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CRANIAL SUTURE CLOSURE IN THE FRANCISCANA DOLPHIN, *Pontoporia blainvillei* (GERVAIS AND D'ORBIGNY, 1844)

Daniela L. del Castillo^{1,3}, David A. Flores^{2,3*},
and Humberto L. Cappozzo^{1,3,4}

¹ Laboratorio de Ecología, Comportamiento y Mamíferos Marinos, División Mastozoología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" Av. Ángel Gallardo 470 (C1405DJR), Buenos Aires, Argentina.

² División Mastozoología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" Av. Ángel Gallardo 470 (C1405DJR), Buenos Aires, Argentina.

³ CONICET. Consejo Nacional de Investigaciones Científicas y Técnicas, Av. Rivadavia 1917 (C1033AAJ), Buenos Aires, Argentina.

⁴ Fundación Azara - Universidad Maimónides, Hidalgo 775 7mo (C1405BDB), Buenos Aires, Argentina.

[Correspondencia: Daniela L. del Castillo <dld.castillo@gmail.com>]

* Present Address: Unidad Ejecutora Lillo, CONICET-Fundación Miguel Lillo. Miguel Lillo 251, 4000 Tucumán, Argentina.

ABSTRACT. Cranial suture closure and its bilateral asymmetry in the franciscana dolphin, *Pontoporia blainvillei*, were studied. Our results showed that the closure of cranial sutures exhibit low variability associated to total body size, with the exception of the premaxilla-maxilla suture which showed some correlation with body size. The cranial sutures of franciscana dolphins showed closure with no directional asymmetry, in accordance with the results found in dolphin species studied to date. Our results support the idea that different species of dolphins exhibit distinct patterns of suture closure, associated with their specific evolutionary histories and functional demands, and that there is no general common pattern.

RESUMEN. Fusión de suturas craneales en el delfín franciscana, *Pontoporia blainvillei* (Gervais and D'Orbigny, 1844). Se estudió la fusión de suturas craneales y su asimetría bilateral en el delfín franciscana, *Pontoporia blainvillei*. Nuestros resultados mostraron que el cierre de suturas presenta baja variabilidad asociada a la longitud corporal total, exceptuando la sutura premaxilar-maxilar, cuyo estado de fusión mostró cierta asociación con el tamaño. Las suturas no mostraron asimetría direccional en su patrón de cierre, en concordancia con los resultados encontrados para las especies de delfines estudiadas hasta ahora. Nuestros resultados apoyan la idea de que diferentes especies de delfines exhiben distintos patrones de cierre de suturas asociados con su historia evolutiva y sus demandas funcionales específicas, y que no hay un patrón común general.

Palabras clave: Asimetría. Cráneo. Franciscana. Odontocetos. Suturas.

Key words: Asymmetry. Franciscana. Odontocete. Skull. Sutures.

Skeletons deposited in scientific collections are useful for performing studies addressing different subjects such as anatomy, evolution or ecology (e.g., Alberch, 1985; Miller, 1985; Suarez and Tsutsui, 2004). Although this material usually lacks valuable biological information such as age or state of maturity, the detection of morphological characters associated to body size is always welcome. Cranial sutures of mammals are among the most variable characters in relation to age and size; they change in both morphology and fusion stages during growth (e.g., Flores et al., 2006; Segura and Flores, 2009; Sánchez-Villagra, 2010; Denuncio et al., 2011; Flores and Barone, 2012; Segura, 2013). Such changes are associated with functional demands and regional growth of the skull. The forces acting on function and growth patterns of skulls of terrestrial mammals—during head movements and mastication—are relatively well known (e.g., Herring, 1972; Behrents et al., 1978; Jaslow, 1990; Herring et al., 1996; 2001; Hylander and Johnson, 1997), and the sequence of suture closure in several groups (such as pigs, carnivores or primates) has been mostly analyzed in a functional framework, in relation to localized tension and compression strains on the skull during various activities (e.g., Herring and Mucci, 1991; Herring and Teng, 2000). Suture closure has also been addressed from an evolutionary point of view (e.g., Wilson and Sánchez-Villagra, 2009; Rager et al., 2013; Segura, 2014). However, stress patterns of skulls in highly specialized mammals such as dolphins are profoundly different than those of non-cetacean mammals, due to strong modifications associated with telescoping of the skull (Fish et al., 2003).

