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O DESENVOLVIMENTO DO BIOSONAR DA TONINHA, *Pontoporia blainvillei*

(ODONTOCETI: PONTOPORIIDAE)

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**O DESENVOLVIMENTO DO BIOSONAR DA TONINHA, *Pontoporia blainvillei*
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Aprovada em de de 2013 .

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“Our perception of how dolphins utilize their sonar in the wild is based on extrapolation of knowledge obtained in 'laboratory' experiments - we do not have the foggiest idea of how dolphins utilize their sonar in a natural environment.”

Au'1993

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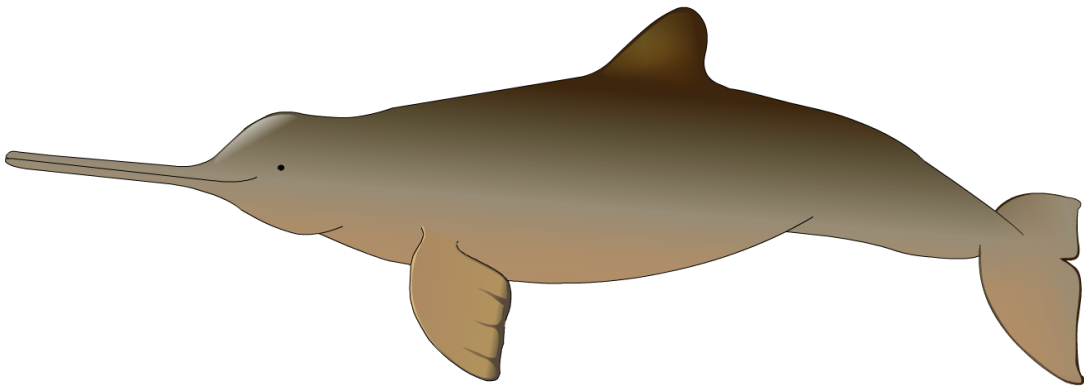
RESUMO

Pontoporia blainvillei é o golfinho mais ameaçado do oceano Atlântico sul ocidental devido à intensa mortalidade acidental durante atividades pesqueiras. A alta taxa de captura de indivíduos com menos de três anos de idade sugere a imaturidade funcional no uso da ecolocalização. Neste trabalho é utilizado o diagnóstico por imagem a partir de tomografias computadorizadas (n=2) e ressonâncias magnéticas (n=3), bem como dissecações de cabeças frescas (n=4) obtidas a partir de animais acidentalmente capturados em redes de pesca, para investigar as mudanças ontogenéticas das estruturas envolvidas na produção e recepção de ondas sonoras para o comportamento de ecolocalização. Ainda, uma análise comparativa de uma série ontogenética de 69 sincrânios foi realizada para elucidar uma relação entre osteologia e as estruturas moles do biosonar (musculatura facial, passagem nasal e gorduras especializadas), bem como descrever as transformações da mandíbula ao longo do desenvolvimento. A tomografia computadorizada fornece uma sequência de cortes (*slices*) com 1 mm de espessura nos planos sagital, coronal e axial, sendo cada pixel de qualquer plano interligado nos três planos. Assim, com o auxílio do programa Materialise © Mimics torna-se possível a manipulação e quantificação (volume, superfície e densidade) das estruturas analisadas em ambiente tridimensional (3D). Os indivíduos analisados revelaram a alta variabilidade morfológica que as toninhas apresentam na forma do biosonar ao longo da ontogenia, e as distintas taxas de desenvolvimento entre estruturas de mesmo aparato funcional (aparato produtor e receptor de sons de alta frequência). A formação da *Bursae cantantes* e do osso maxilar, por exemplo, apresentam distintas taxas de desenvolvimento em sua forma e são importantes estruturas para a funcionalidade do aparato produtor do som. O complexo timpano-periótico representa a estrutura que se desenvolve mais precocemente; ao contrário da mandíbula, que até a fase adulta apresenta sinais de não maturação da estrutura. À luz do vasto conhecimento a respeito da história de vida da espécie ao longo de sua distribuição, como a biologia alimentar e reprodutiva, são discutidos não só para relacionar as modificações do biosonar com a crescente capacidade de explorar a diversidade de presas no ambiente ao longo da ontogenia, mas como a ontogenia pode interferir no sucesso adaptativo da espécie visto sua história evolutiva. O conhecimento das modificações na ontogenia do biosonar em *Pontoporia blainvillei* pode ajudar na compreensão das limitações do seu uso por indivíduos imaturos e gerar subsídios para a conservação da espécie.

Palavras-chave: ontogenia; diagnóstico por imagem; anatomia funcional; heterocronia; recepção do som; nervo trimêneo; extinção.

Capítulo I

O BIOSONAR DOS ODONTOCETOS: "GOLFINHOS-DE-RIO"



Pontoporia blainvillei

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“Perhaps because of the beauty of external form, the great swimming performance, acute sense of hearing, superior intelligence and playfulness of the dolphins, it has often been imagined that the anatomy of cetaceans is somehow quite novel and different from that other mammals, including the Man.”

Purves’ 1972

A subordem Cetacea é a linhagem evolutiva mais diversa dentre todos os mamíferos marinhos (Rice, 2009). Seus representantes apresentam características únicas ao longo de todo eixo do corpo adaptadas a um ciclo de vida exclusivamente aquático. Dentre essas características, incluindo a redução da cintura pélvica a um par de ossos vestigiais e a transformação dos membros anteriores e da cauda em nadadeiras funcionais, as modificações na região da cabeça desses animais melhor explicam o sucesso adaptativo dos cetáceos (Miller, 1923; Cranford et al., 1996; Pyenson et al., 2012).

O processo de telescopagem refere-se à “migração” dos orifícios respiratórios desde a porção anterior do rosto, como encontrado em grupos ancestrais (Cetartiodactyla: Archeoceti), para a região do dorso da cabeça (cetáceos atuais). O encurtamento da região posterior do crânio, desde a base do rosto até os côndilos occipitais; a redução do diâmetro anteroposterior de ossos individuais (exceto parietal); e o deslizamento de um osso sobre outro ou interdigitação sobre os mesmos caracterizam a migração dos orifícios respiratórios para o topo da cabeça (Miller, 1923). Segundo Cranford *et al.* (1996), “...*This single term (telescopagem) was a unfortunate choice because the probable forces behind the process for each suborder was so different, as were the end results.*” Cladisticamente, não há sentido em nomear do mesmo modo processos distintos nos quais as variações morfológicas desse processo são determinadas a partir de novidades evolutivas surgidas independentemente em cada grupo. Embora a visão evolutiva do autor seja contraditória à sistemática filogenética, ele descreve minuciosamente as estruturas envolvidas nesse “processo” em cada grupo vivente de Cetacea e inclui uma chave de identificação baseada em características relacionadas ao processo da telescopagem a nível de família e gênero. Segundo Miller (1923), os cetáceos desenvolveram duas principais formas da telescopagem, diferindo, principalmente, na posição da porção posterior da maxila.

As duas principais linhagens evolutivas de Cetacea apresentam padrões muito distintos em suas história de vida, principalmente aqueles relacionados aos hábitos alimentares. Em mysticetos (Cetartiodactyla: Mysticetii), a porção posterior da maxila projeta-se obliquamente para baixo e para trás da margem anterior do processo supraorbital do osso frontal. As baleias verdadeiras incluem os maiores animais já viventes no planeta terra (Baleia azul, *Balaenoptera musculus*), desenvolveram cerdas bucais queratinizadas provindas da região do palato ao invés de dentes (Goldbogen, 2010) e uma grande mandíbula e tecidos associados que periferam o rosto. Associado à larga distensão da boca, esses animais podem se alimentar de milhões de pequenos crustáceos por dia em grandes abocanhadas de água (Goldbogen, 2010).

Nos odontocetos (Cetartiodactyla: Odontocetii) a porção posterior da maxila desliza por cima do osso frontal (Miller, 1923), permitindo o desenvolvimento da musculatura associada à região facial e do nariz (i. e. *musculus maxilonasolabialis*). Os dentes na mandíbula, pré-maxila e maxila permitiram os odontocetos diversificar seus hábitos alimentares, explorando diferentes ambientes como regiões oceânicas, costeiras, estuários e rios (Berta et al., 2006). Ainda, desenvolveram um mecanismo de orientação através da emissão de pulsos ultrasônicos discretos, com a capacidade de interpretá-los ao serem refletidos pelo ambiente, denominado sistema de ecolocalização ou biosonar (Griffin, 1944; Au, 2009).

O biosonar evoluiu independentemente em diversas linhagens dos vertebrados, como guácharos (Aves: Caprimulgiformes) (Griffin, 1953), andorinhões (Aves: Apodiformes) (Medway, 1959), morcegos (Mammalia: Chiroptera) (Maxim, 1912), e odontocetos (Norris et al., 1961). Em cetartiodáctilos terrestres, o som é produzido no complexo laríngeo através da passagem de ar nas cordas vocais ou por outras estruturas da laringe. O som produzido por esse mecanismo seria 99% refletido em contato direto com a água, exigindo um meio sólido ou líquido que conduza as vibrações da laringe para o ambiente (Schenkkan, 1973). Somente comprovado por Norris *et al.* (1961), hoje sabe-se que o biosonar em odontocetos é gerado através da passagem do ar ao longo das vias e sacos de ar presentes no complexo nasal, provocado por movimentos de abertura e fechamento da laringe (Houser et al., 2004), que, com o auxílio do ossos do hióide, mantém a alta pressão de ar necessária para realizar os sons ultrasônicos (Huggenberger et al., 2008). Cada passagem de ar possui uma estrutura chamada lábios-de-macaco (*monkey lips*), onde o ar passa e cria “estalos” (ondas sonoras) em uma série de eventos, resultado da abertura e rápido fechamento da estrutura (Cranford and Amundin, 2003; Dubrovsky et al., 2004; Cranford et al., 2008b). Esses estalos produzidos são conduzidos pela *bursa cantantis* anterior (Cranford 1988) até o *melon*, onde as ondas sonoras são focadas para o ambiente (Norris et al., 1961; Evans and Prescott, 1962; Purves and Pilleri, 1983; Cranford et al., 1997; Aroyan, 2001). Esses pulsos são refletidos pelo ambiente e recebidos pela mandíbula que, através dos corpos gordurosos presentes na janela mandibular, são conduzidos para a bula timpânica e decodificados no cérebro (Bullock et al., 1968; Norris, 1968; Oelschläger, 1986; Huggenberger et al., 2008).

De fato, o domínio da ecolocalização em odontocetos é desenvolvido a partir de um aprendizado. Estudando a ontogenia da ecolocalização em *Tursiops truncatus*, Hendry (2002) observou que um filhote não ecolocaliza nas primeiras fases de vida e necessita de um longo acompanhamento materno até atingir a maturidade da ecolocalização. Gardner *et al.* (2007) afirmam que, entre outros fatores, a baixa concentração de gordura especializada envolvida no aparato acústico de *Phocoena phocoena* indica que o sistema sensorial da ecolocalização não é funcionalmente maduro ao

nascimento e necessita de uma combinação de tempo, maturação fisiológica e desenvolvimento comportamental para obter a funcionalidade encontrada nos adultos. Motivados pela mortalidade em massa das baleias-bicudas-de-Cuvier, *Ziphius cavirostris*, provocada por exposição a sons de alta intensidade (Evans and England, 2001), Cranford et al. (2008a) descrevem a anatomia geométrica (baseada em imagens tridimensionais) das estruturas envolvidas na produção e percepção do som de um neonato e um adulto, e definem algumas diferenças em relação a forma dessas estruturas. O conhecimento a respeito do desenvolvimento da ecolocação, juntamente com a não maturação fisiológica das estruturas envolvidas no sistema acústico em odontocetos é utilizado na presente dissertação de mestrado como ferramenta para investigar impactos de natureza humana em uma espécie criticamente ameaçada nos seus primeiros anos de vida.

A toninha, *Pontoporia blainvillei* (Fig. 1), é um cetáceo odontoceto endêmico da zona costeira do Brasil, Uruguai e Argentina, e pode ser considerado a espécie mais ameaçada entre os cetáceos do Oceano Atlântico sul ocidental (Praderi et al., 1989; Secchi et al., 2001; Secchi et al., 2003). O limite norte de sua distribuição não ultrapassa Itaúnas (18°25'S-30°42'W), no Espírito Santo, e estende-se até Golfo Nuevo (42°35'S-64°48'W), na Argentina (Fig. 2) (Siciliano et al., 1994; Crespo et al., 1998). Possui padrão peculiar na sua distribuição, não demonstrando ser contínua (Siciliano et al., 2002a; Siciliano et al., 2010). Os autores definem duas áreas onde não há registros para a espécie, uma entre Cabo Frio (22°52'S-41°57'W, costa leste do Rio de Janeiro) e Ubatuba (23°28'S-45°01'W, norte de São Paulo) e outra entre Regência e Itabapoana (19°40'S e 21°18'S, no Espírito Santo). O fato pode estar associado à transparência da água e a profundidade (Siciliano et al., 2002b), uma vez que a espécie tem preferência por águas túrbidas e profundidades que dificilmente superam os 30-35m (Pinedo et al., 1989; Danilewicz et al., 2000; Secchi and Ott, 2000; Danilewicz et al., 2009).

