

Non-metric characters in two species of *Sotalia* (Gray, 1866) (Cetacea, Delphinidae)

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(With 12 figures)

Abstract

Analyses of non-metric characters of the skull and cervical vertebrae were performed among samples of dolphins of the genus *Sotalia* from the north, northeast and south Brazilian coast (*S. guianensis*) and also samples from the Amazon River Basin (*S. fluviatilis*) as part of an osteological descriptive study. The results demonstrated that there was a higher percentage of occurrence of *fenestrae* in the occipital region (66%) and cervical ribs in the cervical vertebrae (87%) in the riverine species. The vomer in wide shape was more frequent in the riverine species (57%), followed by the intermediate (32%) and narrow shape (11%), that was found to be more frequent in the marine species (66 to 76%). In relation to the lacerate anterior foramen, it was observed that an open/elongated shape is more common in the riverine species (88%). Most samples in the marine species present this foramen divided by a spike shaped projection (72 to 98%). The ventrally visible location of the hypoglossal foramen was more often observed externally displaced in *S. guianensis* (88 to 98%), while in *S. fluviatilis*, most samples (87%) presented this foramen internally displaced to the jugular notch, and not visible in ventral view. The fluvial species seems to present neoteny (or maintenance of juvenile characters in adults) in relation to the position of the pterygoids and in development of lacerate anterior foramen.

Keywords: Morphology, *Sotalia*, osteology, skull, cervical vertebrae.

Caracteres não métricos nas duas espécies de *Sotalia* (Gray, 1866)

Resumo

Este é um trabalho osteológico descritivo entre exemplares do gênero *Sotalia* da costa Norte, Nordeste e Sul do Brasil e exemplares fluviais da bacia amazônica, analisando caracteres não métricos no crânio e nas vértebras cervicais. A frequência de ocorrência de fenestras na região occipital (66%) e de costelas cervicais (87%) foi maior na espécie fluvial (*S. fluviatilis*). Na espécie fluvial, a forma do vômer largo foi mais frequente (57%), seguida da forma intermediária (32%) e estreita (11%). A forma do vômer estreito foi mais frequente na espécie marinha (*S. guianensis*) (66 a 76%). Em relação ao forâmen lacerado anterior, foi observado que a forma aberta/alongada é mais comum na espécie fluvial (88%). Na espécie marinha, a maioria dos exemplares apresenta este forâmen dividido por uma projeção em forma de espinho (72 a 98%). A localização do forâmen hipoglossal visível ventralmente foi mais observada em *S. guianensis* (88 a 98%), enquanto que em *S. fluviatilis*, a maioria dos exemplares (87%) apresentou este forâmen deslocado internamente à reentrância jugular, não podendo ser observado em vista ventral. A espécie fluvial parece apresentar neotenia (ou manutenção de caracteres juvenis no adulto) em relação ao posicionamento dos pterigoides e ao desenvolvimento do forâmen lacerado interior.

Palavras-chave: morfologia, *Sotalia*, osteologia, crânio, vértebra cervical.

1. Introduction

The genus *Sotalia* (Gray, 1866) was until recently considered monospecific, however recent molecular genetics (Cunha et al., 2005; Caballero et al., 2007), and geometric morphometric (Monteiro-Filho et al., 2002)

studies revealed the existence of two species: the marine species *Sotalia guianensis* (P.J. van Bénédén, 1864) (gray dolphin) and the riverine species *Sotalia fluviatilis* (Gervais, 1853) (tucuxi).

The marine species is broadly distributed along the tropical and subtropical Atlantic coast of South and Central America, having been recorded from Florianópolis, Santa Catarina, Brazil (27° 35' S and 48° 34' W) (Simões-Lopes, 1988; Borobia, 1989) to Honduras (15° 58' N and 85° 42' W) (da Silva and Best, 1996). The riverine species is endemic to the Amazon Basin, occurring from Belém (at the mouth of the Amazon River), in Brazil, to the rivers of Peru, Colombia and Ecuador (Borobia et al., 1991, da Silva and Best, 1996).

Osteological descriptions for the genus *Sotalia* have been published by Miranda-Ribeiro (1936); Casinos et al. (1981); Borobia (1989); Menezes and Simões-Lopes (1996); da Silva and Best (1996); Alves Júnior and Monteiro-Neto (1999); Avila et al. (2002); Fettuccia and Simões-Lopes (2004), Simões-Lopes (2006). With the exception of Simões-Lopes (2006), these studies were mainly based on traditional studies of morphometrics. There are no previous comparative studies using non-metric characteristics such as, for example, the com-

parison of forms or presence and absence of determined characters for this genus. Therefore, this study aims to compare the two species of the genus *Sotalia* using non-metric characters.

2. Material and Methods

A total of 149 specimens were analysed from five distinct Brazilian states: Mammal Collection of National Institute for Amazônia Research (INPA), Manaus, Amazonas (AM); Emilio Goeldi Museum (MPEG), Belém, Pará (PA); Aquatic Mammals Laboratory (LMA) of the Department of Ecology and Zoology, Federal University of Santa Catarina (UFSC), Florianópolis, Santa Catarina (SC); as well as the Osteological Archive of the Association of Research and Preservation of Aquatic Ecosystems (AQUASIS), Caucaia, Ceará (CE) (Tables 1-4). The INPA collection contains riverine specimens (*S. fluviatilis*) from the Amazonas State (AM), marine specimens from the coast of the Amapá (AP) and es-

Table 1. List of *Sotalia fluviatilis* analysed from the northern region (Amazon State, Brazil), deposited at INPA's mammals collection. F - female, M - male, I - indeterminate gender. N = 44.