Cranial sutures have been principally interpreted as indicators of maturity in odontocete mammals, although it has been demonstrated that it is not possible to generalize their usefulness as maturity indicators, because each species seems to express its own pattern of cranial suture closure across age or size (e.g., Dailey and Perrin, 1973; Mead and Potter, 1990; Van Waerebeek, 1993; Calzada et al., 1997; Chen et al., 2011). For instance, in the pantropical spotted dolphin (*Stenella attenuata*), the spinner dolphin (*S. longirostris*), the bottle nose dolphin

(*Tursiops truncatus*) and the striped dolphin (*S. coeruleoalba*), the fusion of the premaxillary-maxillary suture, which is related to size, is a reliable indicator of physical maturity (Dailey and Perrin, 1973; Mead and Potter, 1990; Calzada et al., 1997). Alternatively, in the dusky dolphin (*Lagenorhynchus obscurus*), the fusion of the frontal-supraoccipital suture is a reliable indicator of sexual maturity (Van Waerebeek, 1993), whereas in the Risso's dolphin (*Grampus griseus*) closing of fronto-interparietal, nasal-frontal and maxillary-premaxillary sutures are reliable indicators of sexual maturity (Chen et al., 2011). On the other hand, directional asymmetry is a feature known to be present in odontocete skulls, and has been widely studied (e.g., Ness, 1967; Cranford et al., 1996; Yurick and Gaskin, 1998), although so far it has not been reported in suture closure (Chen et al., 2011; Jordan, 2012).

The franciscana dolphin, *Pontoporia blainvillei*, is a small dolphin endemic to the southwestern Atlantic Ocean, which was categorized as vulnerable (Reeves et al., 2012). This dolphin belongs to the monotypic family Pontoporiidae (McGowen et al., 2009), occurring from south-eastern Brazil (Siciliano, 1994) to northern Patagonia in Argentina, and inhabits coastal-marine waters, from the coast to the 30-m isobath (Crespo et al., 2010). Although there are several studies of cranial morphology of this species (e.g., Burmeister, 1867; Flower, 1867; Pinedo, 1991; Mazzetta, 1992; Higa et al., 2002; Ramos et al., 2002; Trimble and Praderi, 2008; Negri, 2010; Del Castillo et al., 2014), none of them has focused on variability of suture closure or identification of directional asymmetry on suture closure during growth. The aim of this study is to determine the relation between body size of *P. blainvillei* and the fusion (or closure) pattern of cranial sutures, as well as to determine if the species shows directional asymmetry in suture closure.

We analyzed 156 skulls of franciscana dolphins (83♀, 73♂) of a complete ontogenetic series deposited at the mammal collection of the Museo Nacional de Historia Natural from Uruguay (see **Supplementary Material**). Additional information available, such as the total

body length (TL, in cm), was recorded. Because sexual maturity and age data of the sample were unknown, we use body size (=TL) as a proxy of age (see Kasuya and Brownell, 1979). Male dolphins were considered as sexually mature when TL was equal or greater than 131 cm. Females were considered as sexually mature when TL was equal to or greater than 140 cm. Taking in consideration previous reports on suture closure in different dolphin species (see above), we focused our analyses on those sutures that have proved to be useful for determining approximate age or sexual maturity in dolphin skulls (**Fig. 1**):

- Premaxilla-maxilla, on the most dorsal and posterior region (PM-MX) (Gonzalez, 2002; Jordan, 2012).
- Squamosal-parietal (SQ-PR) (Chen et al., 2011).
- Parietal-frontal (PR-FR) (Galatius, 2010).
- Squamosal-exoccipital (SQ-EO) (Chen et al., 2011).
- Nasal-frontal, on the posterior region (NS-FR) (Chen et al., 2011).

Following the codification proposed by Chen et al. (2011) for *G. griseus*, we assigned a value between 0 and 3 in relation to the degree of suture closure observed (observations were made with naked eye):

0. Bones can move freely; there is no fusion.
1. Bones cannot be moved; junction between them is clearly visible at all points.
2. Partial obliteration of the suture line or joint, due to advancing fusion.
3. Complete obliteration of the suture line or joint.

