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Cranial development and directional asymmetry in Commerson's dolphin, *Cephalorhynchus commersonii commersonii*: 3D geometric morphometric approach

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Commerson's dolphin, *Cephalorhynchus commersonii*, is one of the smallest species of odontocete cetaceans. We aimed to study the postnatal cranial ontogeny of *C. commersonii* through geometric morphometric technique, analyzing the postnatal ontogeny of the symmetric and asymmetric components of shape and providing information about sexual dimorphism affecting cranial shape and size. We digitized 57 landmarks in a sample of 139 crania of an ontogenetic series. Our results indicate that *C. commersonii* presents sexual size dimorphism of cranium in adults, but not shape dimorphism. Major changes between juveniles and adults were associated with lengthening of the rostrum and accentuation of telescoping, as observed in other odontocetes. We found that the degree of asymmetry has a very subtle but still significant change during ontogeny, which may have functional implications. We also observed little general variation in skull shape during postnatal development, supporting the idea of the conservatism of young-like characters in adults of *C. commersonii*. In accordance with this, we detect a very early attainment of stability of shape and size, being statistically similar in males and females. Differences in overall cranial shape and growth patterns in *C. commersonii* and *Pontoporia blainvillei* can be functionally associated to specific modes of feeding, suggesting also differences in the melon morphology.

La tonina overa, *Cephalorhynchus commersonii*, es una de las especies de odontocetos más pequeñas. El objetivo de este trabajo fue estudiar la ontogenia craneana postnatal de esta especie a través de técnicas de morfometría geométrica, analizando la ontogenia postnatal de la componente simétrica y asimétrica de la forma, considerando el posible dimorfismo sexual en forma y tamaño del cráneo. Se digitalizaron 57 landmarks en una muestra de 139 cráneos. Los resultados obtenidos indicaron que *C. commersonii* presenta dimorfismo sexual en el tamaño del cráneo en ejemplares adultos, mientras que no se detectó dimorfismo sexual ligado a la forma. Los principales cambios de forma entre juveniles y adultos estuvieron ligados al alargamiento del rostro y a la acentuación del telescopamiento, como se ha observado en otros odontocetos. Se encontró que el nivel de asimetría direccional tiene un cambio sutil pero significativo durante la ontogenia, lo que podría tener implicancias funcionales. Se observó, como tendencia general, una variación de forma moderada durante la ontogenia postnatal, evidencia que apoya la hipótesis de que los adultos de esta especie retienen caracteres juveniles. En concordancia con estos resultados, se encontró que se alcanzó muy tempranamente la estabilidad en la forma y en el tamaño del cráneo, y no se detectaron diferencias en estos valores para machos y hembras. Las diferencias en patrones de forma y de crecimiento craneales en *C. commersonii* y *P. blainvillei* pueden estar asociados funcionalmente a modos específicos de alimentación, lo que también sugiere diferencias en la morfología de melón.

Key words: asymmetry, *Cephalorhynchus commersonii*, cranial ontogeny, geometric morphometrics

During the postnatal ontogeny in mammals, the cranium of suckling young develops structures and a specific morphology associated with obtaining of different feeding habits and behavior in adult age stages. The ontogeny has been largely studied on terrestrial and partially aquatic mammals with carnivorous habits (e.g., Flores et al. 2003; Brunner et al. 2004; Tanner et al. 2010; Segura et al. 2013; Tarnawski et al. 2014; Flores et al. 2015; Segura 2015) and on cetaceans (e.g., Kurihara and Oda 2007; del Castillo et al. 2014; Nakamura and Kato 2014; del Castillo et al. 2015). In the last group, ontogenetic studies also address issues such as directional asymmetry (DA—Yurick and Gaskin 1988), sexual dimorphism (Calzada et al. 1997; del Castillo et al. 2014), and morphological evolution (Galatius 2010; Galatius et al. 2011; Sydney et al. 2012).

Asymmetry is defined as a deviation of an organism (or a part of it) from perfect symmetry and is composed by 2 different categories (Van Valen 1962). Fluctuating asymmetry (FA) occurs when the mean of the differences between sides in the studied character do not differ from 0. DA occurs when one side of a bilateral trait always develops more than the other side (Van Valen 1962) and is known to affect the cranial morphology of odontocete cetaceans on a wide range of magnitudes, from subtle (e.g., *Pontoporia blainvillei*) to strongly marked asymmetries (e.g., *Physeter macrocephalus*) (Ness 1967; Mead 1975; MacLeod et al. 2007). DA has been associated with sound production mechanisms (e.g., Yurick and Gaskin 1988; Berta et al. 2014; see Mead 1975 for a review of the hypotheses relating to odontocete skull asymmetry), although some recent studies suggest that it is in association with feeding needs (i.e., left-shifted nares correspond to a left-shifted larynx, which should enable asymmetric odontocetes to swallow larger prey than they could if they were symmetrical—MacLeod et al. 2007). Even though DA has been widely studied (Ness 1967; Yurick and Gaskin 1988; MacLeod et al. 2007), its postnatal ontogeny in cetaceans has been poorly addressed.