Collection number	Sex	Age class	Locality	Collection number	Sex	Age class	Locality
INPA 005	I	adult	Japurá River	INPA 054	M	calf	Amazonas River
INPA 007	I	adult	Tefé Lake	INPA 055	I	adult	Amazonas River
INPA 008	I	adult	Tefé Lake	INPA 056	F	adult	Amazonas River
INPA 009	M	juvenile	Negro River	INPA 057	F	adult	Amazonas River
INPA 015	F	calf	Japurá River	INPA 059	M	juvenile	Marchantaria, Solimões River
INPA 016	I	adult	Japurá River	INPA 060	M	juvenile	Marchantaria, Solimões River
INPA 017	M	adult	Japurá River	INPA 062	F	adult	Tefé Lake
INPA 018	I	calf	Japurá River	INPA 065	M	calf	Japurá River
INPA 020	I	adult	Japurá River	INPA 067	I	adult	Japurá River
INPA 024	I	adult	Japurá River	INPA 069	F	adult	Negro River/ Anavilhanas
INPA 026	M	juvenile	Purus River	INPA 071	F	adult	Japurá River
INPA 029	F	juvenile	Tefé Lake	INPA 072	I	adult	Pará River
INPA 038	F	calf	Japurá River	INPA 073	F	adult	Purus River
INPA 039	M	immature	Japurá River	INPA 074	M	adult	Purus River
INPA 040	F	adult	Amanã Lake	INPA 080	M	calf	Catalão, Negro River
INPA 041	M	adult	Negro River/ Anavilhanas	INPA 081	M	juvenile	Cabaliana Lake, Manacapuru
INPA 043	M	juvenile	Japurá River	INPA 082	F	calf	Tapajós River
INPA 047	M	adult	Juruá River	INPA 093	M	adult	Tocantis River/ Tucuruí
INPA 050	F	immature	Amanã Lake	INPA 097	F	juvenile	Negro River
INPA 051	M	calf	Amazonas River	INPA 113	M	adult	Solimões River
INPA 052	M	adult	Amazonas River	INPA 149	I	adult	Coari Grande River
INPA 053	F	adult	Amazonas River	INPA 151	I	adult	Coari Grande River

Table 2. List of *Sotalia guianensis* analyzed from northern region (Amapá and Pará States, Brazil), deposited at INPA and MPEG mammals collections, respectively. F - female, M - male, I - indefinite gender. N = 26.

Collection number	Sex	Age class	Locality	Collection number	Sex	Age class	Locality
INPA 120	M	juvenile	Amazonas Estuary	INPA 133	M	juvenile	North of Amapá
INPA 121	M	juvenile	Amazonas Estuary	INPA 134	F	adult	North of Amapá
INPA 122	M	juvenile	Amazonas Estuary	INPA 135	F	calf	North of Amapá
INPA 123	M	adult	North of Amapá	INPA 136	M	calf	North of Amapá
INPA 124	F	juvenile	North of Amapá	INPA 137	M	calf	North of Amapá
INPA 125	F	juvenile	Amazonas Estuary	INPA 138	F	juvenile	North of Amapá
INPA 126	M	juvenile	North of Amapá	INPA 139	F	juvenile	North of Amapá
INPA 127	M	calf	North of Amapá	INPA 140	M	juvenile	North of Amapá
INPA 128	M	calf	North of Amapá	INPA 141	F	adult	North of Amapá
INPA 129	M	adult	North of Amapá	INPA 142	F	adult	North of Amapá
INPA 130	F	juvenile	North of Amapá	INPA 143	F	adult	North of Amapá
INPA 131	F	calf	Amazonas Estuary	MPEG 24548	I	adult	Marajó Island
INPA 132	F	calf	Amazonas Estuary	MPEG 10945	F	juvenile	Marajó Island

Table 3. List of *Sotalia guianensis* analysed from the Northeast region (Ceará state, Brazil), deposited at AQUASIS's collection. F - female, M - male, I - indeterminate gender. N = 41.

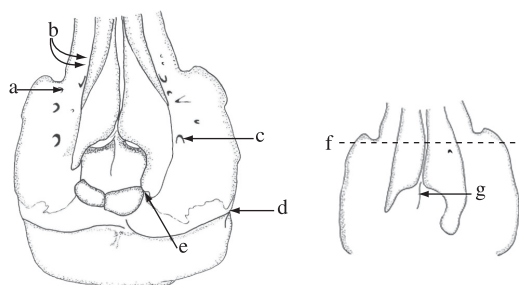
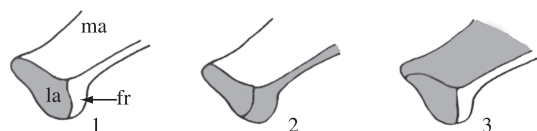
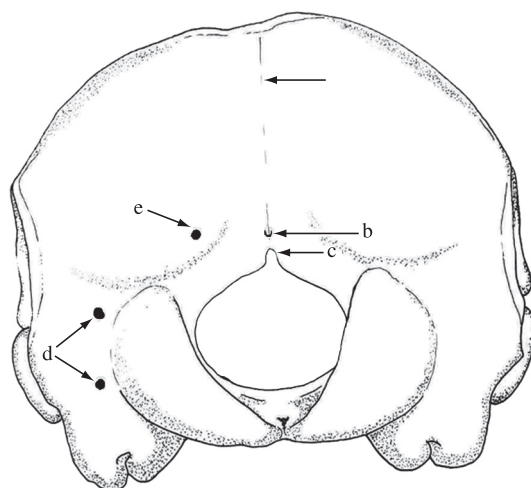
Collection number	Sex	Age class	Locality	Collection number	Sex	Age class	Locality
Aq 002	M	adult	Caucaia	Aq 210	F	adult	Paracuru
Aq 004	I	juvenile	Fortaleza	Aq 212	F	adult	Fortaleza
Aq 012	I	adult	Fortaleza	Aq 213	M	calf	Fortaleza
Aq 013	M	adult	Fortaleza	Aq 214	F	juvenile	Caucaia
Aq 023	M	adult	Caucaia	Aq 215	I	adult	São G. Amarante
Aq 026	I	adult	Caucaia	Aq 218	M	juvenile	São G. Amarante
Aq 036	F	adult	Fortaleza	Aq 222	F	adult	Fortaleza
Aq 038	M	adult	Caucaia	Aq 231	M	adult	Caucaia
Aq 039	I	adult	São G. Amarante	Aq 232	M	adult	Fortaleza
Aq 040	I	calf	São G. Amarante	Aq 234	M	adult	Caucaia
Aq 041	I	immature	Fortaleza	Aq 236	I	adult	São G. Amarante
Aq 042	M	adult	Fortaleza	Aq 239	M	adult	Fortaleza
Aq 058	F	adult	Fortaleza	Aq 240	I	immature	Paraipaba
Aq 071	I	adult	Cascavel	Aq 241	I	adult	Caucaia
Aq 084	M	adult	Fortaleza	Aq 247	F	adult	Fortaleza
Aq 132	M	juvenile	São G. Amarante	Aq 250	M	calf	Paraipaba
Aq 134	M	adult	Fortaleza	Aq 251	I	adult	Trairé
Aq 139	I	adult	Itapipoca	Aq 253	M	adult	Fortaleza
Aq 159	I	adult	Fortaleza	Aq 259	M	adult	Fortaleza
Aq 184	F	adult	Fortaleza	Aq 262	I	adult	Bitupitá
Aq 196	I	immature	São G. Amarante	-	-	-	-

