

## Article

## Ontogeny of the skull of *Sotalia guianensis* (Cetartiodactyla: Delphinidae) on the Northern coast of Brazil

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Received 7 December 2019

Accepted 19 August 2020

Published 26 October 2020

DOI 10.1590/1678-4766e2020024

**ABSTRACT.** This study aimed to investigate the ontogenetic development of the skull in the Guiana dolphin (*Sotalia guianensis* Van Bénédén, 1864) through the comparison of 29 morphological non-metrical characters together with the estimated age of 54 specimens derived from four areas on the northern coast of Brazil. The state of each character was associated with the age of each specimen to assess the formation of bone structures, and the degree of fusion of the sutures in each state of the character studied. Nineteen qualitative morphological characters presenting state ontogenetic variations have been analyzed statistically. The analysis depicted that the characters associated with the parietal-frontal suture, parietosupraoccipital, parietoexoccipital, supraoccipital-exoccipital and basioccipital-pterygoid varied according with the age. The results suggest that the physical maturity of the cranium was more premature in the specimens from the Northern Coast, suggesting a geographical adjustment of the species, or a biological response to an intense pressure of by-catch in fisheries over decades on the populations.

**KEYWORDS.** Aquatic mammals, small cetaceans, development, morphology.

**RESUMO.** Ontogenia do crânio de *Sotalia guianensis* (Cetartiodactyla: Delphinidae), na Costa Norte do Brasil. O objetivo do estudo foi investigar o desenvolvimento ontogenético craniano do boto-cinza (*Sotalia guianensis* Van Bénédén, 1864), comparando 29 caracteres morfológicos não métricos aliados às estimativas de idade de 54 espécimes provenientes de quatro áreas da Costa Norte do Brasil. Cada estado de caráter foi associado à idade de cada espécime para avaliar a formação de estruturas ósseas e o grau de fusão das suturas em cada estado de caráter analisado. Foram analisados estatisticamente 19 caracteres morfológicos qualitativos que apresentaram variação nos estados de caráter. A análise revelou que os caracteres que diferiram de acordo com a idade foram aqueles ligados à sutura parietal-frontal, parietal-supraoccipital, parietal-exoccipital, supraoccipital-exoccipital e basioccipital-pterigóide. Os resultados indicaram que a maturidade física do crânio foi mais precoce nos espécimes da Costa Norte, sugerindo uma estruturação geográfica da espécie ou uma resposta biológica a uma intensa pressão de captura acidental em redes de pesca sobre as populações.

**PALAVRAS-CHAVE.** Mamíferos aquáticos, pequenos cetáceos, desenvolvimento, morfologia.

The Guiana dolphin (*Sotalia guianensis* Van Bénédén, 1864) is considered as a “Near-Threatened” (NT) species by the International Union for the Conservation of Nature (SECCHI *et al.*, 2018) and characterized as a Vulnerable State (VU) as to the risk of extinction by the Red Book of Brazilian Fauna Threatened with extinction (ROSAS *et al.*, 2018). This species is described for the Atlantic coast of South and Central America (SIMÕES-LOPES, 1988; EDWARDS & SCHNELL, 2001; FLORES & DA SILVA, 2009; DA SILVA *et al.*, 2010). In its distribution along the Brazilian coast, the Guiana dolphin is loyal to its sites of feeding and reproduction, which are associated to coastal and estuarine environments (DI BENEDITTO & RAMOS, 2004).

A seminal study on the morphometry of the skull of *S. guianensis* verified that the cranial variables were diagnostics, which allowed the elevation of the two forms

to the category of separated species (MONTEIRO-FILHO *et al.*, 2002). MONTEIRO-FILHO *et al.* (2002) and FETTUCCIA *et al.* (2009) observed that in the marine species the cranial cavity, and the zygomatic process are wider.