The pattern of postnatal skull growth and development varies notably in mammals (e.g., Segura et al. 2013; Tarnawski et al. 2014; Flores et al. 2015) and can vary intraspecifically, in species which have sexual dimorphism (e.g., Tarnawski et al. 2014). In most mammals, sexual dimorphism in size is expressed with males larger than females, whereas inverted dimorphism is registered for few terrestrial mammals such as hyenas, which exhibit matriarchal social structure (Frank 1986). Inverted sexual dimorphism is more common in cetaceans, such as *P. blainvillei*, *Phocoena phocoena*, *Platanista gangetica*, *Berardius bairdii*, and species of the genus *Cephalorhynchus* (Kasuya and Brownell 1979; Lockyer et al. 1988; Ralls and Mesnick 2002; Galatius 2005; del Castillo et al. 2014). The inverted sexual dimorphism in size observed on small cetaceans was linked to competition for resources in females, or the capacity for large offspring (with optimal size to maintain body temperature—Ralls 1976).

Cephalorhynchus commersonii commersonii is one of the smallest species of odontocete cetaceans and is included in family Delphinidae. They inhabit coastal waters of South America between 40°S and 56°S (Goodall 1994; Iñíguez et al. 2003). Sexual maturity is reached at 5–6 years of age, and their length at birth is 55–75 cm. Weaning is reached between 0.5 and 1 year of age and average adult length is 134 cm for females and 130 cm for males (Lockyer et al. 1988; Stewart et al. 2002; Perrin et al. 2009; Riccialdelli et al. 2013). Commerson's dolphins present cranial asymmetry and inverted sexual size dimorphism, with females being 5–10% larger than males (Perrin et al. 2009). A recent report has indicated a paedomorphic condition of some skeletal characters. This condition marks the end of their growth and development sooner than other delphinids, and reaching a lower fusion of skeletal elements (Galatius 2010). Such characters were also observed in some porpoises (Phocoenidae—Galatius 2010; Galatius et al. 2011). Although Commerson's dolphins were properly compared to porpoises, their comparison with other small cetaceans of different superfamilies, such as the Franciscana dolphin, *P. blainvillei* (Pontoporiidae) remains unexplored.

The principal aim of our research was to study the postnatal cranial ontogeny of *C. commersonii* through geometric morphometric technique, analyzing the postnatal ontogeny of the DA of the cranium and detecting changes in asymmetry levels. In addition, we provide information about sexual dimorphism affecting cranial shape and its biological significance, and we compare and discuss our results with those previously obtained for *P. blainvillei* (del Castillo et al. 2014) and other odontocetes.

Materials and Methods

Sample.—We analyzed a sample of 139 crania of a complete ontogenetic series of *C. c. commersonii* (65♂, 65♀, 9 unknown sex; Supporting Information S1) deposited on the mammal collection of the Museo Acatushún de Aves y Mamíferos Marinos Australes (AMMA), Tierra del Fuego, Argentina. Age determinations by dentinal Growth Layer Groups (Perrin and Myrick 1980) were available for 91 specimens (Dellabianca et al. 2012), whose ages were observed between 0 and 18 years. Our sample was entirely composed by specimens of the subspecies *C. c. commersonii* (we did not include specimens of the subspecies *C. commersonii kerguelensis*, which inhabits exclusively the Kerguelen Islands in the Indian Ocean—Robineau et al. 2007). Our smallest male specimen was 236 mm in condylobasal length (RNP773), whereas the largest male specimen was 291 mm (RNP1497). For females, our smallest specimen was 249 mm (RNP1693) and the largest was 290 mm in condylobasal length (RNP1896). Because most dolphins experience most changes during the 1st year, an important limitation of our sample is the absence of neonate specimens. However, our sample includes male and female specimens younger than 1 year, which exhibit clear differences (in size and shape) with respect to older specimens (see "Results" section). The smallest specimens of both sexes were similar in size, and, considering that males and females are born at similar lengths (e.g., Neuenhoff et al. 2011; Galatius et al. 2013), we can assume comparable ontogenetic stages for the young individuals for both sexes. Comparing the size of our smallest and largest specimens, it is noteworthy that our smallest specimens are not neonates, but specimens younger than 1 year, which experienced some growth from birth. On the other hand, dolphins are born in a completely precocial stage, exhibiting complete biological abilities for survival (Perrin et al. 2009).

Data acquisition.—We digitized 57 landmarks in each cranium (Fig. 1; Supporting Information S2), modified from Sydney et al. (2012), with a 3D digitizer MX Microscribe. The landmarks were chosen in order to have a good representation of the overall skull shape and in a way that allow us to see important features of development and asymmetry. Each cranium was digitized at least twice, and an average of both configurations was taken.