tuarine specimens (*S. guianensis*) from Pará State (PA). The other collections only possess marine specimens from their respective localities. Forty-four specimens of *S. fluviatilis* and 105 specimens of *S. guianensis* were

analyzed (AP = 24; PA = 02; CE = 41; SC = 38). The marine specimens were divided into 3 large areas: NOR (including specimens from AP and PA), for the specimens from the coast of Amapá and Pará States, CE for

Table 4. List of *Sotalia guianensis* analysed from the Southern region (Santa Catarina state, Brazil), deposited at LAMAg's collection (UFSC). F - female, M - male, I - indeterminate gender. N = 38.

Collection number	Sex	Age class	Locality	Collection number	Sex	Age class	Locality
UFSC1010	I	juvenile	Daniela Beach	UFSC1222	M	immature	Estreito
UFSC1073	I	adult	Biguaçu	UFSC1223	M	calf	Anhatomirim Island
UFSC1079	F	adult	Beira Mar Norte	UFSC1226	M	adult	G. Celso Ramos
UFSC1082	I	adult	Beira Mar Norte	UFSC1236	F	calf	Sambaqui
UFSC1083	M	adult	Beira Mar Norte	UFSC1245	I	juvenile	São F. do Sul
UFSC1104	F	immature	Beira Mar Norte	UFSC1247	I	adult	Cacupé
UFSC1108	M	adult	Beira Mar Norte	UFSC1253	M	juvenile	Beira Mar Norte
UFSC1117	I	adult	Biguaçu	UFSC1266	M	immature	Biguaçu
UFSC1130	F	adult	G. Celso Ramos	UFSC1268	F	adult	Biguaçu
UFSC1174	M	calf	Sambaqui	UFSC1289	F	adult	G. Celso Ramos
UFSC1175	M	adult	São F. do Sul	UFSC1291	M	adult	G. Celso Ramos
UFSC1176	I	adult	Costeira	UFSC1296	M	juvenile	Anhatomirim
UFSC1178	M	juvenile	Sambaqui	UFSC1297	M	adult	G. Celso Ramos
UFSC1179	M	juvenile	Beira Mar Norte	UFSC1302	I	adult	Itapoá
UFSC1180	F	adult	Cacupé	UFSC1307	M	juvenile	Daniela Beach
UFSC1203	F	adult	Anhatomirim	UFSC1311	I	immature	São F. do Sul
UFSC1208	F	adult	Estreito	UFSC1312	M	adult	Estreito
UFSC1218	F	adult	Curtume Beach	UFSC1321	F	adult	Itaguaçu Beach
UFSC1219	F	adult	Costeira	UFSC1327	M	calf	Beira Mar Norte

**Figure 1.** Scheme of Delphinidae skull in dorsal view, showing non-metric characters: a) Asymmetry of position of the two anterior most large maxillary foramina; b) Number of small foramina in the maxillary; c) Number of foramina in the maxillary behind a line at the level of the anterior edge of the external nares; d) Contact between maxillary and occipital; e) Contact between premaxillary and nasal, on right side; f) Asymmetry of position of the two premaxillary foramina; and g) Development of dorsal mesethmoid spine at the anterior margin of external nares. Adapted from Perrin et al. (1982).**Figure 2.** Composition of the anteorbital process, in lateral view, of the left side: 1) formed by lacrimal; 2) formed by lacrimal and frontal; 3) formed by lacrimal and maxillary. la: lacrimal; ma: maxilar; fr: frontal. Adapted from Perrin et al. (1982).**Figure 3.** Scheme of Delphinidae skull in posterior view, showing non-metric characters: a) Medial occipital ridge, projecting above level of the occipital swellings at midheight; b) Accessory foramen above foramen magnum; c) Clear notch in upper margin of foramen magnum; d) Number of fenestrations in occipital, near foramen magnum and in exoccipital region; e) Number of fenestrations in occipital swellings region. Adapted from Perrin et al. (1982).

the specimens off the Ceará coast and SC for specimens from the Santa Catarina coast.

The skulls were compared using non-metric characters, in accordance with Perrin et al. (1982) and two newly proposed characters (Table 5; Figures 1-4). The

Table 5. List of non-metric characters analysed in skulls and cervical vertebrae from specimens of the genus *Sotalia*. Adapted from Perrin et al. (1982) and two new proposed characters (4a e 4g). NI: not illustrated.