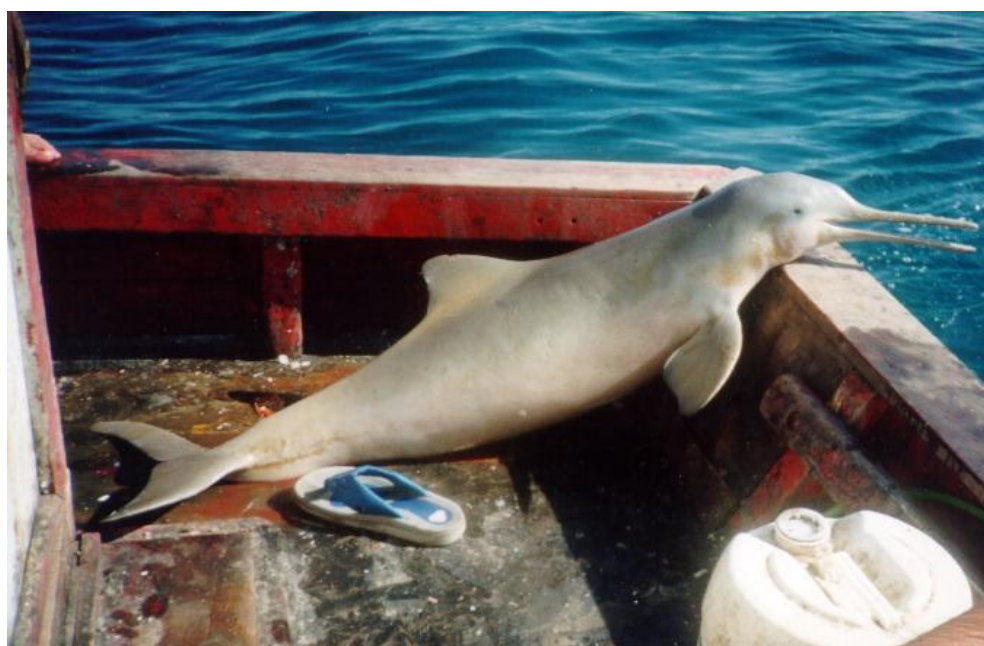


Fig. 1: Registro de captura acidental de uma toninha adulta em redes de pesca no litoral norte do Rio Grande do Sul. Foto: I. B. Moreno.

Com hábitos estritamente costeiros, este odontoceto torna-se vulnerável às ações antrópicas, principalmente no que se refere à captura acidental - *bycatch* - em redes de pesca (Praderi, 1997; Secchi et al., 1997; Kinas and Secchi, 1998; Ott, 1998; Praderi, 2000; Secchi et al., 2003). Curiosamente, mais da metade dos animais, oriundos da captura acidental, analisados nesses trabalhos não ultrapassam os três anos de idade (51%), coincidindo com as primeiras fases de desenvolvimento do biosonar. Vale ressaltar que a maturidade reprodutiva de machos está no intervalo de idade entre os três e quatro anos e que fêmeas possuem cerca de 1,5 anos de intervalo entre gestações, sendo que metade das fêmeas se reproduzem anualmente e a outra metade bianualmente (Danilewicz et al., 2000). Ou seja, a toninha possui a história de vida mais rápida entre os odontocetos e apresenta alta taxa de captura de indivíduos imaturos.

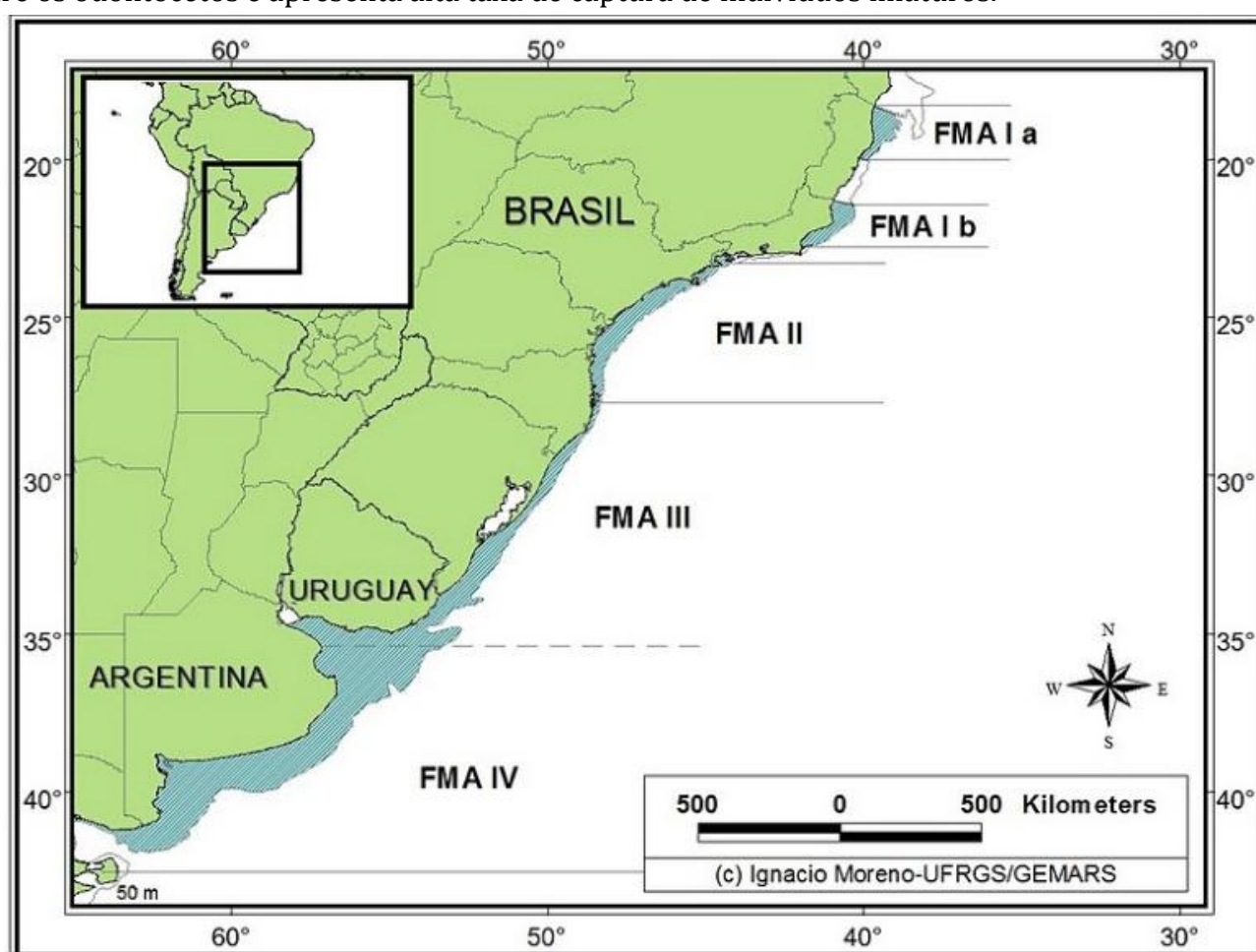


Fig. 2: Mapa da distribuição de *Pontoporia blainvillei* com os limites norte e sul, evidenciando as quatro FMA's propostas por Secchi *et al.* (2003), com modificações de Siciliano *et al.* (2010).

Para fins de manejo, Secchi *et al.* (2003) definem quatro populações para a espécie, as FMAs - *Franciscana Management Area* (Fig. 2) que foram recentemente reestruturadas com base em novas informações disponíveis (Siciliano *et al.*, 2010). A mortalidade de *P. blainvillei* em redes de pesca é

desigual entre as FMAs, sendo que a população que se distribui no litoral do Rio Grande do Sul e Uruguai é a mais afetada pela ação humana, uma vez que a mortalidade estimada por Secchi *et al.* (2004) é de 1500 a 1800 espécimes mortos em redes de pesca por ano. A alta captura de toninhas em redes de fundo (Praderi *et al.*, 1989; Ott *et al.*, 2002) pode estar associada tanto com a menor visibilidade do ambiente demersal (Danilewicz *et al.*, 2009), quanto ao hábito alimentar da espécie (Ott, 1998), em que as presas preferenciais são peixes e cefalópodes demersais (Pinedo *et al.*, 1989; Danilewicz *et al.*, 2002). Assim, Ott (1998) sugere que, durante o comportamento de caça, os indivíduos utilizam o biosonar unicamente para captura de presas e acabam não percebendo a rede de pesca.

A partir dos conceitos básicos da utilização do biosonar por odontocetos (Au, 2009), alguns trabalhos visam à modificação das redes de pesca por material mais denso e, assim, mais perceptível para esses animais (Larsen *et al.*, 2002; Trippel *et al.*, 2003), bem como a utilização de *pingers* que sinalizam a posição das redes com pulsos sonoros (Kraus *et al.*, 1997). A utilização de Sulfato de Bário (BaSO₄) nas redes, como medida de reduzir a captura acidental de *Phocoena phocoena*, foi testada e comprovada por Trippel *et al.* (2003), embora Larsen *et al.* (2002) não apresentem resultados positivos para o mesmo experimento. Ainda, os autores admitem que a utilização de Óxido de Ferro (IO) reduz a captura acidental de *Phocoena phocoena*, no entanto reduz também a captura da espécie visada pela indústria pesqueira o que provavelmente inviabiliza a sua utilização. A utilização de *pingers* em redes de pesca reduz a captura acidental de pequenos cetáceos (Kraus *et al.*, 1997; Bordino *et al.*, 2002). No entanto, estudando o efeito dos *pingers* na captura acidental da toninha, *Pontoporia blainvillei* em águas argentinas, Bordino *et al.* (2002) observaram que esse mecanismo não só reduz a captura deste odontoceto, mas em contrapartida aumenta a interação entre leões-marinhos, *Otaria flavescens*, e a atividade pesqueira, uma vez que estes animais tendem a seguir as embarcações para retirar os peixes das redes trazendo grande prejuízo aos pescadores, o que também inviabilizaria a utilização dos *pingers* em regiões onde existem esses tipos de interações.

O complexo nasal da toninha é descrito na literatura (Burmeister, 1867; Schenkkan, 1972; Cranford *et al.*, 1996; Huggenberger *et al.*, 2010). A ausência da assimetria craniana encontrada em odontocetos e a alta assimetria dos sacos vestibulares de *P. blainvillei* é abordada na literatura como uma peculiaridade em Odontoceti e um enigma em relação à produção do som nessa espécie (Schenkkan, 1972; Huggenberger *et al.*, 2010). Em geral, odontocetos tem a capacidade de produzir dois tipos de som para distintas funções. Os "*clicks*" são ondas sonoras de alta frequência emitidas pelo complexo epicranial e estão relacionadas a ecolocalização (Au, 2009). Os assobios ("*whistles*") são ondas sonoras com frequência modulada de curta duração (Tyack, 2000) produzidas por

movimento de passagem de ar pela laringe e estão associados ao comportamento social das espécies (May-Collado et al., 2007). Essa forma de comunicação é encontrada também em mamíferos terrestres, como os hipopótamos (grupo irmão de Cetacea - Gatesy *et al.*, 1999) que podem produzir sons funcionalmente utilizados para comunicação de no máximo 5KHz (Richardson et al., 1995), como é conhecido para misticetos (Clark, 1990). Em odontocetos, a frequência dos assobios mais comumente encontrada variam entre 5-20KHz (Richardson et al., 1995), sendo que algumas espécies (*e.g. Delphinus delphis, Stenella attenuata, Stenella coeruleoalba, Stenella longirostris, Lagenorhynchus albirostris, Tursiops truncatus e Inia geoffrensis*) podem ultrapassar os 48KHz. Embora a toninha seja considerada um "old-river" (Cranford et al., 1996), numa menção do autor a antiga classificação de Simpson (1945) que trata os chamados "golfinhos-de-rio" como um agrupamento natural e com características plesiomórficas, é capaz de produzir sons atingindo os 148 KHz (Melcón et al., 2012). Hoje, sabe-se que a classificação de Simpson para os "golfinhos-de-rio" (gêneros *Platanista, Lipotes, Inia e Pontoporia*) nada mais é do que evidências de convergências evolutivas entre esses grupos a semelhantes pressões seletivas, sendo as características compartilhadas (rosto fino e comprido, nadadeira dorsal triangular, pescoço flexível, olhos e porte pequenos) adquiridas independentemente pelos grupos (Fig. 3) (Hamilton et al., 2001). Juntamente com *Cephalorhynchus commersoni* e *Phocoena phocoena*, *Pontoporia blainvillei* possui um dos sonares com as maiores frequências já registradas para odontocetos e representa um mistério em relação à sua funcionalidade (Huggenberger et al., 2010).

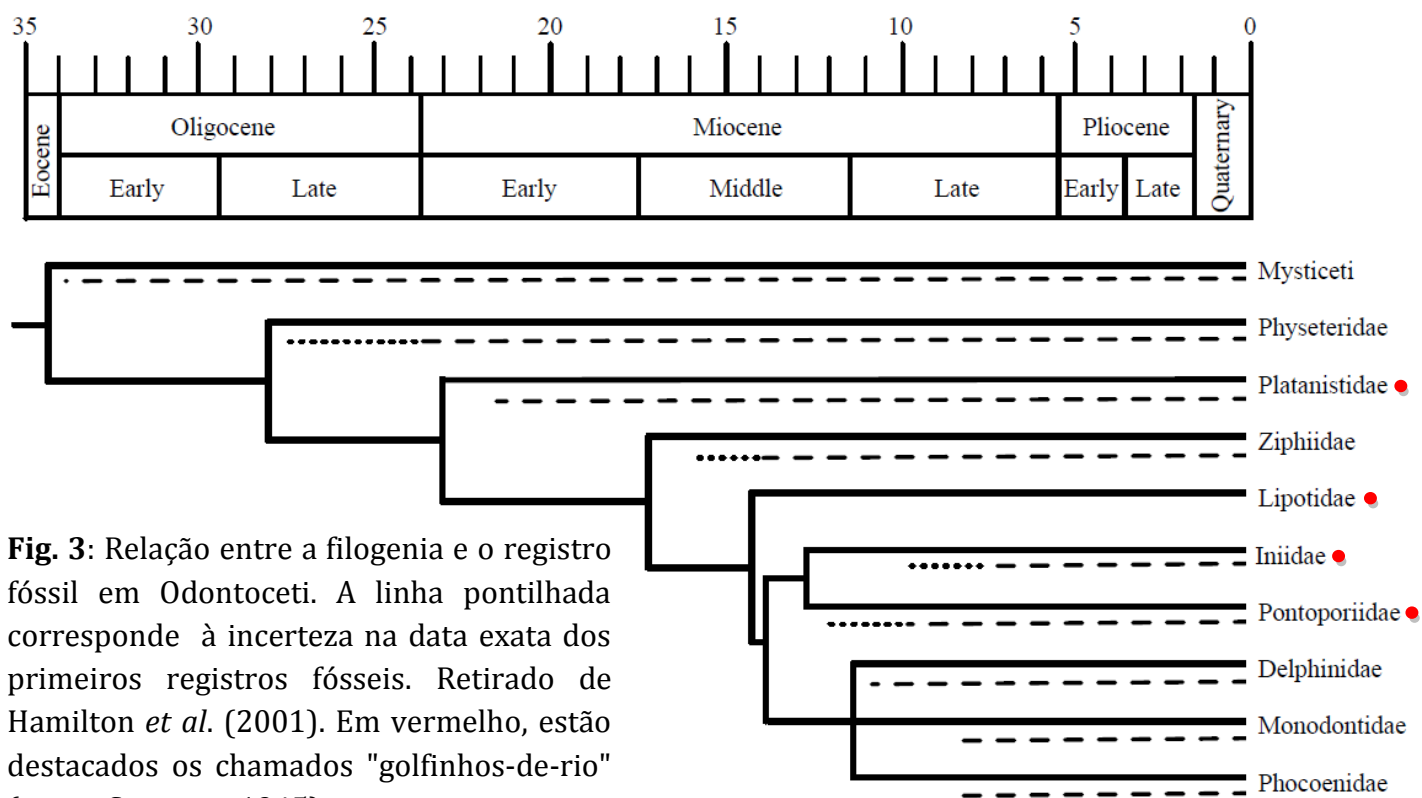


Fig. 3: Relação entre a filogenia e o registro fóssil em Odontoceti. A linha pontilhada corresponde à incerteza na data exata dos primeiros registros fósseis. Retirado de Hamilton *et al.* (2001). Em vermelho, estão destacados os chamados "golfinhos-de-rio" (*sensu* Simpson, 1945).