Symmetric component of shape.—Superimposition of landmark configurations was performed by a Generalized Procrustes Analysis, to remove the spatial variation that does not correspond to form (Goodall 1991; Rohlf 1999). A principal component analysis (PCA) with the covariance matrix of the symmetric component of the shape (Klingenberg et al. 2002) was performed to identify the major components of variation. A linear regression of the symmetric component of the shape versus log centroid size (CS; calculated as the square root of the sum of squared distances of each landmark from the centroid of the landmark configuration—Bookstein 1991; Zelditch et al. 2012) was performed to detect how symmetric component of shape changes in relation to size. For comparison between males and females trajectories in the regression analyses, the angles between regression vectors of both sexes were compared using VecCompare (IMP software package—Sheets 2001), which compares the between-group angle with the 95% confidence interval (95% *CI*) of within-group ranges assessed by a bootstrap procedure (4,900 resamples). If the observed between-group angle is larger than the *CI* ranges of the 2 within-group angles, the directions of the 2 compared vectors were significantly different at $P = 0.05$. Because ontogenetic vectors were not statically different between sexes, data were pooled together and shape variation during ontogeny was analyzed for the entire sample. We included information about size and shape through CS and Procrustes distance (PD) estimations. PD was calculated as the square root of the sum of the squared distances between each landmark of 1 specimen and the configuration of the smallest specimen (in age 0) and was used as an index of shape change. CS and PD were calculated with the software R 2.9.2 (R Development Core Team 2015), plotted versus age, and fitted a nonlinear growth model (von Bertalanffy) to ascertain the 95% *CI*s of the age at which the adult cranial shape and size were stabilized. This analysis was performed on males and females separately:

$$Y \sim A\,(1 - e^{-K\,(\mathrm{Age}\,-\,\gamma)})$$

where Y is the dependent variable (CS or PD), A is the asymptotic dependent variable, K is a growth rate parameter (year − 1), and γ is the age at inflection point (yr). We report age at stability as the estimated age at which the variable reaches 95% of its asymptotic value, which is equivalent to the age-maturity considered by Tanner et al. (2010).

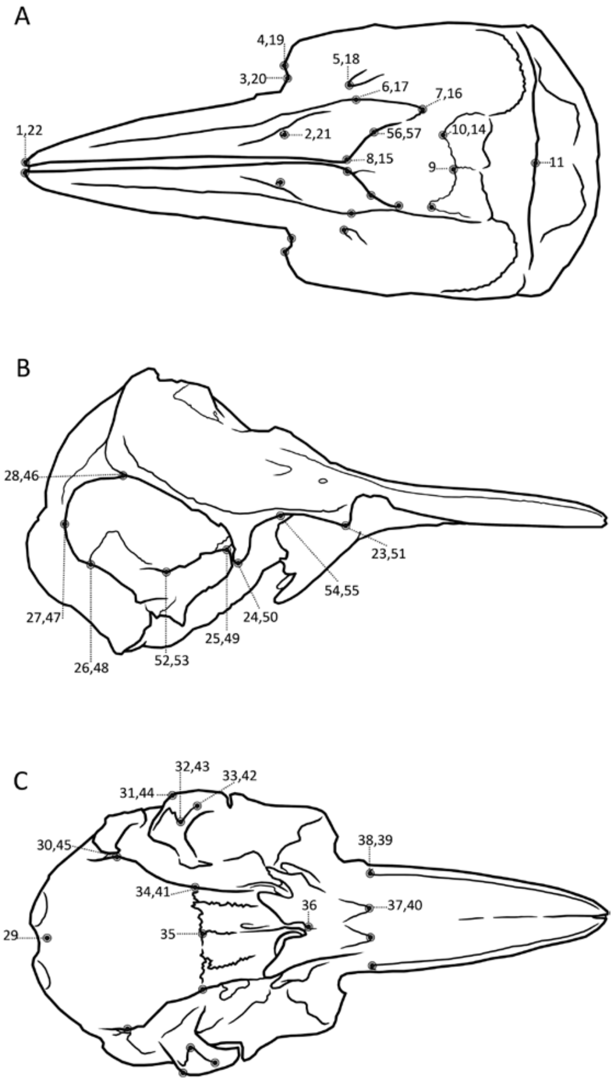

Fig. 1.—Landmarks in A) dorsal, B) lateral, and C) ventral views of the skull of *Cephalorhynchus commersonii*. For landmarks definition, see Supporting Information S2.

Asymmetric component of shape.—A Procrustes analysis of variance (ANOVA) was performed to study the asymmetric component of shape, which allows us to detect significance of different sources of variation, such as interindividual variation, FA, and DA. Besides, the following analyses: PCA, regression, and von Bertalanffy growth model, were performed on the asymmetric component of the shape, in order to study its development. When regression analyses were performed separately for males and females, the regression slopes were not significantly different ($P > 0.05$).

Sexual dimorphism.—Sexual dimorphism was addressed in different ways. We compared positions in the morphospace between sexes and performed comparisons between regression vectors angles and the age at which the stability of different components of both shape and size were reached. Besides, we compared positions in the morphospace of a size-corrected PCA analysis (i.e., PCA of the residuals of the regression of shape into size), to evaluate shape differences between sexes that are not size-related. First, this analysis was performed with the complete ontogenetic series, and then on immature and mature individuals as separate subsets to detect if sexual dimorphism on shape or size was only expressed in adults periods, or dimorphism is already expressed during juvenile stages of growth. Finally, an ANOVA was performed using CS as dependent variable, to analyze sexual size dimorphism. ANOVAs were carried out with the complete ontogenetic series, as well as on immature and mature subsets separately. The normality of the CS was tested with a Shapiro–Wilks test in both our complete sample and cutoff subsets (complete sample: $W = 0.97$, $P = 0.11$; immature subset: $W = 0.95$, $P = 0.42$; mature subset: $W = 0.98$, $P = 0.90$). According to Lockyer et al. (1988), we considered specimens mature when they were over 6 years of age, and immature when they were under 5 years of age. Specimens aged between 5 and 6 years and specimens without estimated age were excluded from the last 2 analyses, in order to avoid dolphins whose maturity stage was intermediate or in doubt (maturity is reached between 5 and 6 years old). All statistical analyses were performed with MorphoJ (Klingenberg 2011), Infostat (Di Rienzo et al. 2008), and R (R Development Core Team 2015).