Several studies associate data on the skull morphology of *S. guianensis* to the estimated age (FETTUCCIA *et al.*, 2009; RAMOS *et al.*, 2010; SYDNEY, 2012). FETTUCCIA *et al.* (2009) studied non-metric morphological features of the skull of *S. guianensis* from different parts of the Brazilian coast, and samples from Suriname, Venezuela, and Colombia. Even though FETTUCCIA *et al.* (2009) only had available a small number of samples from the northern coast of Brazil, which is a region of possible contact between the two species of *Sotalia*. FETTUCCIA *et al.* (2009) highlighted that there is still few morphological information on the populations of *Sotalia* spp. from this region. This study aimed to describe

the development of the skull of *S. guianensis* from different populations of the Northern Brazilian coast. This study provides a more accurate picture of these populations and compares the results to those of FETTUCCIA *et al.* (2009).

## MATERIAL AND METHODS

**Study area.** During the last years, the regular shore surveys performed by the Study Group on Amazonian Aquatic Mammals (*Grupo de Estudos de Mamíferos Aquáticos da Amazônia* - GEMAM) allowed a significant increase in the number of samples of *S. guianensis* in the mammals' collection of the Museum Emilio Goeldi of the State of Pará (MPEG). North Brazilian coast displays heterogeneity of coasts environments (SICILIANO *et al.*, 2008). The samples collected in this study derived from three areas: (1) Amapá coast, (2) Marajó bay and northeastern state of Pará (*Salgado Paraense* region) and (3) Parnaíba river delta, in the transition area between the Amazon coast, and the north-eastern coast of Brazil (Fig. 1).

**Study material.** The osteological material used in this study was composed of 116 skulls of *S. guianensis* (Tab. I) from the mammal collection of Museu Paraense Emilio Goeldi (MPEG), in Belém. Twenty-nine morphological

features were analyzed, following PERRIN *et al.* (1982), FETTUCCIA *et al.* (2009) and MEAD & FORDYCE (2009), adapted (Tab. II). Observations on the development pattern of skull sutures were also performed, according to GALATIUS & GOL'DIN (2011), adapted.

**Estimated age.** The teeth used for the estimation of the age were preserved in a glycerol-ethanol solution (1:1). Analysis of the slices was performed according to the proceedings proposed by HOHN *et al.* (1989) and PERRIN & MYRICK (1980), applying some modifications as suggested by DI BENEDITTO *et al.* (2010) for the enumeration of the Growth Layers Groups (GLG's). The enumeration of GLG's was performed two times by different observers for each specimen, in order to have no interference on the enumeration (DI BENEDITTO *et al.*, 2010). In case of incompatibility in the results, a third reading was performed. The age estimation were used in the morphological description and the statistical analysis in order to assess the ontogenetic development of the skull.

**Statistical analysis.** Fifty-four skulls (see appendix) were used for the statistical analysis. These skulls were used to compare the bone development with the time of formation and fusion of each bone structure.