O objetivo dessa dissertação de mestrado é descrever as diferenças ontogenéticas das estruturas envolvidas no sistema de ecolocalização das toninhas, *Pontoporia blainvillei*, no intuito de começar a entender a mortalidade da espécie nas atividades pesqueiras por capturas acidentais em redes de emalhe, tendo em vista o conhecimento acerca da anatomia funcional do mecanismo de orientação do animal no ambiente. Aspectos da biologia alimentar e reprodutiva são utilizados aqui como ferramentas para compreender a complexidade do biosonar da toninha, bem como propor hipóteses a respeito da funcionalidade de certas estruturas e como essas transformações podem interferir na história de vida e, conseqüentemente, nas pressões evolutivas que a cercam.

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Capítulo II

POSTNATAL DEVELOPMENT OF FRANCISCANA'S (*Pontoporia blainvillei*) BIOSONAR: FUNCTIONAL ANATOMY AND LIFE-STORY*



*"Structure without function is a corpse,
function without structure is a ghost"*

Vogel & Wainwright' 1969

* Manuscrito redigido nas exigências do periódico *The Anatomical Records*.

POSTNATAL DEVELOPMENT OF FRANCISCANA'S (*Pontoporia blainvillei*) BIOSONAR: FUNCTIONAL ANATOMY AND LIFE-STORY

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ABSTRACT

We describe the changes in cephalic anatomy of franciscana dolphin throughout its ontogeny by analyzing three neonate males and two adult male franciscana dolphins using remote imaging technology and hand dissections to compare and contrast the structures involved in sound production and reception. Furthermore, comparisons with an ontogenetic series of 69 skulls are made to elucidate an association between soft tissue and bone changes on epicranial complex and describe the lower jaw formation. By studying the anatomical development of odontocetes orientation mechanism, we provide some insights about biosonar functionality, and understanding how of significant these changes are for these animals' life-story. Primary results revealed topographical changes on franciscana's head, and a great variability on development timing of different functional parts of biosonar anatomy, like Maxilla and *Bursa cantantes* formation and the low modification of timpano-periotic complex compared with the lower jaw ontogeny. Developmental changes on posterior part of right vestibular air sacs follow bone formation modifications, and show great differences on anterior shape throughout the ontogeny, as well as the rostral part of epicranial complex. Our discussion is based on correlate functional aspects of biosonar anatomy with the vast knowledge about life-story of this species. Indeed, shows the relevance of descriptive developmental characters for evolutionary biology.

Keywords: development; anatomic geometry; life-story; "diet shift theory"; bycatch; sound reception; trigeminal nerve.

INTRODUCTION

Toothed whales (Cetartiodactyla: Odontoceti) are cetaceans that developed a complex apparatus on nasal tract and an association between middle ears and lower jaw to respectively produce and receive ultra-sound pulses for echolocation (Norris et al., 1961; Evans and Prescott, 1962; Purves and Pilleri, 1983; Cranford et al., 1996; Aroyan, 2001). Indeed, they use this sonar mechanism to explore and hunt in several environments, like coastal, pelagic and deep waters as well as estuarine and river systems. Increased knowledge about the functional anatomy of biosonar provides subsidies to understand some aspects of the dolphins' life-story, correlating form (or "geometry") and environment (Cranford et al., 2008b; McKenna et al., 2012).

The Pontoporiidae family includes diverse dolphins ranging in age from the late Middle Miocene to the Recent, represented by the last lineage *Pontoporia blainvillei* (Gervais and D'Orgibny, 1844) (Hamilton et al., 2000). Despite such condition, franciscana dolphin is the most endangered species of western South Atlantic Ocean (Praderi et al., 1989; Secchi et al., 2001; Secchi et al., 2003). The major cause of its vulnerability is incidental by-catch in gillnets fishery (Moreno et al., 1997; Secchi et al., 1997; Secchi et al., 2003). Intriguingly, more than half (51%) of captured animals are young (less than three years old) (Kasuya and Brownell Jr, 1979; Crespo et al., 1986; Ott, 2000; Ramos et al., 2000); therefore, echolocation behavior might not have been fully developed, nor learned (Hendry, 2002; Gardner et al., 2007).

The bycatch phenomenon is an interaction between two distinct evolutionary lineages converging to the same source, including humans and the threatened species involved. Larsen et al (2007) report several factors that can be involved in the animal entanglement, including behavioral and by fail net detection using echolocation. In fact, modified composition of fishery gill nets increase the acoustic reflectivity and reduce the mortality in some species (Kraus et al., 1997; Bordino et al., 2002). However, so far, this mitigation effort has not been positively proved for *Pontoporia blainvillei*. The use of acoustic deterrents (pingers) reduces the bycatch in these species but increases the interaction between fishery activity and southern sea lions, *Otaria flavescens*, which are conditioned by a "dinner bell" (Bordino et al., 2002).

The franciscana dolphin's nasal complex is described in detail in literature (Burmeister, 1867; Schenkkan, 1972; Cranford et al., 1996; Huggenberger et al., 2010). Although the extreme complexity of franciscana's biosonar apparatus retains great attention for many authors, its functionality remains a mystery (Cranford et al., 1996; Huggenberger et al., 2010). Even though the biosonar anatomy of Odontoceti and its echolocating function have been well described in works in this field (Cranford et al., 1996; Cranford and Amundin, 2003; Cranford et al., 2008b),

developmental studies are scarce (Rauschmann et al., 2006; Galatius et al., 2011; Moran et al., 2011; Haddad et al., 2012).

Since Norris *et al.* (1961) proved that a blindfolded dolphin can detect objects placed under the rostrum line, it has been accepted that the sound beam formation for echolocation is originated in the epicranial complex, more specifically in the “monkey-lips dorsal bursae” (MLDB) complex (Cranford et al., 2008b). The monkey lips, or phonic lips, produce snap-like noises in a series of events by air passage, specific for each species (Akamatsu et al., 2007), resulted from aperture and quickly closing of the structure, producing a “click” (Cranford and Amundin, 2003; Dubrovsky, 2004; Cranford et al., 2008b). These produced sonar pulses originate vibrations on two small fat bodies named *Bursae cantantes* (Cranford et al., 1996), which are closely placed on the posterior part of the melon terminus. The melon is functionally important to focus sound energy generated in the MLDB complex, thus decreasing acoustic attenuation at the animal-environment interface by impedance matching (McKenna et al., 2012). The high intensity pulses produced by the epicranial complex are reflected by the environment and received by the lower jaw that conducts these vibrations through the mandibular fat bodies in the lower jaw acoustic window to the middle ear or timpano-periotic complex (Bullock et al., 1968; Norris, 1968). The presence of two fatty paths to each bursa complex may reflect two functional sound systems (Huggenberger et al., 2010) and is a particularity in *Pontoporia blainvillei*, as well as the extreme asymmetry of epicranial complex and the unusually symmetry odontocete skull (Cranford et al., 1996).

Developmental studies have been of great interest to evolutionary developmental biologists (Fink, 1982; Smith, 2003; Thewissen et al., 2006). In cetaceans, morphological changes “...in the time of onset or end, or the rate of a development...” (Smith, 2003), or simply heterochrony process (Gould, 1977; Fink, 1982; McNamara, 1986), are proposed at sub-order (*i. e.* Cetacea) (Thewissen et al., 2006), family (*i. e.* Phocoenidae) (Barnes, 1985), and sub-species (*i. e.* *Phocoena phocoena*) level (Galatius et al., 2011). The present study compares the morphology of cephalic anatomy between different stages of development of franciscana dolphin heads with focus on nasal anatomy, containing the sound generating mechanism and the hearing apparatus composed by lower jaw and the timpano-periotic complex. In addition, comparisons with osteological material are made to elucidate an association between soft tissue and bone changes on the epicranial complex, as well as to describe lower jaw formation. The previous knowledge about franciscana's biology and the ontogenetic approach adopted in this research were useful to understand some life-story aspects in this species, including feeding behavior and selective pressures. In our discussion, we will not only focus on the differences in the development timing of some structures involved in biosonar anatomy and the importance of developmental descriptions for phylogenetic studies, but also, in

the light of functional anatomy, how this evolutionary process can be guiding franciscana dolphin, like an arrow (Smith, 2003), to extinction.

MATERIAL AND METHODS

The descriptive changes on biosonar anatomy of franciscana dolphin were based mainly on magnetic resonance imaging (MRI) between one neonate male (6.43mm slice thickness; 0.469mm pixel size) and an adult male (7.99mm slice thickness; 0.586mm pixel size); computed tomography scans (CT) that were collected from thin transverse cross-sections of 1mm thickness by DICOM images format of another neonate male (0.277mm pixel size), and the same adult head (1mm slice thickness; 0.586mm pixel size); and macroscopical dissections (DS) of two adult males, a neonate male and a neonate female (Table 1).

TABLE 1. List of soft material examined

Institution ^a	ID number	Age	Body length (BL)	Sex	Fixation	Method applied
GEMARS	1465	Adult	138.1 cm	M	Frozen	CT, MRI
GEMARS	1441	Adult	155 cm	M	Frozen	DS
GEMARS	1440	Sub-adult	124 cm	M	Frozen	DS
GEMM-Lagos	-	Neonate	68.9 cm	M	Frozen	CT
GEMARS	1472	Neonate	75.5 cm	F	Frozen*/Formali	MRI*/ DS
GEMARS	1417	Neonate	84 cm	M	Frozen	DS
GEMARS	-	Fetus	20 cm	-	Formalin	MRI

Methods applied: CT, computer assisted tomography; DS, macroscopical dissection; MRI, magnetic resonance imaging.

^a GEMARS, Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul, Brazil; GEMM-Lagos, Grupo de Estudos de Mamíferos Marinhos da Região dos Lagos.

All of the examined fresh material was obtained by incidentally caught specimens on fishery activity and are deposited in the Scientific Collection of Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul (GEMARS). The MRI-scans and CT-scans were usually performed in all three planes reviewed by Huggenberger *et al.* (2008). The anatomic geometry was described based on this imaging processing software, including measurements of distances, angles, volume, surface, and density (HU) values (Table 2). Hounsfield units (HUs) express a calibrated measure of electron density within each “voxel” in the three-dimensional image (McKenna *et al.*, 2012), and are arranged on a scale from -1,024H unit to +3,071H unit, adjusted so that -1,024H unit means the attenuation produced by air, and 0H unit means the attenuation produced by water (Robb, 1999). HUs are well correlated with density properties (McKenna *et al.*, 2012), and the volume values are directly comparable in DICOM images format (McKenna *et al.*, 2007). The suite of structures (Table 2) comprises the basic components of sound production and reception apparatus in *Pontoporia blainvillei* that were defined by analyzing images and editing them pixel by pixel on the three planes. Hand dissections follow Schenckan (1972), according to whom “...the different layers of muscles

connected with the blowhole region were dissected layer by layer, keeping adjacent structures intact as much as possible.” In addition, histological sections (HIS) stained with Masson technique (Prophet et al., 1992) were made in the rostral part of the epicranial complex in a neonate specimen (GEMARS 1472) to explore and to characterize the soft tissue.

For comparison purposes, 69 skulls, including 42 males and 27 females, were examined in order to investigate the ontogeny changes of related soft-tissue bones (*i.e.* maxillary and nasal bones) as well as the lower jaw, focusing on alveoli formation. Data including body length (BL) and condyle-basal length (CBL) (Perrin, 1975) of skulls analyzed are given in **comparative material** at the end of the text. Descriptive changes were based on the use of expressions conveying ideas of early and late, or before and after adopted by Miller (1923) to be understood as applying to the process and not to time. In this view, to elucidate a general biosonar bauplan ontogeny. Previous information about franciscana's epicranial complex anatomy reported in the literature was placed in our results to enrich the descriptive changes of the structures. Our discussion is based on functional aspects of biosonar anatomy and the relevance of character definition for evolutionary developmental biology. Terminology follows Mead and Fordyce (2009) and Cranford *et al.* (1996).

RESULTS

In general aspects, the biosonar anatomy of franciscana dolphin reveals a great variability on the ontogenetic timing of some functionally related structures, including sound production and reception apparatus. Although we have been able to describe the main structures of biosonar using high resolution and detail in both calf and adult specimens, some structures of the calf's skull do not appear in the image reconstruction because of the low density of these parts and even the low CT-scan acuity which results in undistinguishable hypointense (Oelschläger et al., 2008) areas for a human operator's decisions (Cranford et al., 2008b). The following sections will provide anatomical descriptions for the ontogeny of biosonar subdivisions.