RESULTS

Symmetric component of shape.—In the PCA, the PC1 summarized 15.62% of the explained variation (Fig. 2A). Along this axis, dolphins that are located towards the positive region (smaller specimens) show relatively short rostra, relatively high and wide braincases, and dorsoventrally compressed and ventrally displaced temporal fossae. Dolphins located towards the negative region of the axis (larger specimens) show proportionally longer rostra, flat and narrow braincases, and tall temporal fossae.

The regression of Procrustes coordinates versus CS was highly significant ($P < 0.01$), and the size explained 5.7% of the shape changes (Fig. 3). Ontogenetic trajectory describes shape variation from smaller crania showing a short and inclined rostrum, broad and tall posterior part of the cranium, toward larger crania showing a longer and less inclined rostrum, and a relatively more compressed neurocranium. In addition, infraorbital and premaxillary foramina were caudally displaced in older specimens, as well as those landmarks surrounding the nares, which were expected according to telescoping of the cranium. The occipital crest was displaced anteriorly, also accompanying the supra-occipital telescoping over the parietal and frontal bones during ontogeny.

The analysis of the ontogenetic shape change through PD of the symmetric component showed important differences between our smaller specimen of 0 and those of 1 year old, reaching an asymptote (i.e., stability of the symmetric component of shape) nearly after. The stability of the symmetric component of shape was reached at approximately 1.76 years for females and 1.21 years for males (Figs. 4A and C). However, there was no detectable difference between sexes when *CI*s were compared (Table 1). CS data also fit von Bertalanffy growth model. Females and males reached stability of this component at approximately 0.97 years of age (Table 1).

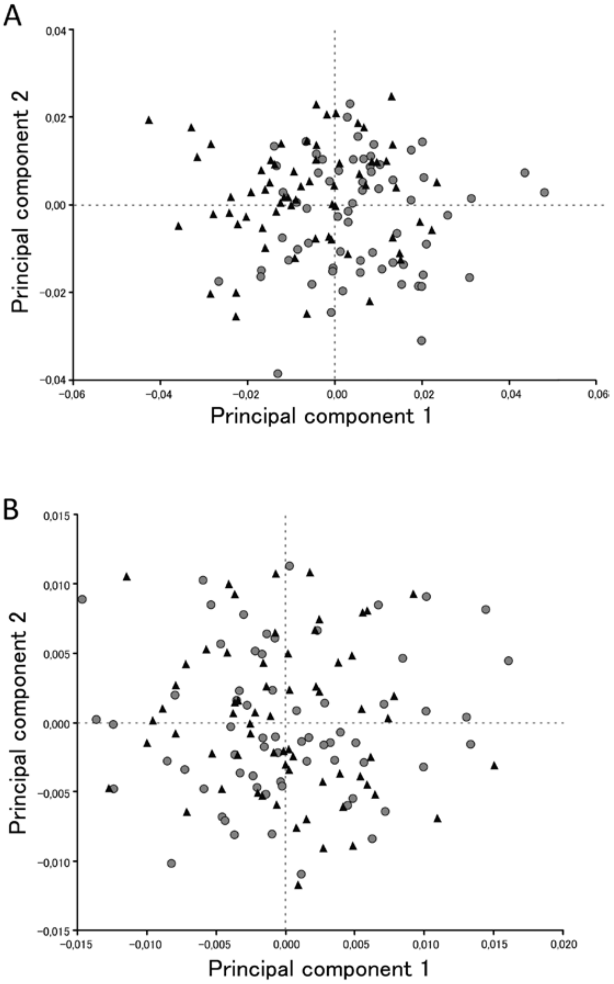

Fig. 2.—PCAs of the 3D shape variables including all landmarks. A) Symmetric component of shape and B) asymmetric component of shape. Circles = males; triangles = females. PCA = principal component analysis.

Asymmetric component of shape.—Procrustes ANOVA showed that DA is present on this sample ($P < 0.01$), as well as FA (Table 2). DA affected principally dorsal cranial region, especially landmarks of the nasal region, associated with air passage (Fig. 5). Shape variation between individuals accounted for 51% of the total variance, whereas variance associated with DA accounted for 34% of the total variance, and the variance associated with FA represented only 10% of the total variance. The variation due to digitizing error represented only 4% of the total variance.

In the PCA of the asymmetric component of the shape, the PC1 summarized 11.91% of the variation (Fig. 2B). Along this axis, dolphins that are located towards the negative (larger specimens) region show an accentuation of the DA. Dolphins that are located towards the positive region (smaller specimens) of the axis show proportionally less asymmetrical crania.