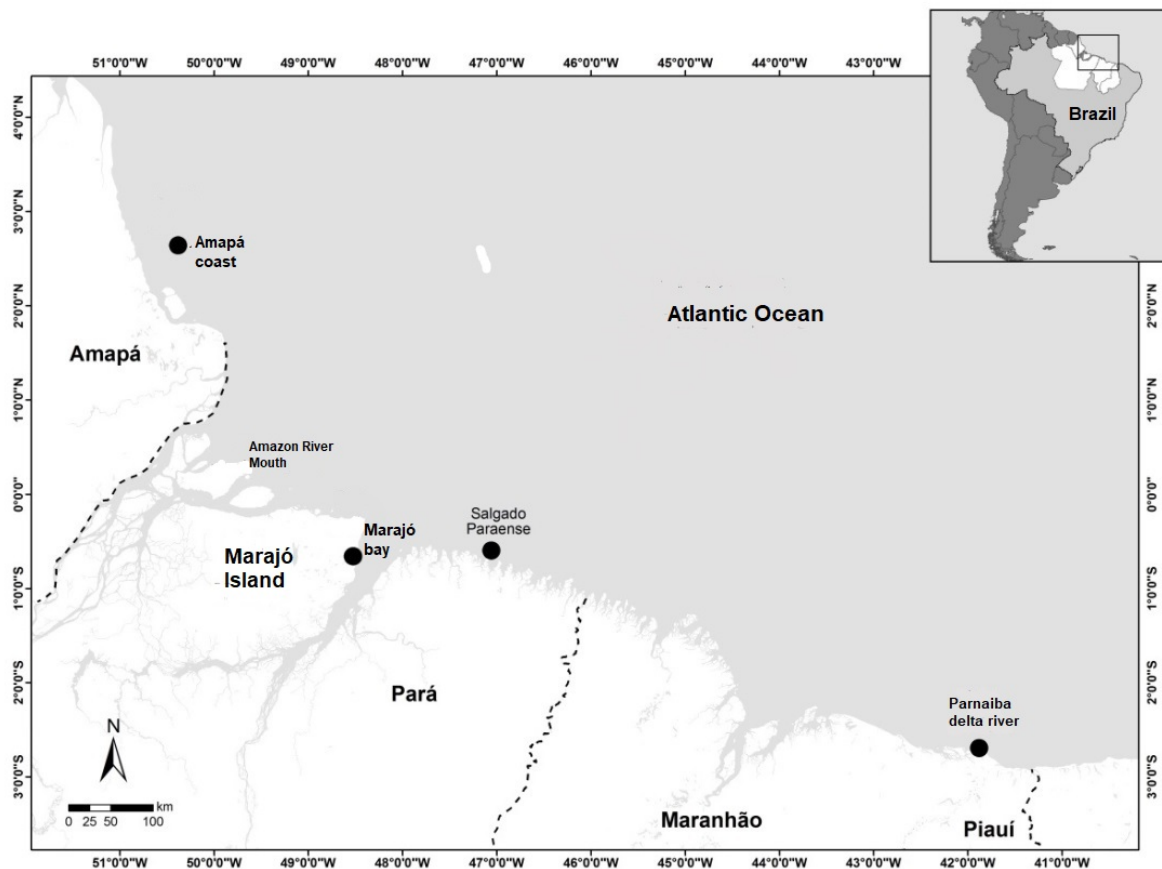


Fig. 1. Localization of the study areas highlighting the localities of origin of the specimen of *Sotalia guianensis* Van Bénédén, 1864 analyzed in this study: Amapá coast (AP), Marajó bay and *Salgado Paraense* region (PA), and Parnaíba river delta (MA/PI). Maura E. Sousa drew the map.

Tab. I. Number of specimens of *Sotalia guianensis* Van Bénédén, 1864 analyzed according to the study area and sex.

Local	Skull			
	Female	Male	Undefined	Total
Amapá coast	1	0	0	1
Marajó Bay	0	3	26	29
Northeastern Pará State	4	1	12	17
Parnaíba river delta	0	4	3	7
General total	5	8	41	54

Tab. II. Morphological features analyzed in the skulls of *Sotalia guianensis* Van Bénédén, 1864.