Development of sound production apparatus

Monkey lips. They are disposed in two pairs on each short nasal passage and are arranged in a series of small wrinkles, which are oriented parallel to the air stream (Cranford et al., 1996; Huggenberger et al., 2010). In our study, the monkey lips of the specimens dissected show the same configuration as described in the literature (Huggenberger et al., 2010), *i.e.* they develop in size and shape in the same way as the nasal passages grow and show the same arrangement in all developmental stages, except for the sub-adult specimen (GEMARS 1440) that reveals a single lip

between each side of posterior nasal passages (Fig.1), similar to a fusion of each side of the structures. The monkey lips could only be observed by hand dissection technique.

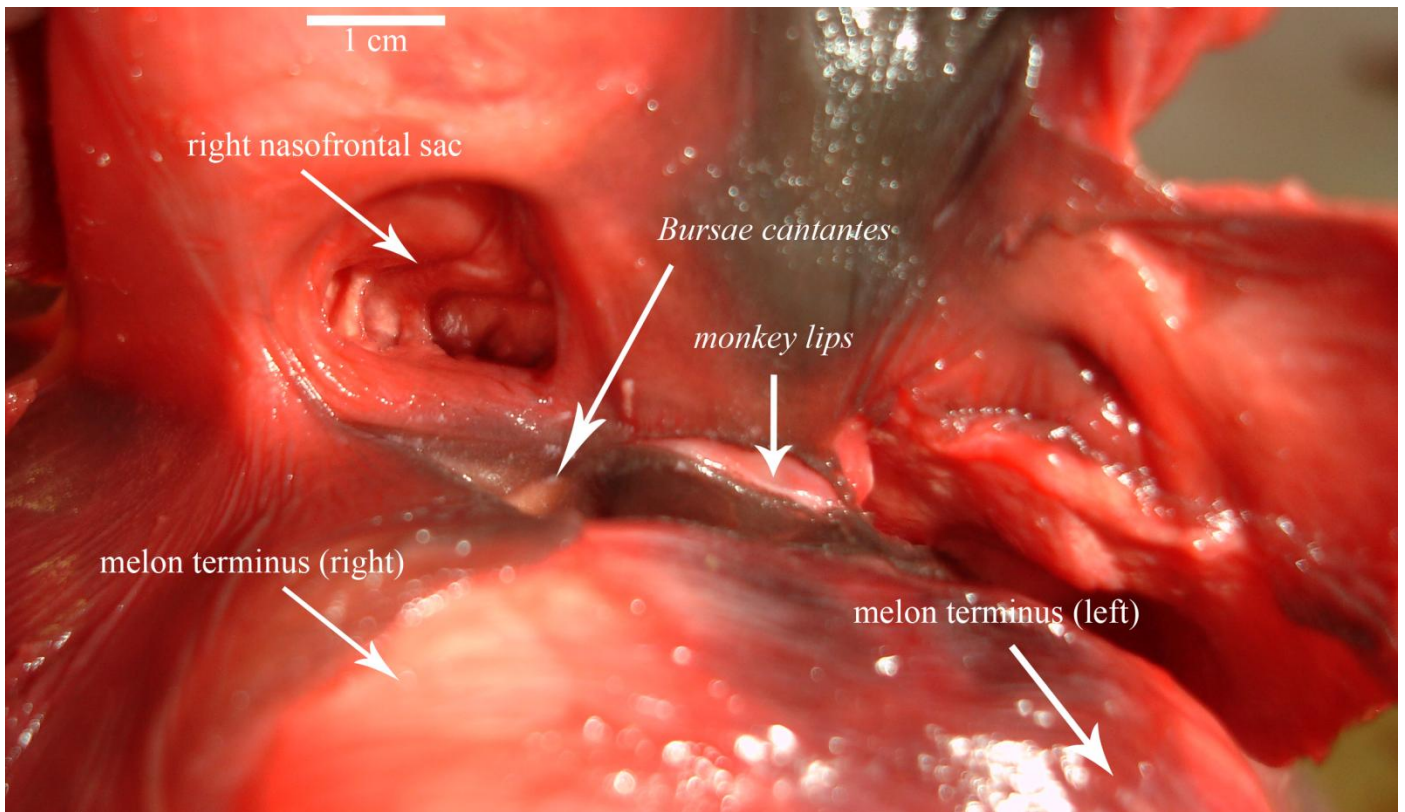


Fig 1. Sub-adult male (GEMARS 1440) dissection showing the main structures involved in sound production. In this frontal view, the tendinous part of *Musculus maxilonasolabialis* was elevated to expose the nasofrontal diverticula, monkey lips and *Bursa cantantes*.

Bursae cantantes. These correspond to two different ellipsoid fat bodies: posterior (PB) and anterior bursa (AB) (Fig. 1). These structures are two small fat bodies perpendicularly placed in relation to the body axis, whose biggest diameter is aligned with the horizontal line that passes between both structures. The PB dimensions show that the width is always greater than the axial length. The neonate specimen exhibits an axial length of 3.74mm and a width of 4.77mm on its right PB; an axial length of 3.2mm and a width of 5.15mm on its left PB. The adult specimen shows an axial length of 4.25mm and a width of 6.91mm on its right PB; an axial length of 4.28mm and a width of 6.41mm on its left PB. As observed for PB dimensions, the AB width is always greater than the axial length. The neonate specimen exhibits an axial length of 2.25mm and a width of 3.08mm on its right AB; an axial length of 1.53mm and a width of 2.73mm on its left AB. The adult specimen's right AB exhibits an axial length of 3.28mm and a width of 6.08mm; an axial length of 3.92mm and a width of 5.31mm on its left AB.

Furthermore, these structures are well aligned with the anterior insertion of nasal bones at dorsal view (Fig. 2). PB, or spermaceti organ (Cranford et al., 2008b), is located on the anterior wall

of the nasal passage and closely adjacent to the anterior monkey lips and below the nasofrontal sacs (Fig. 1, 2, 3). AB is placed on the anterior wall of the nasal passage in the horizontal line of PB and is known to be indistinguishable from the melon terminus. In this study, we could distinguish the limits of this structure from melon terminus on both specimens, although the neonate male presented low differentiation between anterior portion and posterior melon (Fig. 2, 3). If we compare the relative volume between the structure in neonate and adult (Table 2), we will see that PB and AB show distinct timing of formation throughout ontogeny. The relative volumes of PB demonstrate fewer developmental changes than AB.

Melon. The sound lens of franciscana dolphin is composed mainly of lipidic cells and connective tissue fibers as described in the literature (Cranford et al., 1996; Barroso et al., 2012). The developmental changes of the left melon were not as remarkable as the anterior elongation and the great expansion of the anterior part of the right melon (Table 2). The left melon is a triangular fat body that never passes anteriorly through the posterior flattened portion of the right melon (Fig. 2). The posterior part of the right melon is an unusually trumpet or intestine-shaped that first runs anteriorly from the bursa complex through a flattened and laterally curved portion, just above the posterior part of premaxillary bone, and then it extends ventrally and anteriorly to the main body of the structure (Fig. 2). In adult specimens, the right melon runs closest to the surface of the forehead along the anterior-most region of the melon (McKenna et al., 2012), even though it is evident, in the neonate specimen, a distinct form from the adult. The anterior portion of neonate's right melon is marked by an abrupt ventral continuity after the flattened part of the posterior melon (Fig. 2). The two melon pathways develop distinctly in shape dimensions when we compare the structures length and width. The right melon seems to have an offset development comparing to the left melon, which exhibits similar dimensions both in the neonate and adult specimens. The neonate specimen exhibits 60.17mm of right melon length and 10,08mm of left melon length. The adult specimen shows 112.84mm of right melon length and 13.44mm of left melon length. The left melon of a neonate specimen represents 75% of axial length of the same structure in an adult specimen. On the other hand, the right melon of a neonate specimen represents 53% of the same adult structure dimensions. Comparing the width of the posterior part of these two pathways, we observe that the anterior width of the right melon is always larger than the left side. Moreover, these parts may grow proportionally with the posterior part of right and left melon of a neonate specimen exhibiting 8.78mm and 7.71mm, respectively, and 12.94mm and 12.63mm for the same dimensions in the adult specimen. This proportional development was not observed in the right melon anterior part, in which the neonate specimen exhibits 26.68mm as the greatest globular width and 42.1mm for the same dimension in the adult specimen.

TABLE 2. Quantitative tabulation of density (HU), volume and surface values for various structures in the head of a neonate and adult male franciscana dolphin (*Pontoporia blainvillei*), plus measurements for size indexing^a

Structure		Neonate				Adult				Neo/Adult % Vol mm ³
		HU range	HU mean (SD)	Volume mm ³	Surface mm ²	HU range	HU mean (SD)	Volume mm ³	Surface mm ²	
Melon	right	-157/-52	-75.76 (15.04)	13306.54	3619.82	-199/-20	-75.79 (31.75)	67771.22	12945.46	19.63
	left	-172/-52	-74.83 (15.68)	257.52	216.06	-199/-20	-83.32 (40.99)	480.3	376.92	53.61
Anterior bursae	right	-82/-52	-65.08 (12.08)	13.84	23.52	-101/-20	-51.38 (26.55)	52.18	64.53	26.53
	left	-82/-52	-64 (11.28)	8.46	13.79	-101/-20	-52.54 (24.10)	49.09	68.76	17.23
Posterior bursae	right	-97/-52	-72.64 (14.05)	35.76	48.85	-118/-20	-62.23 (30.43)	70.38	83.12	50.81
	left	-97/-52	-69.38 (12.38)	31.53	44.54	-118/-20	-56.12 (27.76)	54.93	72.15	57.41
Tendinous part of <i>M. maxilonasolabialis</i>		68/157	94.56 (17.88)	2788.41	2043.89	44/190	93.78 (25.60)	9485.57	4390.37	29.39
Mandibular fat bodies	right	-82/-7	-59.51 (23.69)	4549.02	2993.78	-166/-37	-92.40 (28.70)	13997.07	8228.64	32.49
	left	-82/-7	-60.45 (22.95)	5038.53	3151.2	-166/-37	-80.36 (23.68)	16471.87	7953.74	30.58
Lower jaw		23/1249	418.05 (193.70)	13016.01	14047.43	60/2229	882.07 (486.59)	56002.81	35901.14	23.24
Connective tissue theca		82/127	97.24 (13.41)	12792.64	7311.69	77/141	93.66 (15.65)	34314.07	18117.53	37.28
Timpanoperiotic complex	right	830/2744	1824.79 (598.75)	2477.19	1967.7	465/3071	2001.05 (872.61)	3242.68	2107.01	76.39
	left	830/2759	1847.10 (602.49)	2436.73	1955.31	465/3071	1991.49 (877.21)	3447.99	2143.14	70.67
Specimen	Total body length (BL)	Condylbasal length (CBL)		Post cranial body length (PCBL)			PCBL / TL			
Neonate	68.9 cm	19.4 cm		49.5 cm			71.8 %			
Adult	138.1 cm	38.7 cm		99.4 cm			72%			
Neonate / Adult %	49.9 %	50.1 %		49.8 %						

^a Comparisons of volume for the structures involved in sound production and reception within the neonate and adult male heads. Morphometrics measurements as BL, CBL and PCBL are included in the table botton for interespecific comparisons (see Cranford 1999; Cranford *et al.* 2008).

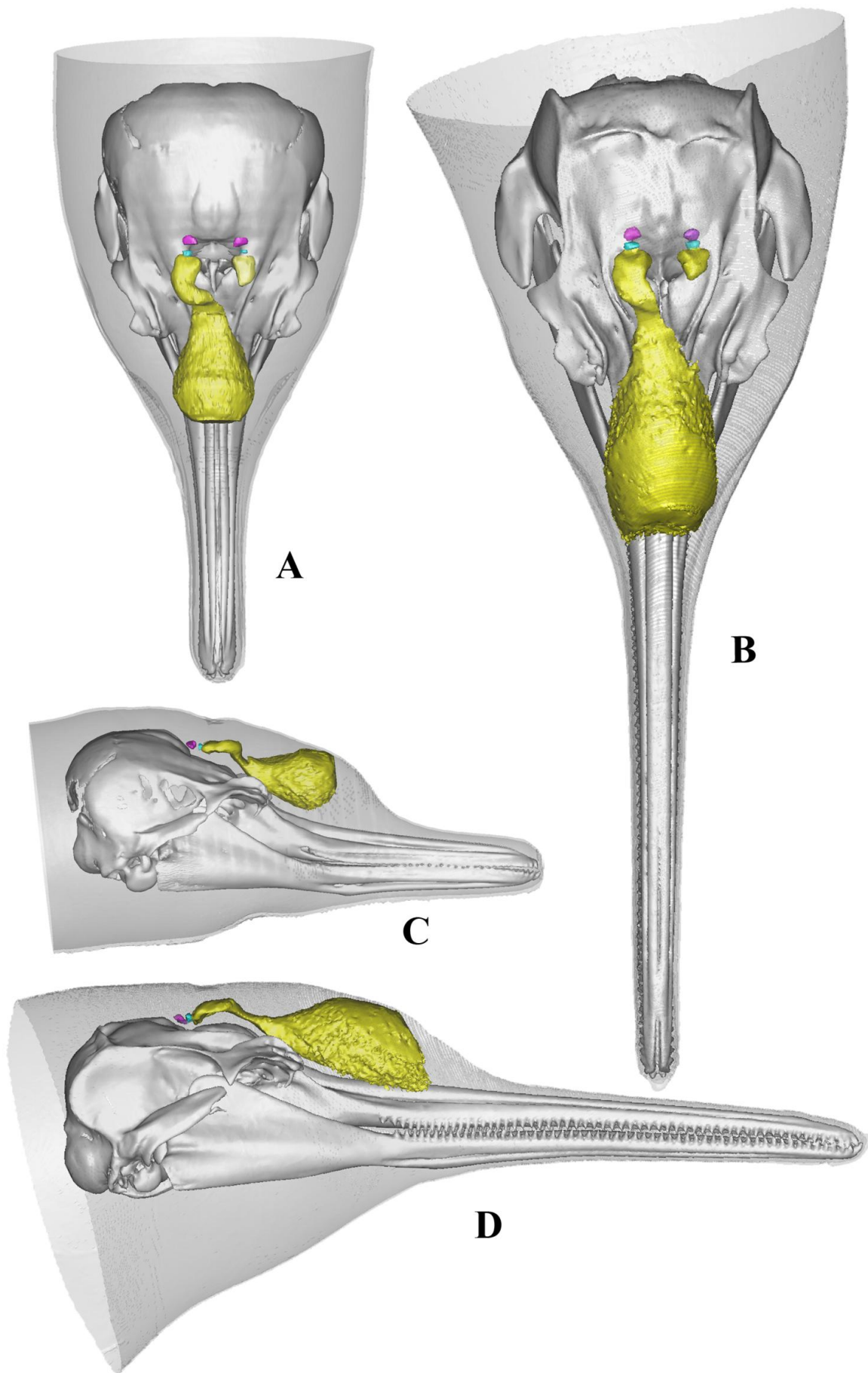


Fig 2. Dorsal (A-B) and right lateral (C-D) views of neonate (CBL: 19.4 cm) and adult (CBL: 38.7 cm) anterior foreheads, showing the skull and lower jaw (white), the skin (gray) and the main structures included in sound production apparatus: melon, yellow; anterior bursa, cyan; and posterior bursa, magenta.