Figure character and character condition	
1	<p>a. Asymmetry of position of the two anterior most large maxillary foramina: 1- symmetrical; 2- left foramen more anteriorly placed; right foramen more anterior.</p> <p>b. Number of small foramina in the maxillary anterior to the anterior-most of the three large foramina.</p> <p>c. Number of foramina in the maxillary behind a line at the level of the anterior edge of the external nares and perpendicular to the long axis of the skull.</p> <p>d. Contact between maxillary and occipital, at point where occipital crest intersects margin of temporal fossa: 1- contact (or space of <1 mm); 2- no contact.</p> <p>e. Contact between premaxillary and nasal, on right side: 1- contact (or space of <1 mm); 2- no contact.</p> <p>f. Asymmetry of position of the two premaxillary foramina: 1- symmetrical; 2- left foramen more anteriorly placed; right foramen more anterior</p> <p>g. Development of dorsal mesethmoid spine at the anterior margin of external nares, between angles of premaxillaries: 1- elevation of the ossified portion of the mesethmoid to, or near to the level of the dorsal surfaces of the premaxillaries; 2- no such elevation.</p>
2	Composition of the anteorbital process, in lateral view, of the left side: 1- formed by lacrimal; 2- formed by lacrimal and frontal; 3- formed lacrimal and maxillary.
3	<p>a. Medial occipital ridge, projecting above level of the occipital swellings at mid-height: 1- present; 2- absent, or not projecting above swellings.</p> <p>b. Accessory foramen above foramen magnum: 1- present; 2- absent.</p> <p>c. Clear notch in upper margin of foramen magnum: 1- present; 2- absent.</p> <p>d. Number of fenestrations in occipital, near foramen magnum and in exoccipital region.</p> <p>e. Number of fenestrations in region of occipital swellings.</p>
4	<p>a. Shape of the vomer among posterior process of the pterygoids: 1- wide; 2- intermediate; 3- narrow.</p> <p>b. Anterior contact between pterygoid hamuli: 1- open (gap > 1 mm); 2- closed.</p> <p>b. Posterior contact between pterygoid hamuli: 1- open (gap > 1 mm); 2- closed.</p> <p>d. Shape of posterior projection of left pterygoid hamulus: 1- longer than wide ($y > x$); 2- wider than long, or equal ($x > y$).</p> <p>e- Vomer's posterior alignment in relation to pterygoids's lamellar process: 1- anterior; 2- aligned; 3- posterior.</p> <p>f- Number of fenestrations in region of basoccipital.</p> <p>g- Shape of the anterior lacerate foramen (right): 1- open; 2- with projection spine form; 3- narrow.</p> <p>h- Visibility, in ventro-occipital view of mesially directed hypogossal foramen between basoccipital and exoccipital process (jugular notch): 1- visible; 2- not visible.</p>
NI	Cervical rib: 1- present; 2- absent.

cervical vertebrae were analyzed according to the presence or absence of cervical ribs.

In order to observe ontogenetic variation, the characters were evaluated by age classes (calf, juvenile, immature and adult) (adapted from Dawbin et al., 1970). Variations between the sexes were not analysed in this study due to the small sample size.

The terminology used for skeletal bones followed Flower (1885), Kraglievich (1937), Lessertieur and Saban (1967), Rommel (1990) and Simões-Lopes (2006).

3. Results

Of the 22 non-metric characters analysed, only six were informative for the distinction between the two species.

3.1. Fenestrae

A high frequency of *fenestrae* in the occipital region was observed, near the foramen magnum in *S. fluviatilis* (66%; $n = 44$). In *S. guianensis* the percentage of occurrence of *fenestrae* varied between 31% (specimens from NOR, $n = 26$), 10 % (CE, $n = 41$) and 13% (SC, $n = 39$).

The number of *fenestrae* near the condyle was also larger in the riverine species, varying from one to four per individual. In both species, these structures were found in all age classes.

In the marine species, the specimens from CE and NOR exhibited one to three *fenestrae*, while those from SC exhibited only one to two. *Fenestrae* can occur only on one side (more common in the marine species) or on

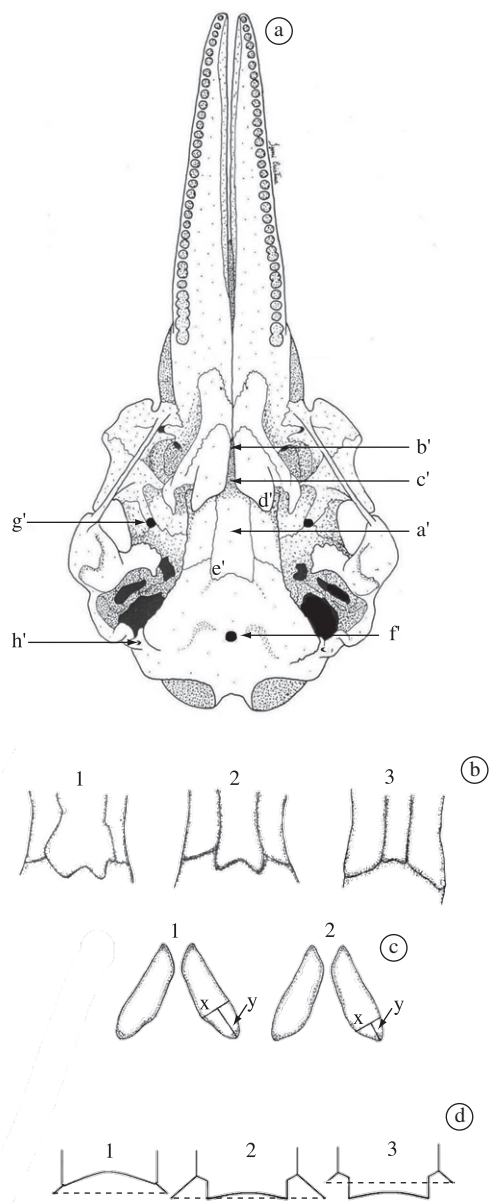


Figure 4. a) Skull of *Sotalia fluviatilis* in ventral view, showing non-metric characters (adapted from Perrin et al., 1982): a') shape of the vomer among posterior process of the pterygoids: 1) wide; 2) intermediate; 3) narrow; b') anterior contact between pterygoid hamuli; c') posterior contact between pterygoid hamuli; d') shape of posterior projection of left pterygoid hamulus: 1) longer than wide ($y > x$); 2) wider than long, or equal ($x > y$); e') vomer's posterior alignment in relation to pterygoids's lamellar process: 1) anterior; 2) aligned; 3) posterior; f') number of fenestrations in basoccipital region; g') Shape of the anterior lacerate foramen (right); h') visibility, in ventro-occipital view of mesially directed hypoglossal foramen between basoccipital and exoccipital process (jugular notch). b) Detail of vomer shape (character a'); c) Detail of hamular process shape from left pterygoide (character d'); d) Detail of alignment from posterior border of vomer (character e'). Skull design from Izeni P. Farias.