Features and study of the features
1. Fontanelle: (0) Opened ; (1) Closed
2. Nasal septum: (0) Not formed; (1) In formation.
3. Individualization of the alveoli: (0) Not formed; (1) Developing; (2) Formed.
4. Nasal bone: (0) Not sutured; (1) Sutured
5. Squamoparietal suture: (0) Not fused; (1) fusion is not apparent on the external surface of the skull; (2) partial fusion apparent on the external surface of the skull; (3) complete fusion.
6. Frontoparietal suture: (0) Not fused; (1) fusion is not apparent on the external surface of the skull; (2) partial fusion apparent on the external surface of the skull; (3) complete fusion.
7. Parietosupraoccipital suture: (0) Not fused; (1) fusion is not apparent on the external surface of the skull; (2) partial fusion apparent on the external surface of the skull; (3) complete fusion.
8. Parietal/exoccipital suture: (0) Not fused; (1) fusion is not apparent on the external surface of the skull; (2) partial fusion apparent on the external surface of the skull; (3) complete fusion.
9. Supraoccipital/exoccipital suture (0) Not fused; (1) fusion is not apparent on the external surface of the skull; (2) partial fusion apparent on the external surface of the skull; (3) complete fusion.
10. Pterygopalatine suture (0) Not fused; (1) fusion is not apparent on the external surface of the skull; (2) partial fusion apparent on the external surface of the skull; (3) complete fusion.
11. Maxillopalatine suture (0) Not fused; (1) fusion is not apparent on the external surface of the skull; (2) partial fusion apparent on the external surface of the skull; (3) complete fusion.
12. Vomerobasioccipital suture (0) Not fused; (1) fusion is not apparent on the external surface of the skull; (2) partial fusion apparent on the external surface of the skull; (3) complete fusion.
13. Basioccipital-pterygoid suture (0) Not fused; (1) fusion is not apparent on the external surface of the skull; (2) partial fusion apparent on the external surface of the skull; (3) complete fusion.
14. Asymmetry in the position of the two foramina of the maxilla in a more anterior position (0) Symmetrical; (1) Left foramen in a more anterior position; (2) Right foramen in a more anterior position.
15. Asymmetry in the position of the two premaxillary foramina: (0) Symmetrical; (1) Left foramen in a more anterior position; (2) Right foramen in a more anterior position.
16. Number of small foramina in the maxilla, anterior to the most anterior of the three large foramina.
17. Number of foramina of the maxilla after the anterior line of the external nasal opening and perpendicular to the skull axis.
18. Dorsal development of the mesethmoid ridge on the anterior edge of the nasal opening between the angles of the premaxillae. (0) Elevation of the ossified portion until the mesethmoid, or until the height of the dorsal surfaces of the maxillae; (1) Without elevations.
19. Composition of the antorbital process in its lateral left view: (0) Lacrimal; (1) Lacrimal and frontal; (2) Lacrimal and maxillary
20. Medial occipital crest, elevating at the average height of the occipital region (0) Present; (1) Absent.
21. Accessory foramen to the <i>Foramen Magnum</i> : (0) Present; (1) Absent.
22. Evidence of a notch on the superior border of the <i>Foramen Magnum</i> : (0) Present; (1) Absent.
23. Number of fenestras associated with the condyles, close to the <i>Foramen Magnum</i> .
24. Shape of the vomer between the posterior processes of the pterygoid: (0) Inverted calyx; (1) Intermediate; (2) Parallel.
25. Anterior contact between the pterygoids: (0) Contactless (separated by a distance > 1.0 mm); (1) With contact
26. Posterior contact between the pterygoids: (0) Contactless (separated by a distance > 1.0 mm); (1) With contact
27. Shape of the extremity of the hamular process of the pterygoid (left): (0) $y > x$ ; (1) $x > y$ .
28. Shape of the anterior lacerate foramen (right): (0) Opened or extended; (1) With a spine-shaped projection; (2) Narrow.
29. Hypoglossal foramen below the basioccipital fossa (visible ventrally) (0) Present; (1) Absent.

The exclusion from the analysis of the qualitative data not associated to the development and displaying variable distribution among the specimens, according to FETTUCCIA *et al.* (2009) and SIMÕES-LOPES (2006), was necessary to associate the characters with the age estimates (features 16, 17, and 23). Besides these, more eight characters (features 1, 2, 21, 23, 25, 26, 27 and 29) were excluded, as they did not present any significant variation among the states of the character. In this form, just 19 characters (3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 18, 19, 20, 22, 24 and 28) were used in the statistical analysis to assess the ontogenetic development in the skulls of *S. guianensis*.

For the statistical analysis, the ages were allocated in six categories: The categories expressed as years of age were: 0-6; 7-12; 13-18; 19-24 e 25-30.

Data did not display a normal distribution. For this reason, the *One-Way* analysis of variance (ANOVA) could not be used, and the non-parametric analysis of variance of Kruskal-Wallis was chosen. This analysis was used to test the presence of differences in the individually considered characters.

To verify the association between the characters and the areas of study an ordination of the variables was performed using a Principal Component Analysis (PCA) of the *Gower* distance (LEGENDRE & LEGENDRE, 1998). This analysis generalizes the *Gower* distance coefficient to determine the use of various types of variables as long as it calculates the distances. In this case, there were two types of variables: binary and ordinals. Only the two first axes of the PCA were selected to represent the results. All the analyses were performed using the statistical software R (3.0.2 version) (R DEVELOPMENT CORE TEAM, 2010) using the *ade4* package.