Although the regression of asymmetric component against the log-transformed CS revealed that DA shows a significant

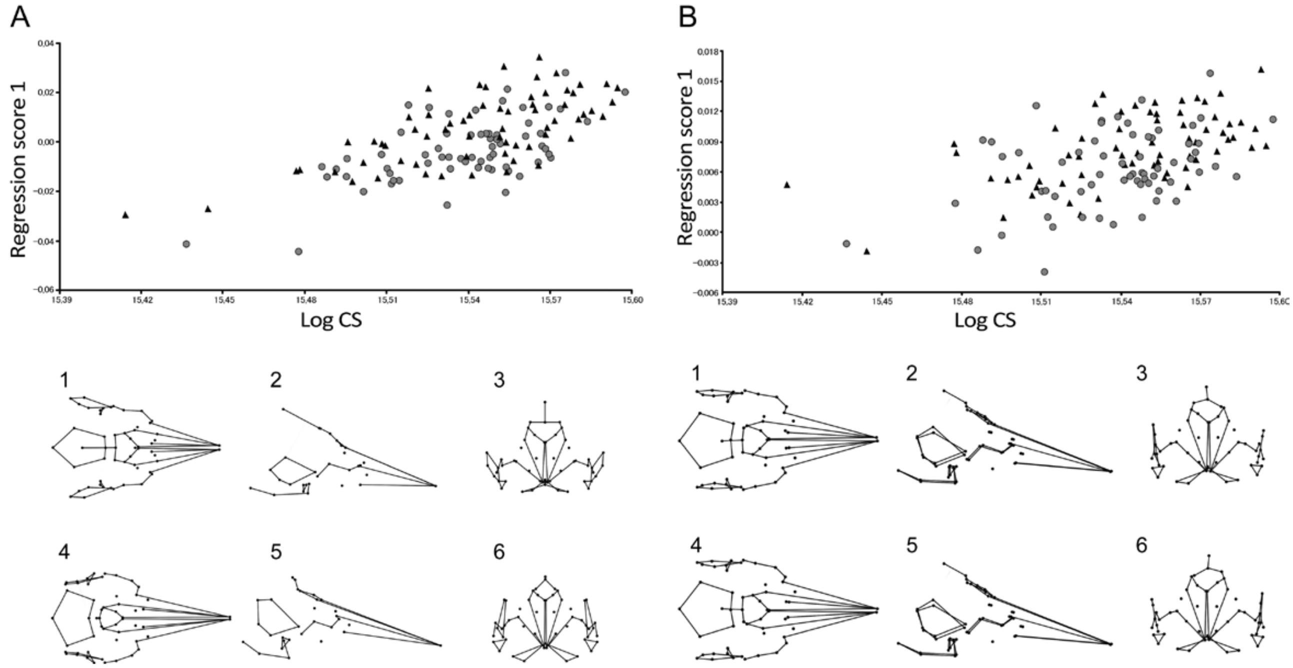

Fig. 3.—Regression of Procrustes distance from average shape versus log CS. A) Symmetric component of shape and B) asymmetric component of shape. Triangles = females; circles = males. (1, 4) dorsal; (2, 5) lateral; (3, 6) frontal views of lower and upper size extremes, respectively (shape differences magnified ×2). CS = centroid size.