In addition, we calculated a sutural index (SI) for each specimen by adding the assigned value of each suture on the left and right sides (Galatius, 2010). In order to explore the sutural change in relation to TL, we performed a bivariate relation of both variables. We employed a non-parametric Kruskal-Wallis test to evaluate differences of SI between mature and immature subsets (Jordan, 2012), and between sexes. Finally, we performed a Wilcoxon test of paired

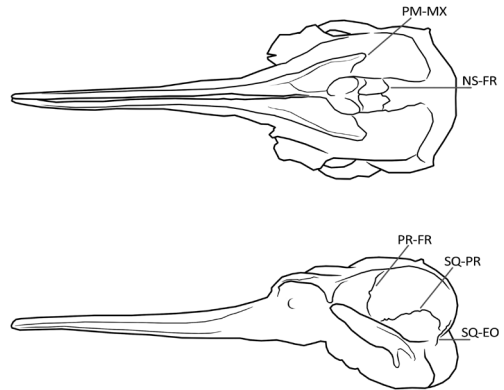


Fig. 1. Franciscana dolphin (*P. blainvillei*) skulls in a dorsal (up) and lateral (down) view, showing the sutures examined for fusion states. PM-MX: premaxilla-maxilla, SQ-PR: squamosal-parietal, PR-FR: parietal-frontal, SQ-EO: squamosal-exoccipital, NS-FR: nasal-frontal.

observations for each suture analyzed in order to test for directional asymmetry in suture closure (Chen et al., 2011). Collected data was analyzed with Infostat (Di Rienzo et al., 2008).

Cranial suture closure showed extremely low ontogenetic variability in *P. blainvillei* (**Fig. 2**). PM-MX and SQ-EO were the most and least variable respectively in closure condition in relation to size. As a general trend, larger specimens showed more advanced PM-MX closure but complete fusion was rarely achieved in remaining sutures (**Fig. 2**). Moreover, a complete obliteration of the suture line (i.e., stage 3), was not observed in any suture of our sample, not even in the larger specimens, such as MNHN 4548 (TL: 174 cm) and MNHN 4661 (TL: 163 cm). Dispersion diagram of SI vs. TL (**Fig. 3**) showed that most specimens had a SI between 10 and 12, and only eight specimens showed higher or lower values. Four that showed higher values were mature and 1 immature, and the 3 with lower values were immature. Significant differences were obtained in SI values between mature and immature dolphins (Kruskal-Wallis test: N Immature = 110, Median = 10; N Mature = 39, Median = 11; $H = 11.91$; $p < 0.01$), with a high level of overlap between both age classes (**Fig. 3**). No significant differences were obtained in SI value between males and females (Kruskal-Wallis test: N Males = 70, Median = 10;

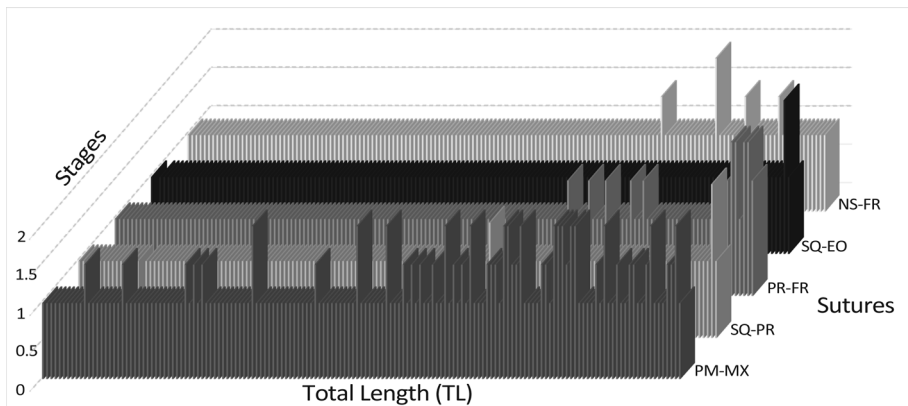


Fig. 2. Fusion stages for cranial sutures analyzed in relation to total length (TL) of 153 franciscana dolphins (*P. blainvillei*) from Uruguay. TL ranges from 83 to 174 cm (see **Supplementary Material**). Scores recorded on the left and right side of the cranium were averaged. PM-MX: premaxilla-maxilla, SQ-PR: squamosal-parietal, PR-FR: parietal-frontal, SQ-EO: squamosal-exoccipital, NS-FR: nasal-frontal.