both sides of the occipital condyle (more common in the riverine species). In newborn and young specimens, other openings in the occipital region (located above the fenestrae) were observed, corresponding to the fontanelles, formed by the union of the exoccipital, parietal and supraoccipital bones (Figure 5).

In the region of occipital protuberance, in general, the occurrence of fenestrae was less frequent: 4.5% in *S. fluviatilis* ($n = 44$), 10% for *S. guianensis* of CE ($n = 41$), 5% for specimens from SC ($n = 38$) and no occurrence for marine specimens from NOR ($n = 26$). In some specimens of the two species, small fenestrae of irregular contour in the basioccipital were observed. In the marine species, such fenestrae occurred in 2% ($n = 41$) and 8% ($n = 39$) of the specimens from CE and

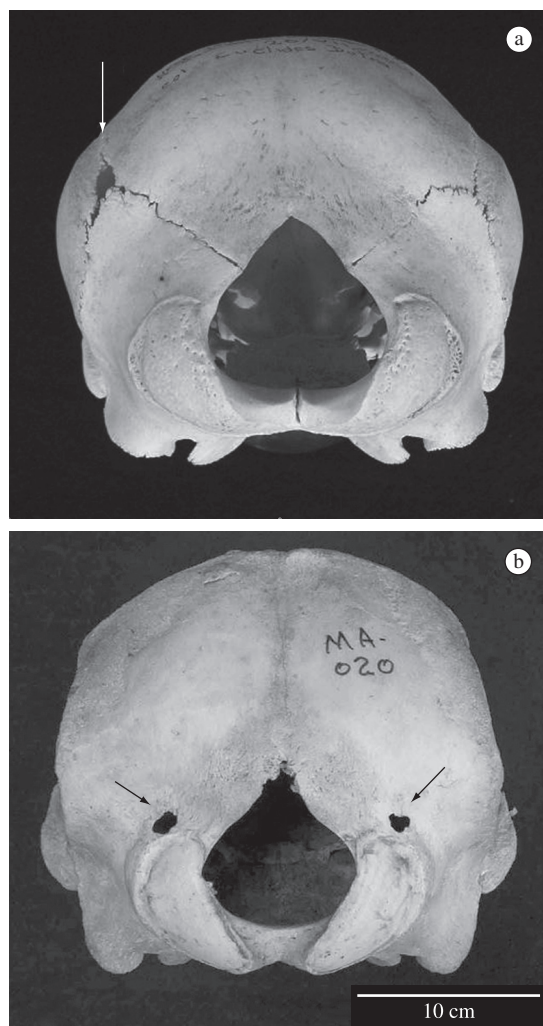


Figure 5. Skull of *Sotalia* in posterior view. a) Calf of *S. guianensis* (SC), indicating the sutures (black arrows) and fontanelles (white arrow) in occipital area. b) Adult of *S. fluviatilis* (AM), indicating the fenestrae next from condile occipital (black arrows). In the calf skull the fenestrae are located below the sutures of occipital area.

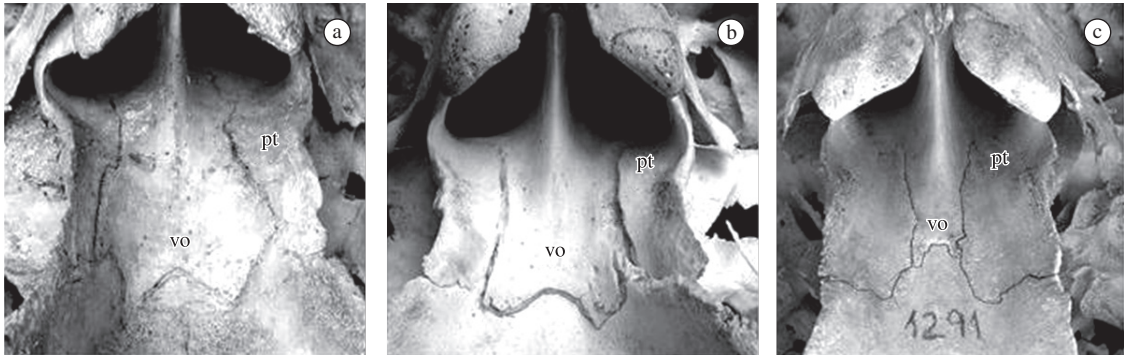


Figure 6. Shapes of the vomer observed in the genus *Sotalia*: a) wide; b) intermediate; and c) narrow. vo: vomer, pt: posterior process of pterygoide.

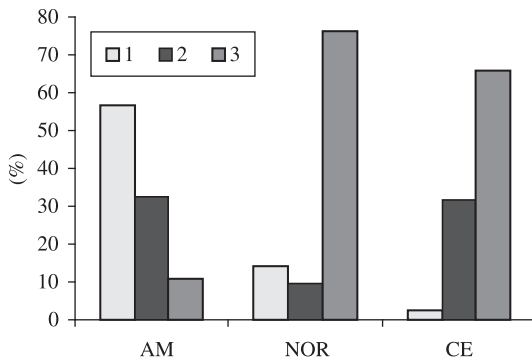


Figure 7. Variation of the vomer shapes in the genus *Sotalia*: 1- wide; 2- intermediate; 3- narrow. AM- Amazonas, CE- Ceará, NOR (samples from AP and PA together).