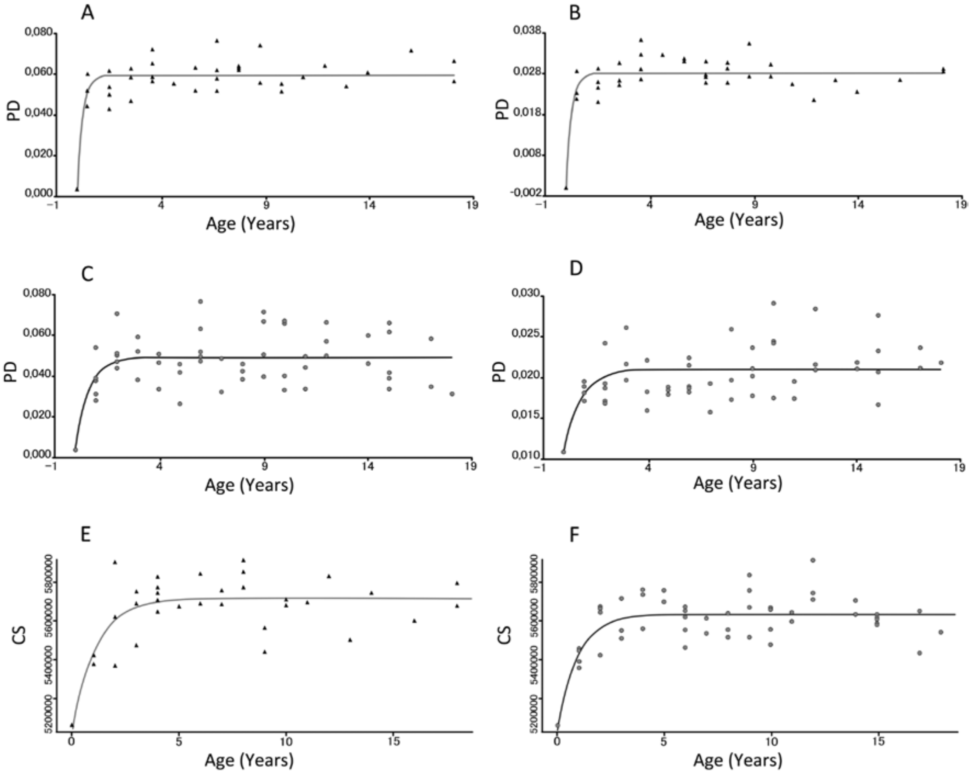

Fig. 4.—von Bertalanffy growth model for the PD (respect to the smallest specimen of our sample) and CS relative to age (GLGs) for females (A, B, E) and for males (C, D, F) of *Cephalorhynchus commersonii*. A, C) Symmetric component of shape. B, D) Asymmetric component of shape. E, F) CS. CS = centroid size; GLGs = Growth Layer Groups; PD = Procrustes distance.

($P < 0.05$) increase during ontogeny (Fig. 3), the percentage of variation explained by this regression is low (1.2%), compared to symmetric component of shape regression.

The analysis of the ontogenetic shape change through PD of the asymmetric component showed the largest difference is between our smallest specimen (age 0) and those of 1 year old

Table 1.—Growth models. Age (in years) in which the stabilization of shape is reached for males and females of *Cephalorhynchus c. commersonii* on symmetric components, asymmetric components, and centroid size, expressed as confidence intervals (95% *CI*s).

Symmetric component of shape	Females	1.761	0.787–3.322
	Males	1.216	0.567–1.699
Asymmetric component of the shape	Females	1.499	0.849–5.048
	Males	1.215	0.619–1.808
Centroid size	Females	0.970	0.564–1.70
	Males	0.975	0.992–1.190

Table 2.—Procrustes analysis of variance of skull shape asymmetry. DA = directional asymmetry; FA = fluctuating asymmetry.

Factor	Mean squares	Sum of squares	*d.f.*	*F* value	*P* value
Individual	0.439	3.789e-5	11,592	4, 78	< 0.0001
Side (DA)	0.293	3.663e-3	80	462, 10	< 0.0001
Individual * Side (FA)	0.088	7.927e-3	11,040	4, 63	< 0.0001
Residual	0.038	1.714e-6	21,976		

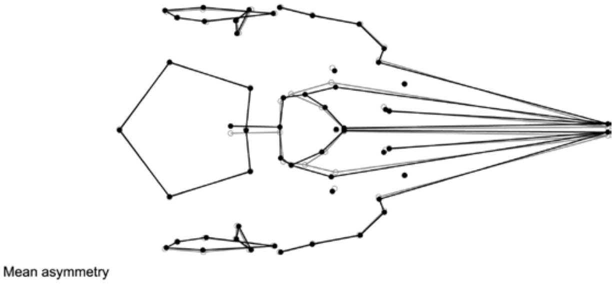

Fig. 5.—Mean cranial asymmetry of *Cephalorhynchus commersonii*, dorsal view. Black outline and closed circles: mean asymmetric shape component. Grey outline and open circles: mean symmetric shape component.

Table 3.—Comparison of cranial shape variation explained by size and sexual dimorphism in *Cephalorhynchus commersonii* and *Pontoporia blainvillei* (del Castillo et al. 2014).

	C. commersonii	*P. blainvillei*
% Shape variation explained by size	5.7	54.1
Sexual shape dimorphism	Absent	Nasal region, mature dolphins
Sexual size dimorphism	♀ > ♂, mature dolphins	♀ > ♂, mature dolphins
Total shape variance	0.0026	0.0035
Size variance	0.0021	0.0091
Allometric shape variance	0.0009	0.0023

but was markedly lower than the differences observed on the symmetric component of shape. Stability of this component was reached at 1.49 years for females, and 1.21 years for males (Figs. 4B and D). There was no detectable difference between sexes when *CI*s were compared.

Sexual dimorphism.—PCA and size-corrected PCA (not shown) of both symmetric and asymmetric components of shape showed that there are no conspicuous shape differences between males and females, neither in the complete datasets (Fig. 2) nor in the cutoff subsets (not shown). As mentioned above, we did not find shape differences associated with sexes in the regression analyses, and von Bertalanffy growth models failed to detect sexual dimorphism in reaching stability of shape (Table 1). Finally, sexual dimorphism in size was not detected in the complete data set and in the immature data set (complete dataset: $n = 127$; $F = 2.15$, $P = 0.15$; immature dolphins: $n = 33$; $F = 1.66$, $P = 0.21$). However, we detected sexual dimorphism in mature dolphins, where females showed higher CS than males ($n = 46$; $F = 5.95$, $P = 0.02$).

Comparison of our results (Table 3) with those obtained for *P. blainvillei* (del Castillo et al. 2014) reveals that the percentage of shape variation in relation to size (same set of landmarks) is strikingly different in both species, being notably lower in *C. commersonii*. Sexual shape dimorphism was only detected in *P. blainvillei*, whereas sexual size dimorphism showed the same pattern in both species (i.e., affecting only mature dolphins).