Although the right melon seems to have a growth related to the epicranial complex length (neonate: 65,05mm; adult: 126,72mm) (Huggenberger et al., 2010), the shape of the anterior part exhibits a series of modifications. In CT and MRI scans of neonate specimens, we see different tissue properties between the melon and the connective tissue theca (above), and between the melon and skull (below) that not correspond to lipidic structures (Fig. 2,3).

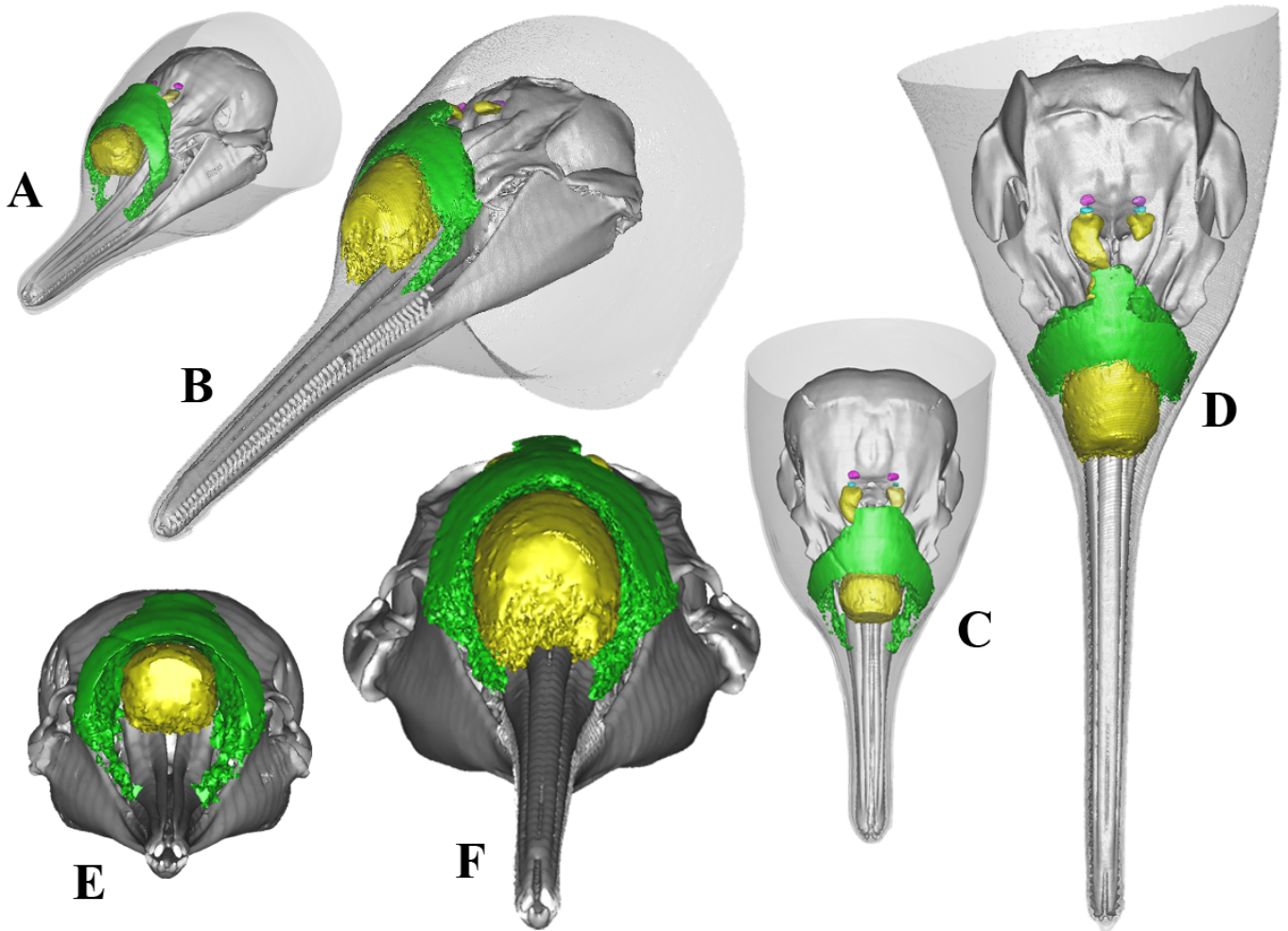


Fig 3. This image shows the sound production apparatus (melon, yellow; anterior bursa, cyan; and posterior bursa, magenta) of neonate (CBL: 19.4 mm) and adult (CBL: 38.7 mm) specimens and the connective tissue theca (Ctt), green, in three views: **A-B**.diagonal; **C-D**, dorsal; **E-F**, frontal. In all three views it is possible to see the gap formed by different tissue properties between the melon and the Ctt in neonate specimen.

In most delphinids, the anterior portion of the epicranial complex is composed of fat (melon), dense connective tissue, and rostral muscles (Mead, 1975). Franciscana dolphin is well known for not possessing this rostral musculature (Huggenberger et al., 2010), although histological analysis of anterior forehead shows a series of longitudinal and transversal muscle fibers, respectively, just below and ventrolateral to the melon in the neonate specimen (Fig. 4). The developmental changes of the right melon reveal a great ventrally expansion of the anterior part, with respect to the early involution of the rostral muscles. The anterior expansion of the right melon globular part is seen by

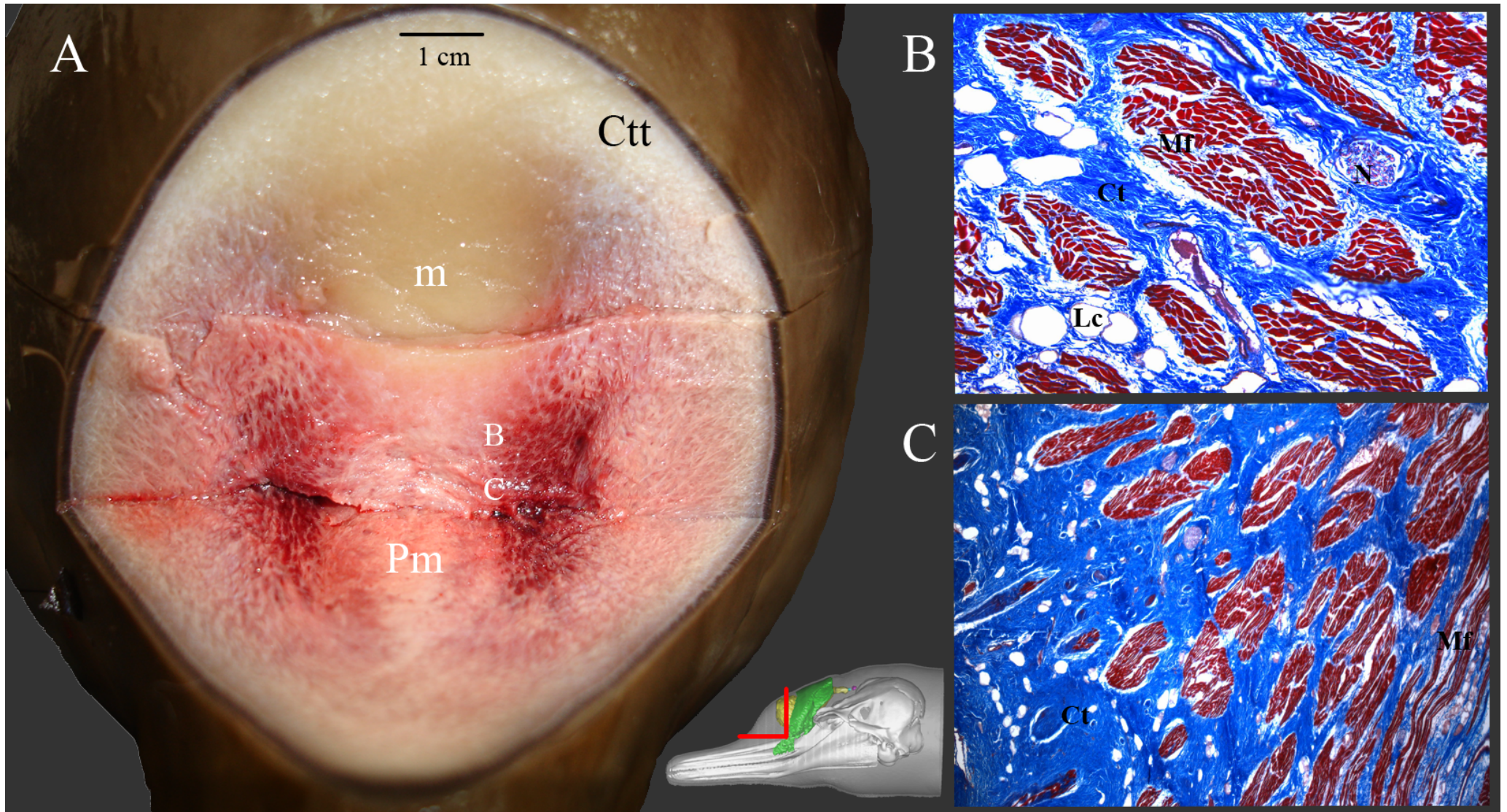


Fig 4. **A.** Frontal section of a neonate female (CBL: 18.7 cm) showing the rostral musculature below and around the melon (**m**). (**Ctt**=connective tissue theca, **Pm**=premaxillary bone). **B.** This image shows the rostral musculature associated with fat bodies and connective tissue just below the melon. (**Mf**=muscle fibers, **Ct**=connective tissue, **Lc**=lipidic cells, **N**=nerve). **C.** Close to the bone, the fat bodies seem scarce and the main structures are connective tissue (**Ct**), as well as longitudinal and transversal muscle fibers (**Mf**).

the gap formed between the connective tissue theca and the right melon. This gap, just anterior to the caudal portion of the premaxillary bone where the second layer of *M. maxillonasolabialis* is located (Huggenberger et al., 2010), extends to the anterior portion of both sides of the great melon in neonate specimen (Fig. 3). In addition, comparing the elevation angle of the *Bursae cantantes* between neonate (18.9°) and adult (16.9°), we see topographical changes of the biosonar apparatus throughout the ontogeny (Fig. 2A-B, 3E-F).

Premaxillary air sacs. These are invaginations of the nasal tract disposed just below the caudal part of the melon at both sides and are comparable to the delphinids, differing primarily in size (Mead, 1975). No significantly changes are found in this structure throughout ontogeny, except by size growth observed in our dissections (not documented).

Nasofrontal air sacs. These are located in the ventral invagination of tendinous part of the left maxillonasolabialis muscle (Fig. 1). The right nasofrontal sac is always bigger than the left side, and shows invaginations of the lateral wall of this diverticulum containing slips of the intrinsic musculature.

Vestibular air sacs (VS). The great asymmetry of franciscana dolphin's epicranial soft tissue is mainly marked by the high hypertrophy level, or "hyperdevelopment" (Schenkkan, 1972) of the VS (Cranford et al., 1996; Huggenberger et al., 2010). The right VS is delimited posteriorly by the ascendant process of maxilla and anteriorly by the line that passes transversally across the anterior end of the caudal premaxillary portion. Moreover, the rostral part of the right sac runs to the left side. In our dissections, it was possible to identify internal invaginations forming many small sacs on the anterodorsal profile of the right VS in all adult specimens (Fig. 5). This feature is present in the sub-adult specimen, but not well developed. In the dissected neonate specimens, the anterodorsal bound is smooth, without any invaginations, and convex. The ventrolateral profile also presents these internal invaginations although they are less developed in all newborn specimens. The anteroventral edge of the same sac changes from a convex shape in neonate specimens to a slight concavity to the left side in adults (Fig. 5). The caudal portion of the right VS changes both its form and arrangement in the epicranial complex throughout the ontogeny. In neonate specimens, the posterior edge of the right VS is round and never achieves the nuchal crest nor the lateral edge of the maxillary bone posterior part. On the other hand, adult specimens present the caudal profile of the right VS reaching the posterior limits of the nuchal crest, and the same VS runs close to the lateral dimensions of the maxillary bone. Comparing osteological material, the caudal portion of the maxillary bone has close similarity to the right VS development (Fig. 6). In both genders, this region of the maxillary bone posterior part. On the other hand, adult

specimens present the caudal profile of the right VS reaching the posterior limits of the nuchal crest, and the same VS runs close to the lateral dimensions of the maxillary bone.