## RESULTS

The minimum age of the specimen found in this research was one year. The maximum age was of a 29-year-old specimen.

**Non-metric morphological feature.** Among the 29 non-metric morphological features analyzed (Tab. II), seven were discharged, as they did provide no information to assess the ontogenetic development. Three of these features were quantitative (16, 17, and 23), and four did not display variations among the states that have been analyzed (21, 25, 26, and 29). Eleven characters (1, 2, 4, 10, 14, 15, 18, 19, 24, 27 e 28) displayed individual variations in most of the specimen, id est, the analyzed state were observed in different ages. One specimen (n=1) at the age of one-year did not display any fusion of the frontoparietal, supraoccipital, parietal-exoccipital, supraoccipital, exoccipital, maxillopalatine, vomero-basioccipital, and pterigo-basioccipital sutures (characters 6, 7, 8, 9, 11, 12 e 13). These structures were partially or completely fused from the age of six years onwards.

As refers to the individualization of the dental alveoli (character 3), specimen between one and ten years of age did

not display formed dental alveoli (State 0). The alveoli in development (State 1) and formed (State 2) were visible in specimen between seven and 21 years of age, and between six, and 29 years of age respectively.

The squamoparietal suture (character 5) did not display fusion (State 0) in specimens between one and 16 years of age. Mature specimen, aged between 27, and 29 displayed the complete fusion of this suture (State 3). The medial occipital crest, elevating at the average height of the occipital region (character 20) and the notch on the superior border of the *Foramen Magnum* (character 22) were visible in individuals from the age of six years onwards.

**Statistical analysis.** The Principal Component Analysis (PCA) of the *Gower* distance (LEGENDRE & LEGENDRE, 1998) displayed no visible clusters among the specimen, as refers to the sampled areas (Fig. 2), age group (Fig. 3), or sex (Fig. 4). This observation suggests that the characters of the skull do not differ among the tested treatments.

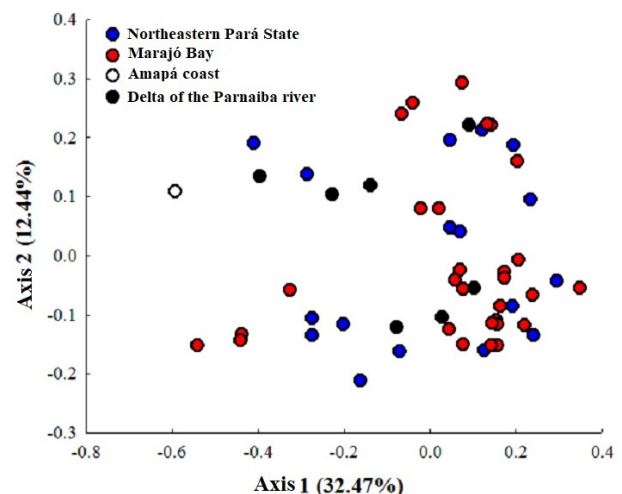


Fig. 2. Principal components (PCA) ordinating the characters of the skull of *Sotalia guianensis* Van Bénédén, 1864 according to the sampling location of each specimen.

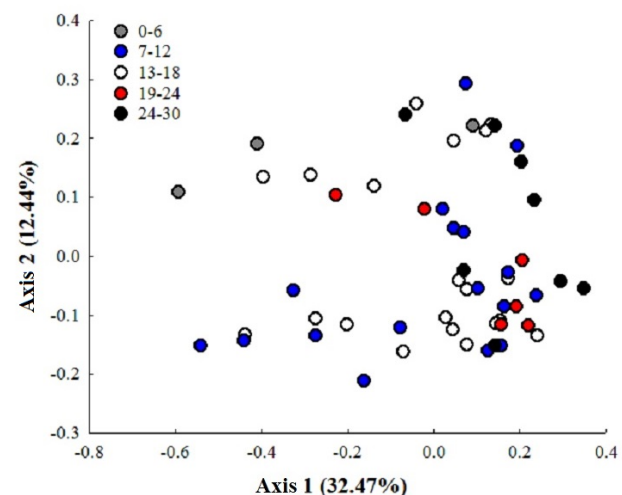


Fig. 3. Principal components (PCA) ordinating the characters of the skull of *Sotalia guianensis* Van Bénédén, 1864 according to the age.