Discussion

Cranial ontogeny of C. c. commersonii.—The shape changes observed in the cranium during the postnatal development of *C. commersonii* included a relative narrowing of the braincase and a relative elongation of the rostrum, in agreement with the common pattern observed in odontocete and most terrestrial mammals (e.g., Moore 1966; Galatius et al. 2011; Sydney et al. 2012; Segura et al. 2013; del Castillo et al. 2014; Flores et al. 2015).

The cranial telescoping showed a weak accentuation during postnatal ontogeny, evidenced by the anterior displacement of the occipital crest and by the caudal displacement of the dorsal infraorbital foramina in larger specimens. Moderate shape change during the postnatal ontogeny of *C. commersonii* is probably widespread in delphinids and related to specializations to the aquatic environment. In odontocete cetaceans, most of the morphogenesis of the skull in functional terms is already present at birth (e.g., Oelschläger 2000), as the newborns must be fairly developed, with all their biological abilities for survival in such extreme environmental conditions; i.e., they must be able to swim, have visual capability, hear and vocalize immediately after birth (Perrin et al. 2009). Indeed, dolphins are more precocial than most terrestrial mammals (e.g., Abdala et al. 2001; Segura et al. 2013; Flores et al. 2015). Our results indicate that components of shape (symmetric and asymmetric) showed no differences between males and females (PCAs), nor the period in which both sexes reached stability (i.e., asymptote; Table 1). In both sexes, the final shape was obtained after weaning, but before sexual maturity. On the other hand, although we did not detect differences on the age at which stability of CS is reached (von Bertalanffy model), we detected that mature female crania were larger than that of males. Such differences are common in some small cetaceans (Kasuya and Brownell 1979; Goodall et al. 1988; Lockyer et al. 1988; Ralls and Mesnick 2002; Galatius 2005; Panebianco et al. 2012; del Castillo et al. 2014), and it has been suggested that this sexual dimorphism may be an adaptation for carrying large offspring (Ralls 1976). However, the significant greater size of the female skull can be a consequence not only from a different pattern of allometric growth, but also attributable to a growth extension of females compared to males (i.e., bimaturism—sensu Leigh 1992).

DA represented a percentage of total variance notably higher than FA (i.e., 34% and 10%, respectively; Table 2). In addition, the percentage explained by DA was very large compared with other mammal species (e.g., humans—Lotto and Gonzalez 2014; nonhumans primates—Willmore et al. 2005; rodents—Burgio et al. 2009), which is expected for the typical asymmetrical condition of dolphins. Size explained only 1.2% of shape variation of asymmetric component, which is an extremely low percentage, although the regression was significant ($P = 0.02$). This confirms the almost despicable change in shape during growth, and the presence of asymmetry from early stages of development. The DA in odontocete skulls is related to biosonar (see Haddad et al. 2012; Berta et al. 2014), for which such asymmetry is functionally important since birth. The fact that asymmetric component of shape fitted to the growth model proposed, suggests an imperceptible increase of asymmetry with age in *C. commersonii*, which may have positive effects in echolocation abilities from birth.

Comparison with other odontocetes.—The telescoping of the skull deepens weakly during growth; this trend has also been observed in not-closely related species of small odontocetes such as *P. phocoena*, *Lagenorhynchus albirostris*, and *P. blainvillei*, suggesting that it may be a plesiomorphic and conserved feature among odontocete cetaceans (Galatius 2010; Galatius et al. 2011; del Castillo et al. 2014). Size explained only 5.7% of shape variation ($P < 0.001$) of symmetric component, a lower percentage if compared with other small dolphin previously studied (e.g., *P. blainvillei*—del Castillo et al. 2014; Table 3). This indicates little variation in skull shape of *C. commersonii* during postnatal development, supporting the idea of the conservatism of young-like characters in adults (Galatius 2010; Galatius et al. 2011). Although both dolphins are among the smaller odontocetes, the strong development of the rostrum of *P. blainvillei* does not exist in *C. commersonii*. Indeed, in *P. blainvillei*, del Castillo et al. (2014) found that a high percent of cranial shape variation can be explained by allometric scaling (54.1%; an order of magnitude higher than that of *C. commersonii*). Moreover, when rostral landmarks of *P. blainvillei* were experimentally eliminated, size explained 10.9% of shape variation (see del Castillo et al. 2014), still a value almost twice than obtained for the complete data set in *C. commersonii.* Differences in overall cranial shape and growth patterns in *C. commersonii* and *P. blainvillei* are functionally associated to specific modes of feeding, as suggested by Werth (2006a, 2006b). Long and slender rostra with many teeth, such as that of *P. blainvillei*, are associated with raptorial feeding strategies, which involve a rapid closure of the mouth to capture prey (del Castillo et al. 2014). Alternatively, short and blunt rostra with small and round mouth openings are associated with suction feeding, which involves drawing water and prey into an enlarged oral cavity, from rapid retraction and depression of the tongue (Werth 2006a). However, *Cephalorhynchus* species are not obligate suction feeders but are known to use both feeding strategies (Werth 2006b). Our calculation and comparison of the total size variance (variance of LogCS), total shape variance (sum of all eigen-values of the PCA of the asymmetric component of the shape), and allometric shape variance (sum of eigen-values of the PC with significant correlation to Log CS) suggest that although the shape variance is similar in both species (0.0026 versus 0.0035), size variance and allometric variance are higher in *P. blainvillei* (Table 3). This indicates that *Cephalorhynchus* exhibits higher shape variation not associated with size, suggesting higher constraints for morphological variation in *P. blainvillei*.