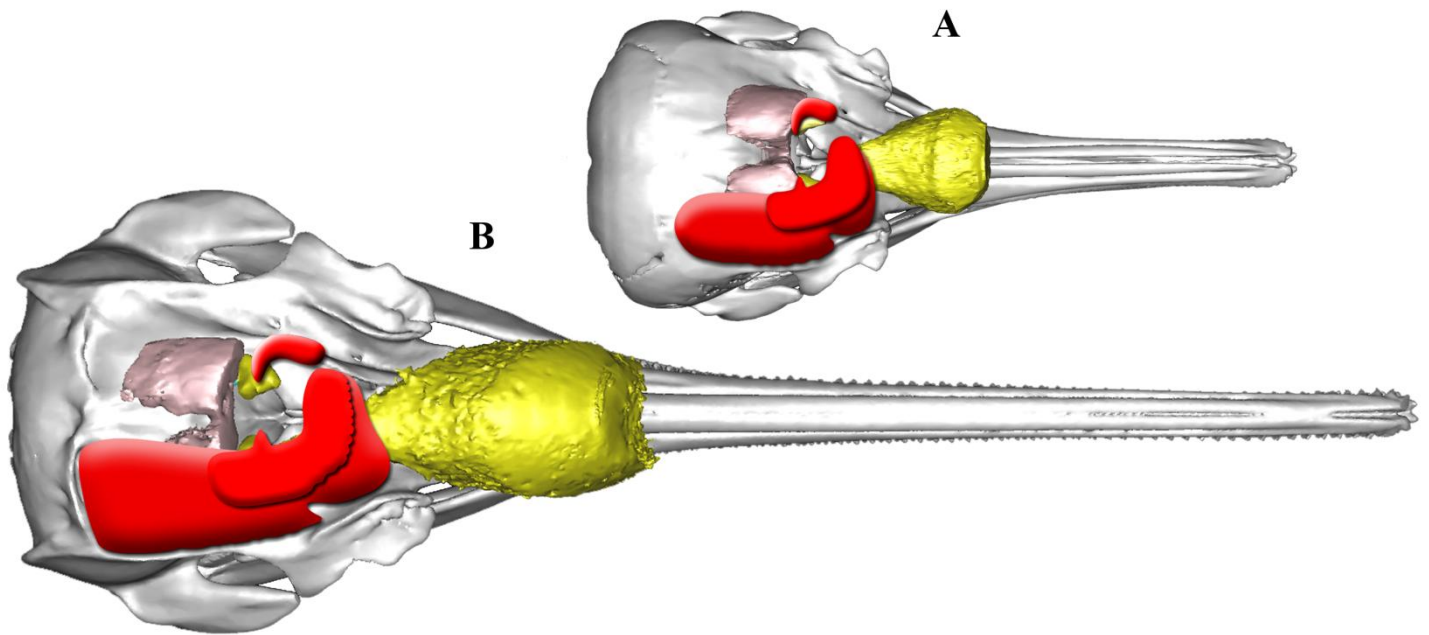


Fig 5. Dorsal view of franciscana dolphin's epicranial complex. In red, schematic representations of right and left vestibular air sacs (Vs). (right and left melon=yellow; tendinous part of *M. maxillonasolabialis*=pink) **A.** Neonate specimen showing a smoothed anterodorsal bound, convexed anteroventral bound, and a round posterior part of right Vs. **B.** Adult and sub-adult specimens present internal invaginations in the right Vs forming many small sacs on its anterodorsal profile. Posteriorly, the Vs reach the limits of the supraoccipital crest, and the same Vs runs close to the lateral dimensions of the maxillary bone.

Comparing osteological material, the caudal portion of the maxillary bone has close similarity to the right VS development (Fig. 6). In both genders, this region shows a round profile just before and on the immediate contact of this bone with frontal, supraoccipital and interparietal bones to form the nuchal crest (n=10, CBL range: 22.31-27.59cm) (Fig. 6A-B). When the maxillary bone reaches this crest, the profile shows a change in shape, becoming slightly round or straight on the transversal line of the body axis (n=57, CBL range: 27.68 cm-41.39 cm) (Fig. 6C-F). In addition, the lateral profile of the ascendant process of the maxilla, just after the orbit region, develops from a round or convex shape to a concave form at the line that transversally passes across the premaxillary bone posterior end. The premaxillary caudal part grows vertically from or below the line that passes through the anterior insertion of nasal bones (n=19, CBL range: 22.31-33.89cm) (Fig. 2A) surpassing this line throughout the ontogeny (n=48, CBL range: 27.68-42.27cm) (Fig. 2B).

Development of sound reception apparatus

Lower jaw. In *Pontoporia blainvillei*, the rostrum formation presents topographical changes mainly on alignment with the skull, and shows distinct development timing between its upper and lower portions. In young specimens, the ventral profile of each lower jaw ramus is convex, with the

ventral process formed by the posterior end of mandibular symphysis projected ventrally (Fig. 2A-B, 7). This process ventrally passes through the line between the angular process of the lower jaw and the anterior tip of rostrum (n= 23, CBL range: 22.31-33.89cm) (Fig. 2A, 8C). Throughout the ontogeny, however, the rostrum seems to change its curvature angle when it grows distally, and the profile turns from a convex profile of the mandible to a concave angulation of the same structure. This feature is marked by the surpassing of the ventral process formed by the posterior end of mandibular symphysis through the line that passes between the angular process and the mandibular tip (n= 46, CBL range: 27.68-42.27cm) (Fig. 2B, 8D).

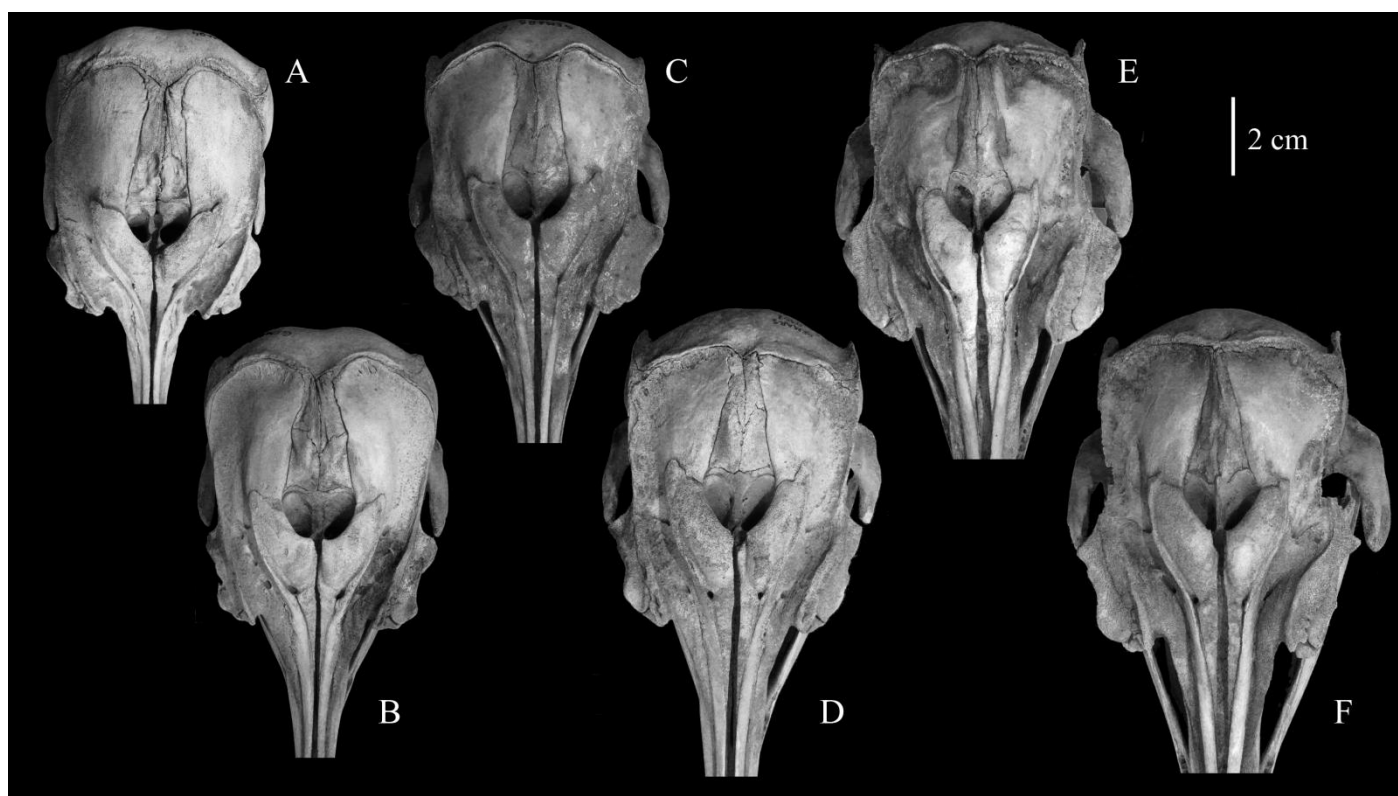


Fig 6. Dorsal view of six skulls in distinct developmental stages including a neonate (A), a calf (B), two sub-adult (C, D) and two adults (E, F) showing the modifications of the ascendent part of the maxillary bone and the formation of the nuchal crest. A. GEMARS 777, CBL: 22.5 cm. B. GEMARS 533, CBL: 27.6 cm. C. GEMARS 1195, CBL: 30.2 cm. D. GEMARS 452, CBL: 32.7 cm. E. GEMARS 627, CBL: 41.4 cm. F. GEMARS 420, CBL: 41.5 cm.

The dental alveolus of lower jaw develops from posterior to anterior part of the tooth row, like the upper portion of rostrum (*i. e.* maxilla and premaxilla). First, a series of interalveolar septa begins to develop along the posterior walls of alveolar grooves, not surpassing the first half of the alveolar edge (n=29, CBL range: 22.31-35.17cm) (Fig 9). The developed dental alveolus is characterized by the complete closure of interalveolar septa, and begins to develop from the posterior portion of alveolar grooves to the half of the same row (n=19, CBL range: 30.13-39.79cm), passing by the first half of the alveolar edge (n= 9, CBL range: 27.59-40.97cm) and then

all dental alveolus can be seen as well formed (n=13, CBL range: 36.23-42.27cm). Curiously, all specimens that present only interalveolar septa in the posterior end of lower jaw alveolar row don't show any stage of development of this feature in maxillary tooth row. Moreover, the lower jaw alveolar grooves are always more developed than upper tooth rows; and the beginning of maxillary alveolus formation (with dental alveolus developed just in the first half of tooth row) was found just in specimens with well-developed dental alveolus before or after the first half of the alveolar tooth row (n= 7, CBL range: 33.35-39.79 cm).

The **mandibular fat bodies (Mfb)** show a slight elongation toward the anterior portion (Fig. 7). The differences between the axial lengths of both Mfb in the neonate (right: 61,03mm; left: 55,45mm) and the adult (right: 121,1mm; left: 117,61mm) specimens represent this anterior elongation when we compare the neonate's width variation (right: 10,66mm; left: 12,19) with that of the adult (right: 15,51mm; 14,39mm). In addition, a decrease in density (HU) means in the adult Mfb was observed (Table 2). The thin lipidic lamina, or external mandibular fat bodies (Norris, 1968), was observed in neonate and adult specimens but not pictured in 3D images. In both anatomic geometry descriptions, it is possible to see a gap on Mfb that consists of the passage of the trigeminal nerve that cannot be perceived by CT-scans (Fig. 7C-D).

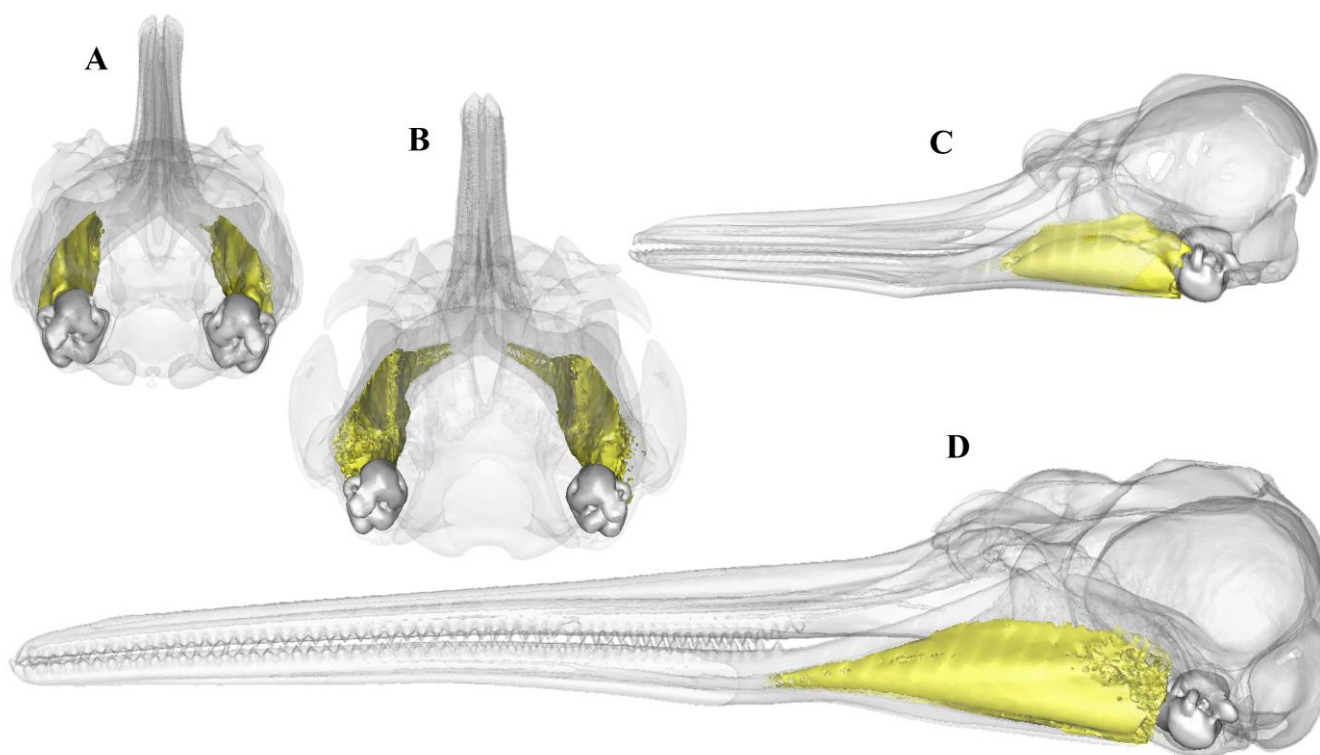


Fig 7. Posterior (A-B) and left lateral (C-D) views of neonate (CBL: 19.4 cm) and adult's (CBL: 38.7 cm) sound reception apparatus showing the skull and the lower jaw (transparent white), each mandibular fat body (yellow) and the timpano-periotic complex (dense white). On the lateral view (C-D), topographical modifications of the lower jaw can be seen by the changes on its curvature angle when it grows distally, and the profile turns from a convex curvature to a concave angulation. In both views, the timpano-periotic complex shows low differentiation related to the mandibular fat bodies and the lower jaw.