SC, respectively. In the riverine species, these *fenestrae* occurred in 9% (n = 43) of the specimens. These openings were not observed in the marine specimens from NOR.

3.2. Vomer

There was a prevalence of one form of vomer for the marine species, and another form for the riverine species (Figure 6). The wide form (wider in the posterior region) was more frequent in the riverine species, occurring in 57% (n = 37) of specimens, followed by the intermediate form (32%) and the narrow form (11%) (Figure 7). In the marine species, the narrow form was most frequent, occurring in 76% (n = 21) of the specimens from NOR and in 66% (n = 38) of the specimens from CE. The intermediate form of the vomer occurred in 9.5% (n = 21) of the specimens from NOR and in 31.5% (n = 38) of the specimens from CE. This characteristic was added later to the analysis, thus the specimens from SC were not included in the analyses. This characteristic seems to be related with individual variation and not with development.

3.3. Pterygoids

The contact, anterior and posterior, between pterygoids exhibited no variation, being separate (gap >1 mm)

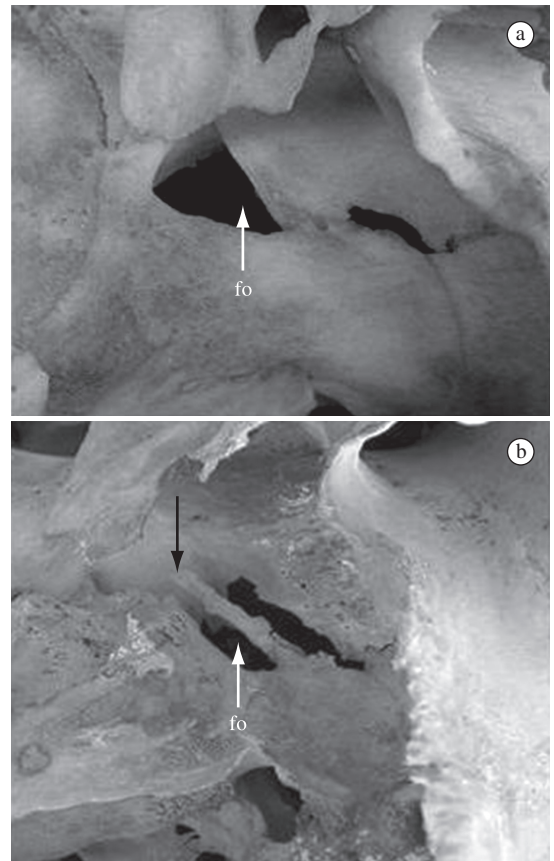


Figure 8. Shape of the anterior lacerate foramen (fo) observed in the genus *Sotalia*: a) open; and b) with spine form projection (black arrow).

in 100% of specimens of both species (except for INPA specimen 130 from AP, whose pterygoides had medial contact). In riverine species it was observed that generally there was a greater distance between pterygoides in the posterior portion, forming an inverted “v”. Young individuals of marine species seems to present this same

greater distance in the posterior portion. This could indicate neoteny in the riverine species, but in order to be able to interpret this variation a more thorough morphometric study is needed.

3.4. Anterior lacerate foramen

The predominant form of anterior lacerate foramen was distinct in the two species (Figures 8 and 9). In *S. fluviatilis*, the majority of specimens (88%, n = 43) exhibited open/elongated anterior lacerate foramen. In *S. guianensis*, the majority of the specimens analysed exhibited foramen divided by a projection in the form of a spine: 72% (NOR, n = 25), 77.5% (CE, n = 40) and 98% (SC, n = 38). This spine projection, which rarely develops in adults of the riverine species, seems to be associated with ontogenetic development in the marine species, leading to the assumption that it is related to neoteny. A more detailed study with a larger number of young and juveniles of both species could provide an answer to this question. In the three marine samples analysed, it was observed that some individual adults exhibited a formation of fusion points between the projection and one side of the lacerate foramen.

3.5. Hypoglossal foramen

The location of hypoglossal foramen next to the jugular notch was considerably higher in *S. guianensis*: 88% (NOR, n = 25), 95% (CE, n = 41) and 98% (SC, n = 39). In this species, this foramen is generally visible in the ventral view, externally displaced to the jugular notch. Conversely, in the riverine species, the majority of specimens (87%, n = 45) exhibited this foramen internally displaced to the jugular notch, not easily observed in the ventral view (Figures 10 and 11). It is worth noting, however, that variation exists in the proximity of this

foramen to the jugular notch in both species, where some individuals exhibit a displaced foramen, being either separated or together with the notch. This characteristic doesn't seem to be related with development.

3.6. Cervical vertebrae

In the cervical vertebrae, projections on the seventh cervical vertebrae (Ce₇) associated with the transversal canal (= vertebral arterial canals), are called pleuroapophyseal plates or cervical ribs (Figures 12). The occurrence of these structures was higher in *S. fluviatilis* (87%; n = 31) than in *S. guianensis* from CE (9%, n = 23)

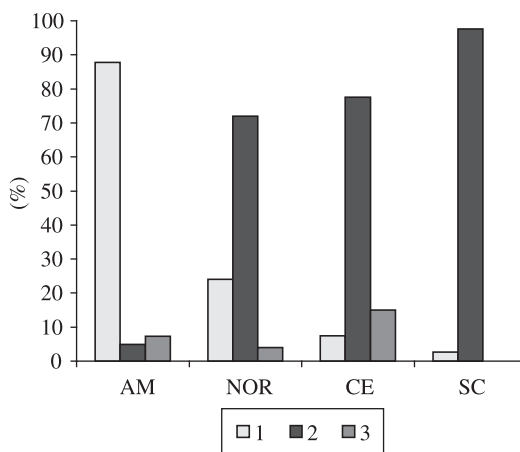


Figure 9. Variation of the anterior lacerate foramen shapes (fo) observed in the specimens of genus *Sotalia*: 1- open; 2- with projection spine form; 3- narrow or partially closed. AM- Amazonas, CE- Ceará, NOR (samples of AP and PA together), SC- Santa Catarina.