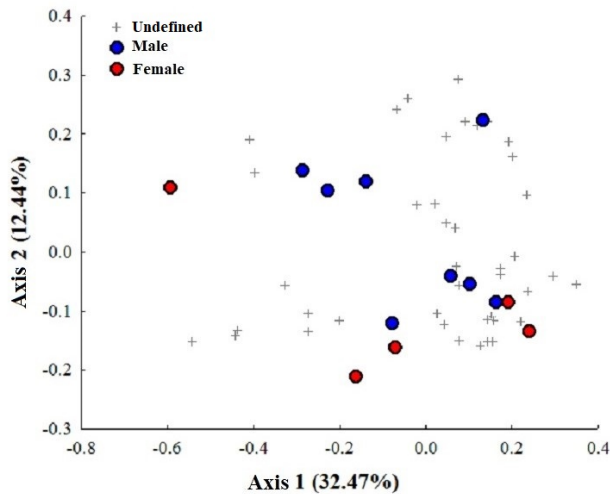


Fig. 4. Principal components (PCA) ordinating the characters of the skull of *Sotalia guianensis* Van Bénédén, 1864 according to the sex.

The analysis of the characters of the skulls individually displayed that some of them differed according to the age group. The characters 6, 7, 8, 9, and 13 differed according to the age of the individuals (Tab. III).

## DISCUSSION

The analysis of the skull development of *S. guianensis* mostly agreed with the results obtained by other studies (FETTUCCIA *et al.*, 2009). According to FETTUCCIA *et al.* (2009) and R. M. A. Ramos (unpubl. data), the formation of the interalveolar septa starts between one and four years of age, and is a good characteristic to classify an individual as an adult. As refers to the individualization of the alveoli (character 3), the specimen aged between one and ten years displayed the interalveolar septa unformed, and specimen of the approximate age of 21 years displayed the interalveolar septa in development. These data corroborate with the results of R. A. M. Ramos (unpubl. data): individuals from the Southeastern coast with the age of until 20 years old displayed partially developed interalveolar septa.

Former studies with *S. guianensis* suggest that the fusion in the parietosupraoccipital suture (character 7) occurs early (FETTUCCIA *et al.*, 2009). Even the same, in our study, one specimen of one year of age did not present this suture fused. This datum suggests the necessity for a more in-depth analysis of this question in a larger sized sample.

Tab. III. Results of the Kruskal-Wallis analysis of each character of the skull of *Sotalia guianensis* Van Bénédén, 1864 according to the age group. Significant results are displayed in bold ( $p$  was considered significant as  $<0.5$ ).

Morphological characters	Description of the character	Degree of freedom	N° of samples	H	P
3	Individualization of the alveoli:	4	54	8.43744	0.0768
4	Nasal bone	4	53	7.09867	0.1308
5	Squamoparietal suture	4	53	5.38563	0.25
6	<b>Frontoparietal suture</b>	4	<b>53</b>	<b>15.6092</b>	<b>0.0036</b>
7	<b>Parietosupraoccipital suture</b>	4	<b>53</b>	<b>13.6536</b>	<b>0.0085</b>
8	<b>Parietal/exoccipital suture</b>	4	<b>53</b>	<b>10.0611</b>	<b>0.0394</b>
9	<b>Supraoccipital/exoccipital suture</b>	4	<b>53</b>	<b>14.0675</b>	<b>0.0071</b>
10	Pterygopalatine suture	4	42	6.90634	0.1409
11	Maxillopalatine suture	4	52	2.36623	0.6687
12	Vomerobasioccipital suture	4	44	4.98379	0.289
13	<b>Basioccipital-ptyergoid suture</b>	4	<b>44</b>	<b>10.314</b>	<b>0.0355</b>
14	Asymmetry in the position of the two maxillary foramina	4	52	6.00889	0.1985
15	Asymmetry in the position of the two premaxillary foramina:	4	51	2.31231	0.6785
18	Dorsal development of the mesethmoid ridge	4	49	3.28296	0.5116
19	Composition of the antorbital process	4	50	1.73558	0.7842
20	Medial occipital crest, elevating at the average height of the occipital region	4	52	3.65766	0.4543
22	Evidence of a notch on the superior border of the <i>Foramen Magnum</i>	4	52	7.42803	0.1149
24	Shape of the vomer between the posterior processes of the pterygoid	4	39	3.69754	0.4485
28	Shape of the anterior lacerate foramen	4	52	2.94035	0.5679