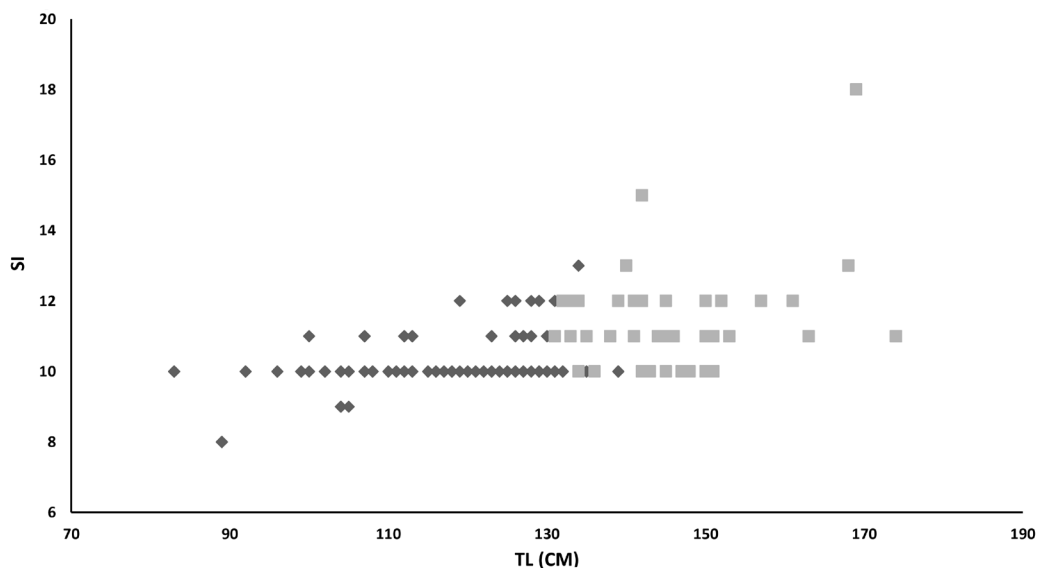


Fig. 3. Cranial sutural index (SI) in franciscana dolphins (*P. blainvillei*) from Uruguay plotted against body total length (TL). Light grey points: mature dolphins. Dark grey points: immature dolphins.

N Females = 83, Median = 10; H = 0.56; p = 0.38). No significant bilateral asymmetry of the sutures analyzed was detected (Wilcoxon Test, **Table 1**). The test for SQ-EO was not performed because all pairs were equal (i.e., all specimens showed the same stage of fusion on their left and right sides).

Although our results exhibit low ontogenetic variability and an almost invariant SI across size

(between 10 and 12) in *P. blainvillei*, the eight specimens with higher and lower SI values were well related with body size, thus suggesting that skulls showed at least an incipient pattern of suture closure and TL in this species. Such findings are not as clear as the sequence of suture closure detected in other species of the Family Delphinidae (e.g., *Stenella* spp., *L. obscurus*, *T. truncatus*, *G. griseus*). We are

Table 1

Wilcoxon matched-pairs signed rank test for bilateral asymmetry in the degree of fusion of cranial sutures in the franciscana dolphin (*P. blainvillei*) from Uruguay. No significant bilateral asymmetry was detected ($p < 0.05$). PM-MX: premaxilla-maxilla, SQ-PR: squamosal-parietal, PR-FR: parietal-frontal, SQ-EO: squamosal-exoccipital, NS-FR: nasal-frontal.

Suture	n	W	P
PM-MX	153	243	0.076
SQ-PR	153	1.5	>0.99
PR-FR	153	16	>0.99
SQ-EO	153	n/a	n/a
NS-FR	153	4	>0.99

aware that we have limited representation of very early stages of postnatal ontogeny, since our sample has rather few very small/neonate specimens. However, in this report we focused in events of suture closure that occur in middle and later stages of growth. We found that SI was not strictly related to size, suggesting that it is not a reliable tool for discrimination of maturity in the species. There was a high degree of overlap between SI values of each group, although significant differences were found between them (Fig. 3). A similar outcome has been presented by Pinedo (1991), who found that fusion of most cranial sutures was weakly correlated with age groups, and that invisibility of the SQ-PR suture, together with some discrete morphological characters of the skull (i.e., bone alveolar separation throughout tooth rows, downward curvature of the rostrum, and fusion of the hyoid bones), showed a better correlation with age and size in *P. blainvillei*. It is noteworthy that Pinedo (1991) found the SQ-PR suture to be completely fused in 2% of her sample (N=853), indicating that, in line with our observations, this condition is rarely achieved, even among very old specimens. It is also important to mention that the method we used to determine sexual maturity presents important limitations. TL may have geographic, temporal and individual variations, which we did not consider. However, the method

proposed by Kasuya and Brownell (1979) was developed with dolphins of the same region of the sample used by us (Franciscana Management Area [FMA] III, Secchi et al., 2003), and most specimens of our sample were collected shortly after those studied by Kasuya and Brownell. Therefore, we believe that the approach we use to define mature and immature dolphins is valid, although these results should be treated with caution when compared with *P. blainvillei* from other FMAs.