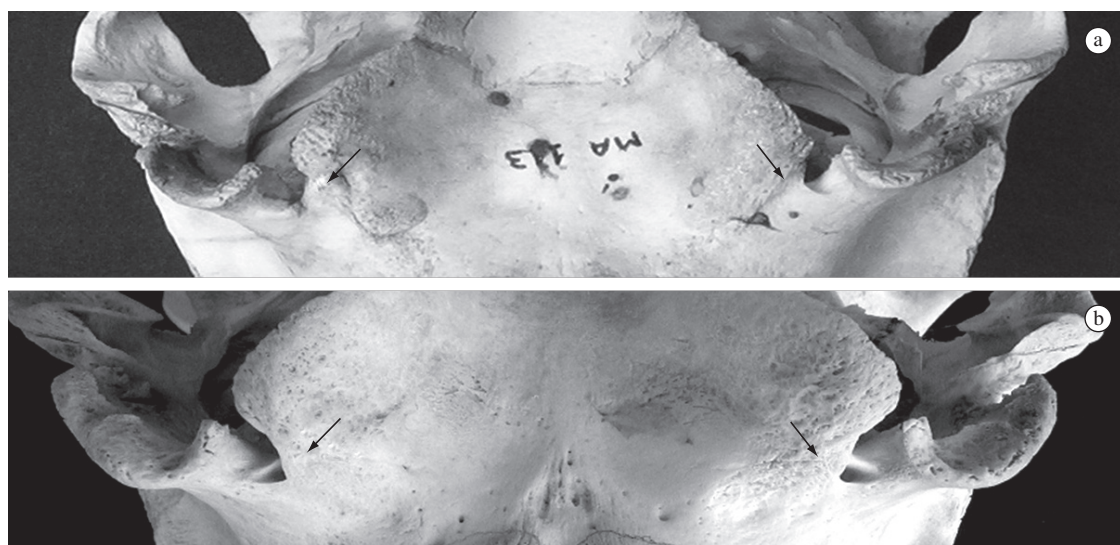


Figure 10. Localization of hypoglossal foramen in specimens of the genus *Sotalia*. a) *Sotalia fluviatilis*, the foramen cannot be observed in ventral view; b) *Sotalia guianensis* (SC), the foramen is dislocated externally to jugular notch and can be observed in ventral view. Structures indicated by the black arrows.

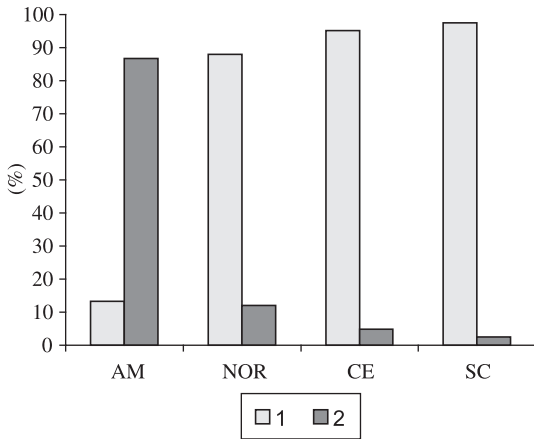


Figure 11. Percentage of the occurrence of hipoglossal foramen: 1- Hipoglossal foramen visible in ventral view; 2- Hipoglossal foramen not visible in ventral view. AM- Amazonas, CE- Ceará, NOR (samples of AP and PA together), SC- Santa Catarina.

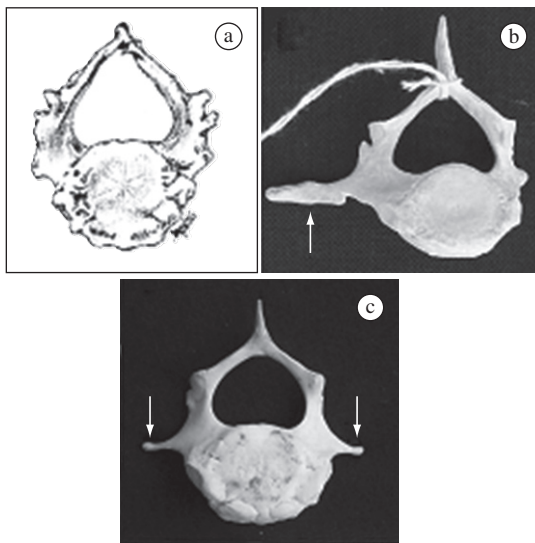


Figure 12. Cervical vertebrae from *Sotalia*. a) Seventh cervical vertebra (Ce7) of *S. guianensis* (normal); b) Ce7 of *S. guianensis* (CE) with cervical rib on left side; c) Ce7 of *S. fluviatilis* (AM) with cervical rib in both sides. Structures indicated from arrows.

and from SC (19%, $n = 32$). Furthermore, the size of the ribs is proportionally smaller in the riverine species than in the marine species. In *S. guianensis*, the cervical ribs were generally observed only on one side (right or left), while in *S. fluviatilis* they were observed on both sides. The UFSC specimen 1117 exhibited this structure on the right side of the third cervical vertebra (Ce₃). The cervical ribs were observed in all age classes.

4. Discussion

4.1. Fenestrae

The presence of *fenestrae* commonly observed in the occipital region, near the condyles of *Sotalia fluviatilis* was also recorded in juveniles and adults of *Pontoporia blainvillei* (Gervais and d'Orbigny, 1844) (Pinedo, 1991). However, in *Pontoporia*, the number of *fenestrae* was greater than that observed for the genus *Sotalia*.