The complete fusion of the supraoccipital/exoccipital suture (character 9) occurred in individuals aged between six, and 29 years. This observation corroborated with the result of FETTUCCIA *et al.* (2009), who described that the complete fusion of the sutures of the occipital complex concurred with the age of sexual maturity of this species, between seven, and 12 years of age.

The characters that refer to the position or counting of the foramina in the maxillary bone (characters 16, and 17) were quite variable among the specimen. Our results corroborate the data presented by FETTUCCIA *et al.* (2009) and SIMÕES-LOPES (2006). According to these authors, the foramina of the facial region of *S. guianensis* are variable as refers to the number, and position. These characters were not informative for ontogenetic development.

The results of the present study confirm the composition of the antorbital process (character 19), mainly formed by the maxillary and the lacrimal bones. FETTUCCIA *et al.* (2009) observed the frequency of the two states in specimens of *S. guianensis* from the Northern Coast (state 0, lacrimal; state 2, lacrimal and maxillary), being the lacrimal and maxillary state, the most common. The results of the present study were similar to those presented by FETTUCCIA *et al.* (2009). This character was not related to ontogenetic development because this state was found in different age groups.

Statistical analyses did not highlight differences associated within the areas of study or to the sex of the individuals. Even though five morphological characters (characters 6, 7, 8, 9, and 13) displayed differences related to age. These characters may, therefore, be considered as useful indicators of the development of *S. guianensis*. GALATIUS *et al.*, 2011 performed a study correlating the age of Phocoenidae and the development of the skull. These authors also highlighted that the modification of state of these sutures (frontoparietal, parietosupraoccipital, parietal-exoccipital, supraoccipital-exoccipital) is consistent with the age of the individuals.

Studies performed with specimens of Guiana dolphin from other areas of the Brazilian coast claim that this species reaches the physical maturity later, at about ten to twelve years of age (FETTUCCIA *et al.*, 2009). The specimens of Guiana dolphin used in this study displayed a more premature skull development, at about six to seven years of age. The population of the northern Brazilian coast might be submitted to different evolutionary pressures, which led to more earlier development.

Mean body length at birth and asymptotic body length are quite plastic traits of vertebrate populations (TANAKA, 2011). Geographical variation, at least in adult body size, has been reported for several species of cetaceans (PERRIN, 1984; PERRIN & REILLY, 1984). For example, CALZADA & AGUILAR (1995) reported differences in body sizes of striped dolphins (*Stenella coeruleoalba*) between the northern and southern regions of the western Mediterranean Sea, as dolphins in Japanese waters are 16-19% longer than those in the western Mediterranean Sea. As previously stressed

(MIYAZAKI, 1977; CALZADA *et al.*, 1996), differences in body size among cetaceans could be the result of habitat diversity and variation used by each population, notably related to productivity, and the density of dolphins present in the region. As such, Guiana dolphins inhabiting waters of the North Brazilian coast are likely affected by density-dependent forces in the body growth rate or, as a result, the age at attainment of sexual maturity.

Our results agree with those presented in previous studies, consolidating the knowledge on the populations of *S. guianensis* from the northern coast of Brazil, as underpinned by the larger amount of samples used. Advocating the results presented by the previous authors, we did not observe sexual or geographical differences among the four areas where the study took place. This observation confirms the uniformity of the populations of the northern coast as refers to these aspects.

