teeth); 16 to 17 prediastemal teeth (vs. 12 to 13); maxillary teeth curved medially (vs. maxillary teeth nearly perpendicular to maxilla); maxilla and

palatine closer to each other in *H. gigas* than in *H. bicinctus*. *Palatine* (Fig. 5) with maxillary process extending from fourth up to eighth teeth (vs. from fourth up to sixth teeth); choanal process extending from sixth up to 11th/12th teeth, with tapered edge extending from fifth up to eighth teeth (vs. choanal process extending from sixth up to eighth teeth with no tapered edge), contacting parabasisphenoid (vs. close to parabasisphenoid but not reaching it); palatine bears 11 to 13 curved teeth of nearly equal size (vs. 10 to 11 teeth). *Pterygoid* bears 24 curved teeth of nearly equal size, and mesolateral portion articulates with ectopterygoid on the level of sixth up to 15th teeth (vs. 15 to 18 teeth, and pterygoid articulates with ectopterygoid on the level of seventh up to 10th teeth). *Ectopterygoid* with anterior edge as an expanded bifurcation, with lateral branch of bifurcation wider than medial (vs. simple bifurcation with branches of equal width) (Fig. 6). *Supratemporal* overlaps much of dorsal portion of prootic,

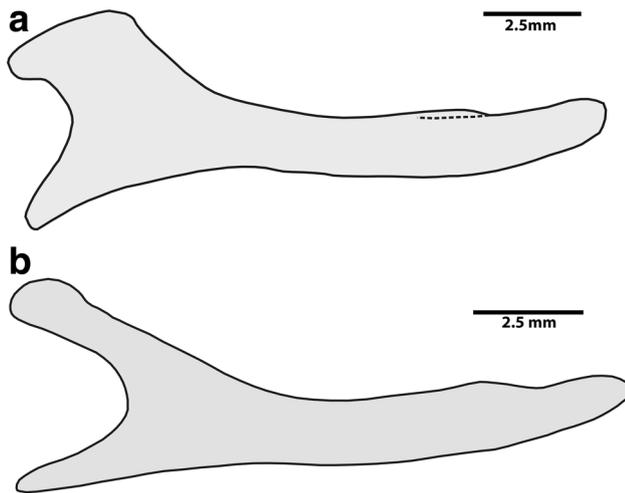


Fig. 6 Ectopterygoid of *Hydrodynastes gigas* (a) and *H. bicinctus* (b) in ventral view

contacting dorsal border of the anterior and posterior foramina of prootic and *fenestra ovalis* (vs. not contacting dorsal border of foramina and *fenestra ovalis*); posterior edge not extending beyond dorsal limit of braincase in lateral view (vs. posterior edge extends beyond dorsal limit of braincase). *Dentary* (Fig. 7) contacts angular on the level of 14th teeth and bears 17 to 19 curved teeth (vs. contacts angular on the level of 11th teeth and bears 15 to 17 teeth). The other characters of the skull showed no differences compared to *H. bicinctus* (see the description in Murta-Fonseca et al. 2015).

Discussion

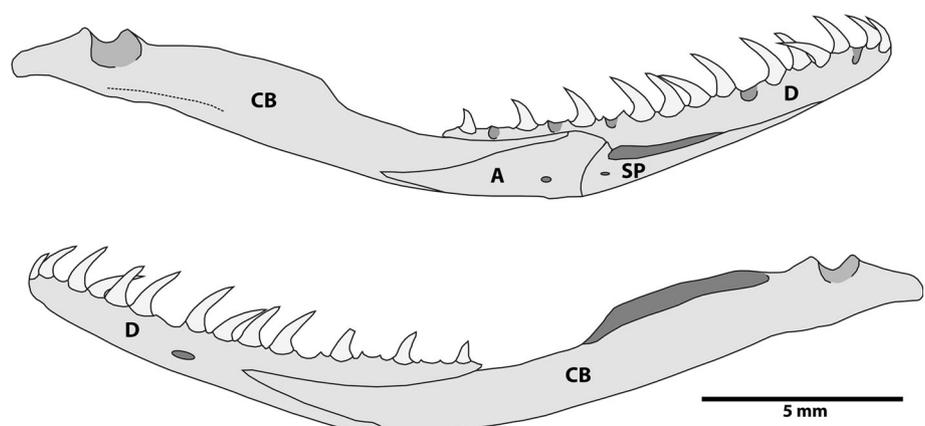
The analyses presented herein reveal a significant ontogenetic allometry in the skull of *H. gigas*. These results were observed in other vertebrates (e.g., Cardini and O'Higgins 2005; Ponssa and Vera Candioti 2012; Blanco et al. 2015),

although it has never been tested for snakes through GM. Other studies, however, showed correlations between the proportions of the structures of the skull and/or proportions between the size of the skull and the size of the snake (e.g., Rossman 1980; Vincent et al. 2004; Natusch and Lyons 2012; López et al. 2013; Hampton 2014).