Timpano-periotic complex. These structures show fewer modifications than all structures involved in the biosonar anatomy. After birth, there is a decrease in its relative size proportionally to the skull (Fig. 7). As to volume values, we see that, although neonate franciscana dolphins' timpano-periotic complex continues to develop, it already corresponds to over 70% of the adult structure (Table 2).

DISCUSSION

Franciscana dolphins represent the only "river-dolphin" form among Odontoceti that inhabit the marine environment and is endemic of coastal waters of Brazil, Uruguay and Argentina (Siciliano et al., 1994; Crespo et al., 1998). Siciliano *et al.* (2002) pointed out that environmental conditions like water transparency and depth may represent the primary factors for two gaps on the distribution of this group, since there are no records for this species within the range of distribution. According to the authors, *Pontoporia blainvillei* exhibits preference for turbid waters, like those enhanced by "big rivers". Phylogenetic studies reveal that the morphological features shared by the so-called river dolphins (*i.e.* long and narrow rostrum, low triangular dorsal fin, flexible neck, small eyes and size) although convergente, represent ecological adaptations for river environments. Trophic studies of this species indicate, at least, 76 prey types including fishes (~80%), crustaceans (~9%) and molluscs (~8%) (Danilewicz et al., 2002b).

Franciscanas from the southern population feed essentially from benthic species while northern populations tend to forage on more pelagic species (Di Benedetto and Ramos, 2001). Moreover, older animals show great variability of food items compared to weaned calves (Rodríguez et al., 2002). In addition, the great diet variation through their ontogeny reveals an estuarine dependence for young specimens, and it is basically composed of shrimps. The first predation activities start at a very young age (2.5-3 months) and at length of approximately 75 cm for northern argentine population. The estimate feeding independence starts at the age of 7 months, when they reach 95 cm in length (Danilewicz et al., 2002b). Riccialdelli et al. (2013) pointed that the ontogenetic diet shift in Commerson's dolphin may be related to the improvement in foraging skills and the expansion of habitats by older animals, as well as the increase in diving capabilities.

The changes observed in the biosonar anatomy in *Pontoporia blainvillei* may complement this ontogenetic diet shift hypothesis and can represent an important tool to investigate the increase in foraging capabilities. The fact that shrimps are the most important diet component in the first predation activities may be related to the limitation of young individuals on the first foraging behaviors. The improvement of biosonar capabilities and the great changes observed in the mainly involved structures throughout the ontogeny may result in the increase in diet components in sub-

adult and adult specimens, which begin to search larger and fast prey, like some fishes and molluscs (Rodríguez et al., 2002).

Gardner *et al.* (2007) pointed that the mastery of echolocation in odontocetes is not inherited, but developed in a combination of time, physiological maturation and learning. The small size and the “countershaded” coloration (Yablokov, 1963; Trimble and Praderi, 2006), along with their rare aerial displays make it difficult to study franciscana dolphins in the wild (Bordino et al., 1999; Melcón et al., 2012). Here, we will discuss some features related to the life-story of this species in the light of previous knowledge about odontocetes's biosonar functional anatomy.

Topographical changes on franciscana's biosonar morphology throughout ontogeny may functionally represent a great change on sound production mechanism. McKenna *et al.* (2012) suggested that the biosonar capabilities are straightly related to the melon morphology among Odontoceti species. In addition, the connective tissue and the rostral muscles act on the melon shape for sound adjustments (Mead, 1975; Harper et al., 2008). The trumpet form that the posterior part of the right melon in *Pontoporia* presents may be modulated by related muscles to obtain a straight beam for sound propagation, resulting in an elongated lens for conducting and filtering the high intensity pulses produced by MLDB complex (McKenna et al., 2012). The presence of rostral musculature in neonate specimens may represent some mastery dependence for using the right-side pathway. In contrast, adult specimens show less mobility without rostral muscles. On the other hand, the left melon reveals similar shape in young and adult specimens and can represent the early mechanism of sound pathway in their life-stories. Each melon corresponds to a distinct sound pathway and is functionally different from its counterpart. In contrast with other dolphins, *Pontoporia blainvillei* is the only odontocete that presents two functional melon pathways. The elongation of the right melon may result in a single narrow signal.

The nasal air sacs of a dolphin's head are important acoustic reflectors in echolocation and sound beam formation (Aroyan et al., 1992). These air spaces are extremely variable, both within a single species and between species (Mead, 1975; Dormer, 1979; Cranford et al., 1996). The “hyperdevelopment” of the right vestibular air sac isolates all sound produced by the right MLDB complex by dorsally reflecting the sound. Another species of the so-called river dolphin, *Platanista gangetica* (Odontoceti: Platanistidae), does not exhibit any vestibular air sacs, although the maxillary crest can reveal functional convergence (Pilleri, 1979). The ascendant part of maxilla develops above the epicranial complex (see Pilleri, 1979; Fig. 10), and exhibits an extensive air sinus which does not communicate with the nasal cavity, but with the periotic sinus and tympanic cavity instead.

The sound reception mechanism may present the same variability as found for sound production apparatus, which is well correlated to the epicranial complex shape. Odontoceti's mandibles serve a variety of functions, mainly feeding and hearing (Barroso et al., 2012), respectively on the anterior and posterior portions of the lower jaw (Perrin, 1975). The most accepted hypothesis for the sound reception pathway was proposed by Norris (1968), according to which the signals pass through the thin external lamina of the mandibular ramus. Cranford et al. (2008a) propose that the ultra-sounds are received by the gular region, where the sound pass below and between the lower jaws, passing through an opening created by the absence of the medial bony wall of the posterior mandibles, mandibular window (Norris, 1968), and then to the bony ear complexes through the internal mandibular fat bodies. Although this idea has not yet been tested in captivity dolphins, many authors have investigated the physical properties related to sound propagation in the mandibular fat bodies (Bullock et al., 1968; McCormick et al., 1970; Møhl et al., 1999; Krysl et al., 2006; Cranford et al., 2008a). In our work, although we are unable to physically demonstrate the acoustical properties of each Mfb in both specimens, the great expansion of the Mfb in adult specimens may increase the sound reception area according to the gular reception theory. The decrease in Mfb density means, in the adult specimen, can represent a specialization of this structure to receive higher pitch frequencies sound reception, with a more effective sound energy decrease for the middle-ears. Although our techniques are unable to detect more precisely some changes on the timpano-periotic anatomy like the ossicles (malleus, incus and stapes) (Cranford et al., 2010) and the cochlea morphology (Ketten, 1994), we believe that the limitations in the ultra-sound reception system in young individuals may result from other parameters observed in this work. Another sound reception hypothesis is that the ultra-sound frequencies used for echolocation are received by the tooth row (Dobbins, 2007), although experimental studies in this respect have never been conducted.

The hypothesis about the advent of echolocation in several vertebrate groups is often associated with environment changes and morphological evolution (Teeling et al., 2005; Lindberg and Pyenson, 2007). Lindberg and Pyenson (2007) stated that the origin of echolocation in odontocetes is related to nocturnal feeding on diel migrating cephalopods and other prey items during the Paleogene. According to the authors, the great morphological changes on biosonar anatomy was documented in fossil records during the Oligocene, like the transition from heterodont to more homodont dentition (Fordyce, 2003) and the first major encephalization increase (Marino et al., 2003; Marino et al., 2004). Moreover, Werth (2006) suggested that suction feeding in odontocetes is consistent with the decline of shelled cephalopods observed in late Oligocene, which may produce stronger echoes than soft-bodied cephalopods (Monks, 2002). Head modifications in some

Odontoceti species like blunt head, short jaws and reduced dentition (the amblygnathous odontocetes: *e. g.* Genera *Globicephala* and *Kogia*) (Werth, 2006), as well as prey-stunning behavior in some cases (Zagaeski, 1987; MacKay and Pegg, 1988) are features related to suction-feeding evolution in this group (Werth, 2006). Toothed whales (odontocetes) show a higher variability on the lower jaw feeding apparatus, which includes the tooth row if present, than the "sound reception" portion (Barroso et al., 2012). In general, smaller dolphins and porpoises have more teeth (*e. g.* *Stenella longirostris*, *Stenella coeruleoalba*, *Delphinus delphis*) (Werth, 2006) and have a diet frequently based on nocturnal preys at deep diving (Perrin and Gilpatrick Jr, 1994; Wursig et al., 1994). Franciscana dolphins do not present deep dive, but have evolved evolve a biosonar bauplan with a great number of teeth (50 pairs on each lower jaw ramus), like an amplified sensor for turbid waters.

The lower jaw is innervated by the trigeminal nerve (Fig. 9) which, along with facial, glossopharyngeal and vagus nerves, completes the four of the 11 cranial nerves that contain both the mechanic and sensitive functional components (Ridgway, 1990). Oelschläger (2008) pointed out that the well-developed trigeminal nerve in dolphins may be involved in the sonar generation and emission by the forehead innervation of this nerve; however, nothing has been mentioned about the sensitive mandibular part of the trigeminal system (Ferguson, 1978). Dolphins' large brain size has attracted great attention from several authors who investigate how they evolve and develop this high encephalization (Marino et al., 2004; Huggenberger, 2008; Oelschläger, 2008). Few works have attempted to understand trigeminal system functions in dolphins' heads (Ridgway, 1990; Oelschläger, 2008). Although the "teeth reception theory" lacks further experimental studies, we believe that the ultra-sounds involved in echolocation behavior are received in the tooth row and perceived by the mandibular part of trigeminal system, making sense in the brain. Furthermore, we do not exclude the "gular reception theory" because we relate this idea to the communication sounds, or the functionally distinct lower frequencies whistles. As pointed out by Oelschläger (2008), "we have only just begun to learn what dolphins really do with their large brains".

In this work, the alveolar grooves formation has revealed to be a good tool to describe and compare the lower jaw morphology throughout its ontogeny. The fact that some of the studied adult specimens exhibit an undeveloped alveolar tooth row in the lower jaw, and most sub-adult specimens show only the first half well-formed (Fig. 8), reflects the offset development of this structure compared to the other main biosonar structures described in this study. Although we have been unable to correlate such a peculiar development of the lower jaw with the massive caught of young specimens in fishery gill nets, the structure involved in the sound reception

mechanism is indeed not as well-developed in neonate specimens as it is in sexually matured individuals (see comparative material) (Danilewicz et al., 2002a). This timing on lower jaw formation can be a result of an evolutionary process that is guided by divergences on the rates of development of related lineages.

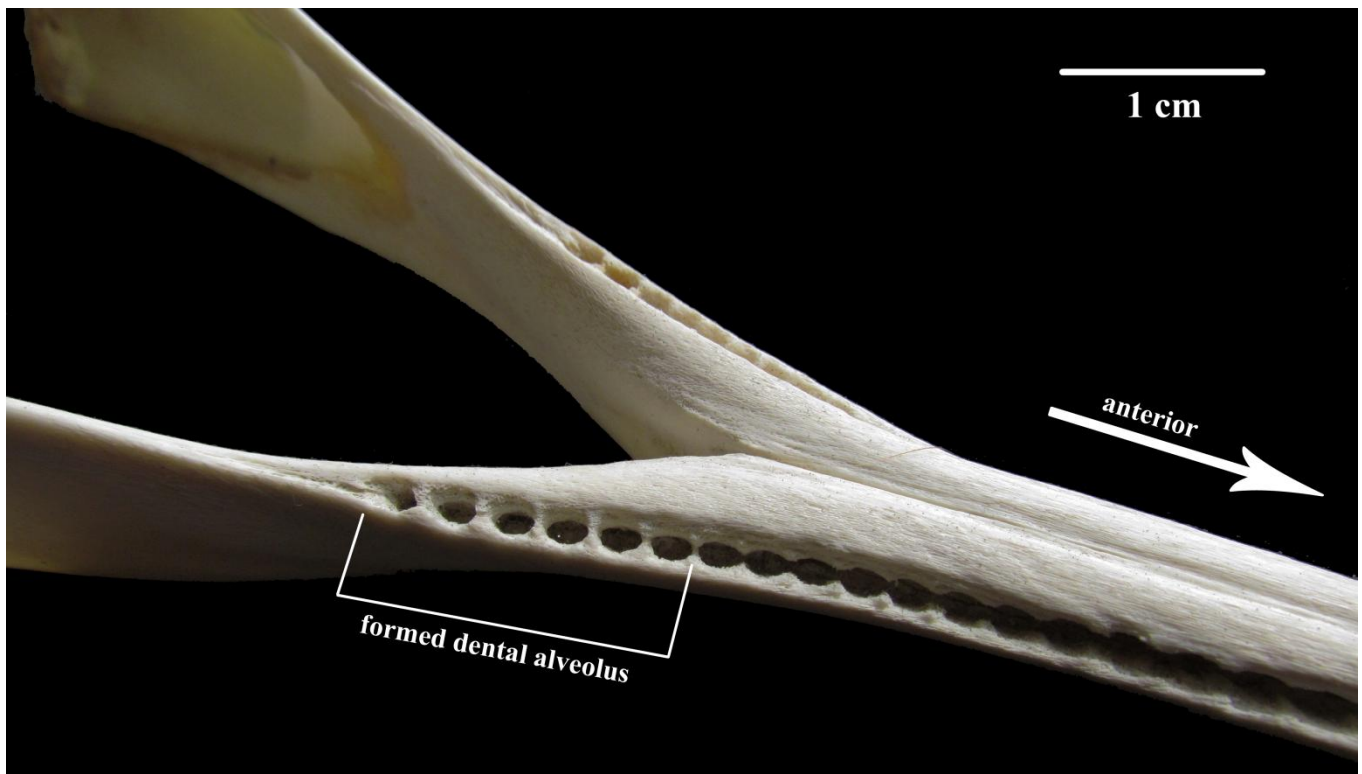


Fig 8. Diagonal view of sub-adult mandibular bone showing six well formed dental alveolus followed by a gradient of undeveloped dental alveolus, which develops anteriorly to the tip of alveolar grooves. GEMARS 1403, CBL: 38.36 cm.