In disagreement with previous studies, we observed that five characters displayed differences according to age (frontoparietal suture, parietosupraoccipital suture, parietal/exoccipital suture, supraoccipital/exoccipital suture, and basioccipital-pterygoid suture). This result suggests that the development of the populations of the northern coast is different compared to other regions.

**Acknowledgments.** To the CAPES for the master degree grant that allowed the performance of this study in the Zoology postgraduate degree of the convention between the Federal University of Pará and the Pará Museum Emilio Goeldi. To all the members of the study group on aquatic mammals of the Amazon (GEMAM) for the help provided during the entire field and laboratory work. To my friend Dr. Yulie Shimano for the help provided with statistical analyses and to the researchers Dr. Larissa Rosa de Oliveira, Dra. Ana Paula M. Di Benedetto e Dr. Paulo Henrique Ott for the main suggestions. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) Finance Code 001.

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Appendix 1. List of the specimen of *Sotalia guianensis* Van Bénédén, 1864 analyzed (M, male; F, female, U, undefined).

Field identification	MPEG	TL (m)	Sex	Local	Estimated age
0	37826	0	U	Northeastern Pará State	18
001	38430	1.50	M	Northeastern Pará State	13
002	38431	0	F	Northeastern Pará State	18
12	38497	1,55	U	Northeastern Pará State	15
30	38447	1.61	U	Marajó Bay	24
31	38448	1.62	U	Marajó Bay	11
40	38457	1.71	U	Marajó Bay	17
96	38750	0	U	Marajó Bay	9
100	38754	0	U	Marajó Bay	10
117	38768	1.69	U	Marajó Bay	21
118	38769	0	U	Marajó Bay	18
135	39440	0	U	Northeastern Pará State	14
138	39443	0	U	Marajó Bay	27
144	39449	0	U	Marajó Bay	13
180	39606	0	U	Marajó Bay	28
206	39618	0	U	Marajó Bay	21
229	39660	1,23	U	Marajó Bay	7
236	39644	1,68	U	Marajó Bay	12
237	39652	0	U	Marajó Bay	8
244	42041	1,60	M	Marajó Bay	13
264	42051	1.60	U	Marajó Bay	28
272	39669	0	U	Marajó Bay	25
284	42057	1.60	U	Marajó Bay	17
291	42045	1.52	U	Marajó Bay	16
294	40997	1.72	U	Northeastern Pará State	28
308	42059	1.58	F	Northeastern Pará State	7
326	42114	1.67	U	Marajó Bay	16
338	42061	0	U	Marajó Bay	28
353	42105	0	U	Northeastern Pará State	26
355	42110	1.74	M	Marajó Bay	11
385	42145	1.43	U	Marajó Bay	10
389	42161	1.73	M	Marajó Bay	14
390	42162	0	U	Marajó Bay	19
403	Not listed	0	U	Marajó Bay	11
420	42191	1.58	F	Northeastern Pará State	13
423	44297	1.14	F	Amapá coast	1
424	44298	0	U	Northeastern Pará State	14
434	44305	0	U	Marajó Bay	14
436	44307	0	U	Marajó Bay	29
452	44321	0	U	Northeastern Pará State	12
462	44331	1.73	U	Northeastern Pará State	11
465	44334	0	U	Northeastern Pará State	11
466	44335	0	U	Marajó Bay	18
470	44339	0	U	Northeastern Pará State	7
472	44341	1.83	F	Northeastern Pará State	19
480	44348	0	U	Northeastern Pará State	6
483	42211	1.71	U	Northeastern Pará State	10
CEMA 22	42074	1.97	M	Parnaíba river delta	11



## Appendix 1. Cont.

Field identification	MPEG	TL (m)	Sex	Local	Estimated age
CEMA 23	42075	1.73	M	Parnaíba river delta	11
CEMA 25	42076	0.00	U	Parnaíba river delta	17
CEMA 50	42089	0.00	U	Parnaíba river delta	14
CEMA 53	42091	1.88	M	Parnaíba river delta	18
CEMA 62	42097	1.50	M	Parnaíba river delta	21
CEMA 66	Not listed	1.80	U	Parnaíba river delta	6