Although the external cranial difference present between *C. commersonii* and *P. blainvillei* not necessarily reflects differences in melon morphology and function of focusing sound (Norris and Harvey 1974; Cranford et al. 1996; McKenna et al. 2012), previous research has reported that cranial morphology may be related with melon morphology (concave facial regions can accommodate larger melons) and, in consequence, it may reflect different capabilities in sound emission mechanisms (Galatius et al. 2011). In this regard, the cranial morphology of these 2 species of different families is very different (the facial region is much more concave in *C. commersonii*), suggesting possible functional differences, involving intensity and directionality of the sound beam (Galatius et al. 2011). However, Morisaka and Connor (2007) showed comparable acoustic repertoires in some species, including *P. blainvillei*, other *Cephalorhynchus* species, some porpoises, and pygmy sperm whales, *Kogia breviceps*.

In *C. commersonii*, the asymmetric component of shape fitted to the growth model proposed (Table 1). Moreover, the regression slope of asymmetric component of shape into size was significant, but the amount of variation for which the regression model accounted was very low, suggesting an imperceptible increase of asymmetry with age, in a similar pattern to *P. phocoena* whose degree of asymmetry was not correlated with cranial length or, by implication, age (Yurick and Gaskin 1988). Adult females and males of *C. commersonii* were similar in shape, while in *P. blainvillei* adult females and males were different in shape of the dorsal part of the premaxillaries and the external bony nares, which may be related to differences in sound production abilities between sexes (del Castillo et al. 2014). According to that hypothesis, *C. commersonii* does not present osteological evidence for differential abilities between sexes. However, even though osteological examination is a good and accessible tool to study morphology and functional implications, it is restricted, as it does not consider soft tissues, important in sound production and communication (Norris and Harvey 1974; Cranford et al. 1996). Osteological observations should be taken as a starting point for developing more detailed studies considering soft tissue anatomy (McKenna et al. 2012), as well as environmental variables, in order to achieve a deeper knowledge about functional issues.

In other species of small cetaceans such as *P. phocoena* and *P. blainvillei*, it was reported that females grow (in size) for a longer period than males (Galatius 2005; Negri 2010). We did not observe this pattern of females growing for a longer period of time in our sample. Further research about intraspecific growth patterns on other species may provide valuable knowledge useful for analyzing this component in a comparative context.

Previous research proposed that *C. commersonii* presents several paedomorphic features such as short rostra, round braincases, small body size, and early attainment of sexual maturity (e.g., Lockyer et al. 1988; Goodall 1994; Galatius 2010) which are shared with porpoises (Galatius et al. 2011). According to Galatius (2010), paedomorphosis in *C. commersonii* is achieved through progenesis (i.e., truncation of development in the descendant species, where the attainment of adulthood and onset of sexual maturity occurs at a younger age than in the ancestor). In accordance with this, our results show a very early attainment of stability of shape, and a very conservative cranial shape and size during their postnatal ontogeny. Although both small dolphins (*C. commersonii* and *P. blainvillei*) exhibit limited suture fusion in adults crania (Galatius et al. 2011; del Castillo et al. 2015), we did not detected, in *P. blainvillei*, the paedomorphic condition assigned for *C. commersonii* in other characters of the skull (e.g., rostrum growth). There was no convergence between both species, as those defined for porpoises and *C. commersonii* (Galatius et al. 2011). As discussed, *P. blainvillei* cranial ontogeny show striking differences with paedomorphic species (Gutstein et al. 2009). However, if other factors are considered, such as the earlier onset of sexual maturity than its closest extant relative *Inia geoffrensis* (Best and da Silva 1989; Ramos et al. 2000), their small adult size, and patent sutures in adults (del Castillo et al. 2015), the idea of paedomorphosis affecting some characters in *P. blainvillei* does not seem unlikely. A detailed study of the fossil record of Pontoporiidae and related groups would shed light on this issue and expand knowledge of evolutionary trends on cetaceans.

In summary, our results indicate that *C. commersonii* presents cranial sexual size dimorphism. Major changes between juveniles and adults were associated with lengthening of the rostrum and accentuation of telescoping in *C. commersonii*, and there was a very subtle change in asymmetry during ontogeny. It would be relevant to assess a more diverse taxonomic sample in the context of the changes of cranial shape and size in odontocete cetaceans, in order to evaluate levels of flexibility of the cranium to evolve in response to selection pressures. Further studies must focus on the analysis and detection of DA and sexual dimorphism during the ontogeny in other odontocete species, in order to reveal if the patterns observed herein are stable and common in delphinids, or if there is a major complexity in the mode of growth and levels of asymmetry in a more speciose sample.

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SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1. List of studied specimens of RNP collection.

Supporting Information S2. Anatomical description of landmarks used.

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