The sutures analyzed in this study only reached stage two of fusion (i.e., without complete obliteration). This finding is not in agreement with those found by Chen et al. (2011) for *G. griseus*, where SQ-PR and PR-FR do reach a complete fusion. Similarly, Jordan (2012) found that stage 3 is reached in PM-MX and NS-FR sutures in *Delphinus* sp. In some terrestrial mammals, suture closure seems to be related to skull size. For instance, in large carnivores as canids, felids and otariids, suture closure or fusion is a common condition in older and larger specimens (Brunner et al., 2004; Segura and Flores, 2009; Denuncio et al., 2011; Segura, 2013), although some exceptions also suggest a phylogenetic signal of suture closure pattern (see Wilson and Sánchez-Villagra, 2009; Rager et al., 2013; Segura, 2014). In this context, Barman et al. (2012) observed a pattern in terrestrial artiodactyls, where small species show a very limited amount of skull suture fusion, hypothesizing that it could be related to the thickness of the skull bones, based on the functional observations of Moazen et al. (2009). As skull bones are thinner in smaller animals, and sutures distribute strain across the whole skull (e.g., Herring, 1972), this might be an important factor for keeping them open, fulfilling the function of energy absorption. Our findings for *P. blainvillei* in comparison with larger Delphinidae species are in accordance with the former hypothesis. *Pontoporia blainvillei* is one of the smallest extant cetaceans, reaching mean standard body length of 153 cm in females and 133.33 cm in males (Kasuya and Brownell, 1979), whereas *Delphinus* sp. and *G. griseus* reach bigger sizes (*D. delphis* 201.21 cm for females, 212.92 cm for males, Murphy and Rogan, 2006; *G. griseus*

270 cm, Amano and Miyazaki, 2004). The recent work of Galatius et al. (2011), detected that bigger species of porpoises (*Phocoenoides dalli*, *Phocoena dipotrica*) generally show further development of cranial sutures than smaller species (*Phocoena phocoena*, *P. spinipinnis*), also supporting the hypothesis of Barman et al. (2012) for artiodactyls. A direct comparison of suture fusion and function of our results with that of terrestrial mammals is not feasible, since the physical processes of tension and compression in specific areas of the skull during mastication and other activities of terrestrial mammals (see Hylander and Johnson, 1994; Rafferty and Herring, 1999; Sun et al., 2004), are not comparable to the forces the cetacean skull is subjected to in the water. Forceful cranial activities which generate mechanical loads on cranial bones and sutures in odontocetes are probably related to prey capture and locomotion (i.e., swimming), and the function of energy absorption could be very limited in the cranial sutures of other areas of the skull (Sun et al., 2004; Loch and Simões-Lopes, 2013).

Galatius et al. (2011) described a paedomorphic condition in Porpoises based on some skeletal characters such as short rostrum and scarce closure of cranial sutures. Further comparisons in a phylogenetic context could shed light on heterochronic process or paedomorphic condition occurred during the evolution of *P. blainvillei*, considering their limited fusion of cranial sutures detected here. However, taking into account the strong development of the rostrum detected in the postnatal ontogeny of *P. blainvillei* skull (Del Castillo et al., 2014) a paedomorphic condition of this species is unlikely.

Finally, the absence of directional asymmetry in any of the sutures of *P. blainvillei* was also registered in other cetacean, such as *Grampus griseus* (Chen et al., 2011) and *Delphinus* sp. (Jordan, 2012). Considering that these species have more asymmetrical skulls than *P. blainvillei* (Ness, 1967; MacLeod et al., 2007) it is not surprising that *P. blainvillei* does not show an asymmetrical pattern of suture closure. Probably, the absence of directional asymmetry of suture closure is a plesiomorphic condition in odontocete cetaceans.

Summarizing, our results indicate that *P. blainvillei* cranial sutures have low variability in relation to body size and do not show directional asymmetry on their closure. Such pattern, also observed in porpoises, suggests a condition not strictly linked to paedomorphic species, as the skull morphology of *P. blainvillei* (specially the rostrum) exhibits strong modifications during its growth. The detection of this condition (i.e., poor fusion of skull sutures) in different clades of dolphins will help understand the phylogenetic significance of the pattern of sutural fusion in the group.

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SUPPLEMENTARY MATERIAL ONLINE

Specimens examined in this study.

https://www.sarem.org.ar/wp-content/uploads/2015/06/SAREM_MastNeotrop_22-1_Castillo-sup1.pdf