The idea of the existence of a negative correlation between size of the head and size of the body in snakes (as well as in other vertebrates) throughout ontogeny is very well supported, that is, the smaller the body, the larger the size of the head proportionally (e.g., Vincent et al. 2004—*Agkistrodon piscivorus*; Natusch and Lyons 2012—*Morelia viridis*; Hampton 2014—*Nerodia fasciata*). However, studies focusing on the correlations between isolated bones of the skull are scarce for snakes, with the notable exceptions of the works of Rossman (1980) with *Nerodia rhombifer*, and Vincent et al. (2007) and Hampton (2014) with *N. fasciata*. We compared our results with such studies since these are the only known approaches dealing with ontogenetic allometry in snakes skull (although not employing GM methods), in order to evaluate the existence of recurrent patterns of allometric growth in the taxa examined. We supported some of the results of Rossman (1980), who also found a positive allometry between nasal length and skull length, and a negative allometry between frontal length and skull length. Likewise, Rossman (1980), Vincent et al. (2007), and Hampton (2014) found a positive allometry between supratemporal length and skull length, a result also supported by our data. On the other hand, Rossman (1980) found no correlation between parietal length and skull length (vs. negative allometry in the present study). This difference regarding the few existent works considering allometry in specific bones of the skull of snakes reinforces the need of further studies to evaluate the existence of recurrent patterns within the group.

Traditionally, correlations between shape and diet have been the main focus of discussion on studies showing the existence of morphological changes in the skull during

Fig. 7 Mandible of *Hydrodynastes gigas* (FML 2156) in medial (superior) and lateral views (inferior). A angular, CB compound bone, D dentary, SP splenial



ontogeny in snakes (especially juveniles vs. adult specimens). There are studies showing allometric changes in feeding apparatus (e.g., Rossman 1980; Vincent et al. 2007; Hampton 2014) and/or ontogenetic changes in diet (e.g., Garcia and Drummond 1988; Daltry et al. 1998; Natusch and Lyons 2012), while these patterns were not found in other studies (e.g., Vincent et al. 2004). The differences in diet throughout ontogeny are usually related to morphological, behavioral, and physiological changes (Natusch and Lyons 2012; López et al. 2013; Hampton 2014). Considering species whose individuals of distinct age classes occupy the same habitats, ontogenetic changes in diet might be a strategy to reduce intraspecific competition (Meik et al. 2010). In the present study, we did not evaluate shifts in feeding apparatus, since we used a dorsal view of the skull, although the suspensorium apparatus, such as supratemporal length, is a good predictor of gape circumference (Hampton 2014). Nevertheless, no evidences of ontogenetic changes in the diet of *H. gigas* are known, precluding inferences on the correlations of skull shape and feeding habits.

The application for the first time of GM for analyses of ontogenetic allometry in the skull shape of snakes showed very satisfactory results and reinforces the method as a powerful tool in this kind of study. Furthermore, we emphasize the importance of analyzing other structures beyond feeding apparatus in GM studies since allometric changes in the skull of snakes are not restricted to these bones. The results presented herein confirm Rossman (1980) who states that ontogenetic changes in skull morphology are of sufficient magnitude to warrant caution in supporting taxonomic decisions based on small samples of randomly selected skulls. We emphasize that the same precaution should be considered for the use of characters related to skull morphology in phylogenetic studies and reinforce that researchers should use only specimens of comparable size classes to codify the states of such characters. Moreover, studies of the skull shape in snakes harbor a bias since they usually deal with a small sample size and therefore underestimate the patterns of variation expressed in the skeletal system (Bell and Mead 2014). This trend may be partially explained by the culture of many modern biologists around the world who consider skeletal preparation as “wasted specimens,” making available only skulls of specimens with incomplete or no data collection (Bell and Mead 2014). We hope that the advent of new technologies to access skeleton morphology without damaging the specimen, such as high-resolution X-ray computed tomography, changes this scenario.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Human and animals rights This article does not contain any studies with human participants or animals performed by any of the authors.

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