In the genus *Sotalia*, the occurrence of *fenestrae* next to protuberances of the occipital region was low compared with the region next to the condyles. In the basioccipital, the presence of *fenestrae* was less frequent in immature specimens than in mature specimens. In *Pontoporia blainvillei* and in *Stenella* the occurrence of this structure was rare and occasional, respectively (Pinedo, 1991; Perrin et al., 1982).

Considering that the *fenestrae* observed next to the condyles in *S. fluviatilis* do not have the same origin as the fontanelles present in newborn individuals, given their different location, the origin and function of these *fenestrae* are not clear.

4.2. Vomer

The cranial floor is not generally included in morphologic studies and revealed interesting results. Simões-Lopes (2006), analysing specimens of *S. guianensis* in the southern region, observed that the laminar posterior process of the vomer is narrower than the lamellar pterygoid processes.

In the same study, the author found the converse in *S. fluviatilis* – where the vomer is broader and the lamellar pterygoid processes narrower. In the present work we verified that this characteristic described by Simões-Lopes (2006) was present in the majority of the marine specimens analysed. However, in the samples from CE and AP, we observed that some specimens also possessed a broad vomer, similar to the riverine species, herein called the “wide form”. Apparently, this characteristic can be used to distinguish the two species, but it is important to note that a small percentage of marine specimens possess a broad vomer just as some riverine specimens possess a narrow vomer. Thus, the use of this characteristic should be considered in combination to others when separating the species.

In relation to the posterior alignment of the vomer, the arrangement anterior to the lamellar pterygoid processes was observed in 100% of the cases for the marine species. In the riverine species ($n = 39$), 18% were observed with the posterior edge of the vomer aligned with the pterygoids, while in another 18% the posterior edge of the vomer extended beyond the pterygoides. Dawbin et al. (1970) attribute the alignment of the vomer in relation to the posterior pterygoid processes to age. For these authors, in sub-adults *Peponocephala electra* (Gray, 1846) the vomer extends to the level of the sutures between the pterygoides and basioccipital and in adults, the vomer extends beyond the adjacent pterygoides. This

pattern was not observed in the current study, since all adults of *S. guianensis* were observed with the posterior suture of the vomer anterior to the pterygoides. Moreover, the variation observed in the riverine species does not appear to be related to ontogenetic development, but rather to individual variation.

4.3. Pterygoides

The pterygoides were found to be medially separated by a projection in the tip of the palatines in all specimens, corroborating the data found in the literature (van Bénédén, 1875; Flower, 1885; Miranda-Ribeiro, 1936, da Silva and Best, 1994; 1996; Avila et al., 2002; Simões-Lopes, 2006). The variation in the form of the posterior projection of the left pterygoide was very subtle between the two species.

4.4. Anterior lacerate foramen

The anterior lacerate foramen is formed by two foramina (the optic foramen and the orbitorotundum foramen). These two structures are divided by a “wall” (Yamagiwa, et al., 1999) here called a spike-shaped projection. In *S. guianensis*, the majority of the adult specimens (between 72 and 98%) exhibited this projection between the optic and the orbitorotundum foramen. On the other hand, the narrow form was only observed in adults, suggesting that with time, this spiny projection fused with one side of the lacerated foramen (as observed in some marine specimens). In *S. fluviatilis*, in contrast, the absence of this projection was more common (88%), and could indicate neoteny.

4.5. Hypoglossal foramen

The location of the hypoglossal foramen varied between the two species. In *S. guianensis* the hypoglossal foramen generally meets between the crest of the basioccipital and the paraoccipital process, more precisely in the jugular notch as it occurs in other species of marine Delphinidae, for example, *Grampus griseus* (Cuvier, 1812) (Yamagiwa et al., 1999) and *Tursiops truncatus* (Montagu, 1821) (Rommel, 1990). In contrast, the hypoglossal foramen in *S. fluviatilis*, in the majority of cases, was found to be internally displaced.

4.6. Cervical vertebrae

The occurrence of cervical ribs was higher (87%) in the riverine species. The presence of pleuroapophyseal plates was initially suggested for some groups of mammals, especially monotremes and marsupials (Lessertisseur and Saban, 1967). Unilateral or bilateral processes in the cervical vertebrae are common in some groups of mammals (including *Homo*), and the costal rudiments are associated with the vertebral or vertebrarterial foramina (Lessertisseur and Saban, 1967). These authors also mention their presence in marine mammals as *Orcinus orca* (Linnaeus, 1758), *Tursiops truncatus* and *Balaenoptera* sp. Such processes have been considered serially homologous to the cervical ribs, also appearing in the literature as costal plates or pleuroapophyseal plates

(Flower and Lyddeker, 1891). The presence of cervical ribs is an intriguing characteristic in comparative anatomy, as these structures are typically observed in reptiles (Paula Couto, 1979; Ferigolo, 1987). In *S. guianensis*, these structures have already been reported in about 22.5% (n = 31) of the specimens of the southern region (Fettuccia and Simões-Lopes, 2004). In this work, considering a larger sample, the observed frequency of cervical ribs in the specimens from SC was 19% (n = 33), and of 9% (n = 23) from CE. Cervical ribs in mammals are examples of atavism (reappearance of an extinct character, common to ancestral lineages that rarely occur in current populations). Other cases of atavism are described in the literature as the occurrence of vestigial posterior members in whales and extra-numeric teeth in bats and sea lions (Bejder and Hall, 2002; Rui and Drehmer, 2004 and Drehmer et al., 2004). According to Hall (1984), there are four basic criteria for the recognition of an atavism: 1) persistence of the characteristic in adult life; 2) absence of this characteristic in the parents or recent ancestors; 3) occurrence in one or a few individuals within a population; and 4) similarity or identity with the same character exhibited by all the members of the ancestral population. Moreover, if the incidence of the character is still relatively high in a population, it is considered a polymorphism (Hall, 1984). Thus, considering the high occurrence of cervical ribs in specimens of the riverine species, these structures do not appear to be atavistic, suggesting the need for a more detailed study with a more representative sample number for a more consistent conclusion.

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