Progenetic evolution is a truncation of somatic development at an immature stage caused by accelerated sexual maturity relative to a nonpedomorphic ancestor (Gould, 1977; Alberch et al., 1979). Galatius *et al.* (2011) suggested that the pedomorphic characteristics described in phocoenids (*i.e.* adult size, amount of allometric development, and degree of fusion of skull sutures and epiphyses) are features related to harbor porpoise's (*Phocoena phocoena*) adaptation for coastal habits. The great differences found on the formation timing of the structures involved in franciscana's biosonar may reflect a similar evolutionary process. The long narrow rostrum of the "old-rivers", for example, may represent an outcome obtained by some toothed whales that diverge from an ancestor without "riverine-snout" by offset formation timing on anterior portions of lower jaw, premaxillary and maxillary bones.

Franciscana dolphin is one of the smallest toothed whales and presents geographic variation, including size and cranial proportions (Kasuya and Brownell Jr, 1979; Pinedo, 1991; Ramos et al., 2000), parasite loads (Aznar et al., 1995), molecular data (Hamilton et al., 2000; Lázaro et al.,

2006), and reproductive strategies (Kasuya and Brownell Jr, 1979; Danilewicz, 2003). Distinct reproductive timing is observed among northern populations (Kasuya and Brownell Jr, 1979; Danilewicz et al., 2000). Moreover, northern populations present smaller asymptotic lengths than southern populations (Barreto and Rosas, 2006). It seems that *Pontoporia blainvillei* presents similar evolutionary parameters as Galatius et al. (2011) found in *Phocoena phocoena*. Our descriptions may be useful for investigating the geographic variation throughout franciscana's distribution using the developmental character construction proposed by Fink (1982) which is awaiting further investigations.

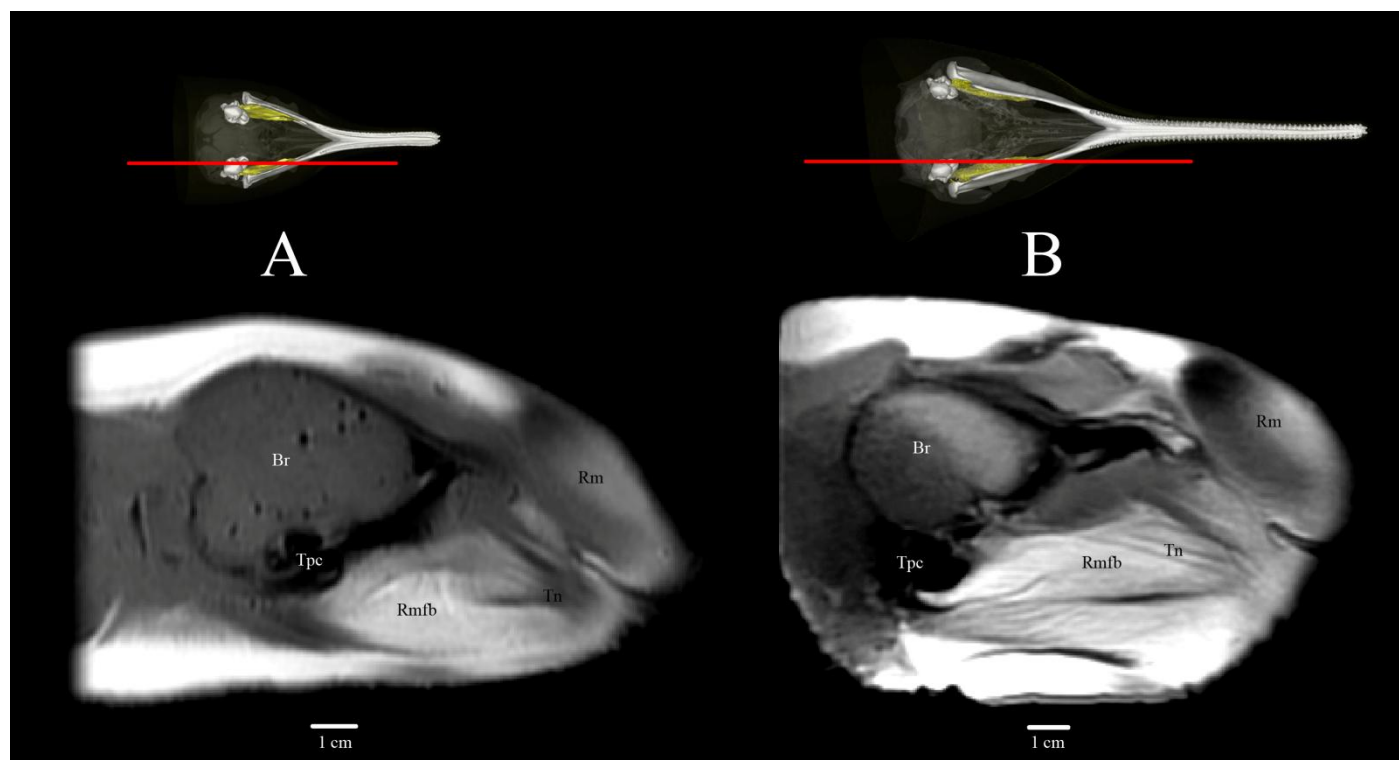


Fig 9. Midsagittal MRI scans of neonate (A) and adult (B) franciscana dolphin heads. (Br=brain, Rmfb=right mandibular fat body, Rm=right melon, Tn=trigeminal nerve, Tpc=timpano-periotic complex).

Although we must be careful with interpretations about functional anatomy (Cranford et al., 1996; McKenna et al., 2012), the peculiar development of franciscana's biosonar can be associated with the massive mortality of young specimens in fishery activities. In fact, *Pontoporia blainvillei* shows the shortest life-story among odontocete species (21 years) and presents high incidentally caught of young individuals (Danilewicz et al., 2000). The great mortality surpass 1400 specimens dead by year on fishery activities in Rio Grande do Sul-Brazil and Uruguay area (FMA III), showing the critic situation of this species (Secchi et al., 2004). It's possible that chemically enhanced gill nets are not effective for this species, distinctly as reported to *Phocoena phocoena* (Cox and Read, 2004). Human impacts and the peculiar features of sound transmission and reception apparatus in *Pontoporia blainvillei* are not only accelerating the perish process of this group, but showing that

we (*Homo sapiens*) have been unable to make sustainable use of the ocean despite the fact that we still cannot understand it in all its complexity.

Comparative osteological material examined: Females GEMARS 1169 (CBL: 23.00 cm, BL: 91.9cm), GEMARS 0777 (CBL: 22.5 cm, BL: 95cm), GEMARS 0502 (CBL: 25.35 cm, BL: 105.5cm), GEMARS 1219 (CBL: 31.13 cm, BL: 117cm), GEMARS 1080 (CBL: 32.28 cm, BL: 80cm), GEMARS 0596 (CBL: 31.99 cm, BL: 113.5cm), GEMARS 1029 (CBL: 32.05 cm, BL: 111.5cm), GEMARS 1135 (CBL: 31.98 cm, BL: 91.5cm), GEMARS 1117 (CBL: 33.89 cm, BL: 118.3cm), GEMARS 0745 (CBL: 33.80 cm, BL: 121cm), GEMARS 0253 (CBL: 38.92 cm, BL: 142 cm), GEMARS 0779 (CBL: 37.39 cm, BL: 149cm), GEMARS 0155 (CBL: 37.45 cm, BL: 145cm), GEMARS 0128 (CBL: 36.13 cm, BL: 147.5cm), GEMARS 1091 (CBL: 36.178 cm, BL: 131.5cm), GEMARS 0391 (CBL: 38.17 cm, BL: 143cm), GEMARS 0177 (CBL: 39.40 cm, BL: 140cm), GEMARS 0179 (CBL: 37.45 cm, BL: 133cm), GEMARS 0440 (CBL: 39.79 cm, BL: 150cm), GEMARS 0748 (CBL: 39.13 cm, BL: 141cm), GEMARS 0780 (CBL: 40.97 cm, BL: 156cm), GEMARS 0482 (CBL: 37.83 cm, BL: 140cm), GEMARS 0509 (CBL: 40.18 cm, BL: 151 cm), GEMARS 0420 (CBL: 41.51 cm, BL: 154cm), GEMARS 1222 (CBL: 41.77 cm, BL: 155.5cm), GEMARS 0252 (CBL: 42.27 cm, BL: 162cm), GEMARS 0627 (CBL: 41.39 cm, BL: 160.5cm). **Males** GEMARS 0336 (CBL: not measured, BL: 102 cm), GEMARS 1170 (CBL: 22.31 cm, BL: 92.5cm), GEMARS 1160 (CBL: 24.09 cm, BL: 92.5cm), GEMARS 1376 (CBL: 25.38 cm, BL: 99.5cm), GEMARS 0533 (CBL: 27.59 cm, BL: 27.59cm), GEMARS 0424 (CBL: 23.42 cm, BL: 97.5cm), GEMARS 1290 (CBL: 27.51 cm, BL: 95cm), GEMARS 0423 (CBL: 25.49 cm, BL: 112cm), GEMARS 1177 (CBL: 27.59 cm, BL: 96cm), GEMARS 0352 (CBL: 27.68 cm, BL: 103cm), GEMARS 1294 (CBL: 30.16 cm, BL: 112cm), GEMARS 0381 (CBL: 31.66 cm, BL: 31.66 cm), GEMARS 1195 (CBL: 30.20 cm, BL: 107cm), GEMARS 0532 (CBL: 34.35 cm, BL: 121cm), GEMARS 0437 (CBL: 30.51 cm, BL: 95cm), GEMARS 0456 (CBL: 33.04 cm, BL: 119cm), GEMARS 0475 (CBL: 32.36 cm, BL: 117.5cm), GEMARS 0977 (CBL: 32.89 cm, BL: 118cm), GEMARS 0323 (CBL: 31.81 cm, BL: 116.5cm), GEMARS 1216 (CBL: 31.85 cm, BL: 114cm), GEMARS 0508 (CBL: 30.13 cm, BL: 117cm), GEMARS 1197 (CBL: 32.59 cm, BL: 125cm), GEMARS 0604 (CBL: 33.20 cm, BL: 122cm), GEMARS 0452 (CBL: 32.74 cm, BL: 124cm), GEMARS 0150 (CBL: 32.09 cm, BL: 122cm), GEMARS 1299 (CBL: 31.54 cm, BL: 117.3cm), GEMARS 1193 (CBL: 35.17 cm, BL: 134.5cm), GEMARS 0490 (CBL: 33.35 cm, BL: 127.5cm), GEMARS 1251 (CBL: 35.97 cm, BL: 127cm), GEMARS 1403 (CBL: 38.36 cm, BL: 137cm), GEMARS 1238 (CBL: 37.69 cm, BL: 137cm), GEMARS 0761 (CBL: 36.27 cm, BL: 130cm), GEMARS 1127 (CBL: 36cm, BL: 126cm), GEMARS 1081 (CBL: 38.35 cm, BL: 136cm), GEMARS 1289 (CBL: 37.24 cm, BL: 128.5cm), GEMARS 0473 (CBL: 36.36 cm, BL: 126cm), GEMARS 0362 (CBL: 36.23 cm, BL: 135cm), GEMARS 0742 (CBL: 36.83 cm, BL: 138cm), GEMARS 0314 (CBL: 38.06 cm, BL:

132.5cm), GEMARS 1121 (CBL: 38.24 cm, BL: 146cm), GEMARS 0408 (CBL: 37.72 cm, BL: 150cm), GEMARS 1124 (CBL: 36.4 cm, BL: 144cm).

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Capítulo III

CONSIDERAÇÕES FINAIS



"Now, my suspicion is that the universe is not only queerer than we suppose, but queerer than we can suppose."

Haldane'1927

Desde a comprovação do sistema de ecolocalização em odontocetos por Norris *et al.* (1961), uma corrida entre anatomistas (Norris, 1968; Cranford *et al.*, 1996; Huggenberger *et al.*, 2008) e físicos (Dobbins, 2007) percorreram esse meio século tentando desvendar as estruturas anatômicas capazes de servir como ferramenta para o sofisticado sonar biológico dos golfinhos; bem como procurando maneiras de reproduzi-los, respectivamente. Ao longo desses anos, as tecnologias aplicadas nesses estudos sofisticaram-se de modo que o hoje é possível avaliar estruturas moles e de difícil "acesso" por parte da técnica convencional de dissecação à mão livre. Embora a utilização da tomografia computadorizada seja uma novidade científica e de grande atenção por muitos autores (Cranford and Amundin, 2003; Cranford *et al.*, 2008a; Cranford *et al.*, 2008b; Huggenberger *et al.*, 2008; Cranford *et al.*, 2010; Huggenberger *et al.*, 2010; Cranford, 2011; Barroso *et al.*, 2012; McKenna *et al.*, 2012) a "dissecação" das imagens torna a utilização dos *softwares* de manipulação de imagem tanto subjetivo quanto uma descrição a partir de dissecações à mão livre, com a experiência do próprio observador. Essa subjetividade na interpretação das imagens já foi abordada na literatura (Cranford *et al.*, 2008b), porém a baixa quantidade de especialistas nesse tipo de pesquisa impossibilita comparações. De fato, a experiência do observador vai ser o fator "chave" da descrição em ambas técnicas de dissecação (*i. e.* material biológico e imagem).

Nesse trabalho, as principais estruturas envolvidas no sistema de produção e recepção do som em *Pontoporia blainvillei* se mostraram não só peculiares em relação à forma encontrada para os indivíduos nos diferentes estágios ontogenéticos, mas também pelo processo de como essas estruturas se desenvolvem. As estruturas, tanto do aparato produtor quanto receptor do som, se desenvolvem em diferentes taxas de desenvolvimento ("*timing*"), como por exemplo a *Bursae* cantantes, que é dividida em bursa posterior e anterior. A bursa posterior é tratada na literatura como homóloga ao órgão espermaceti das cachalotes e a bursa anterior geralmente é associada à porção posterior do *melon*. Essas duas estruturas se desenvolvem em taxas diferentes em *Pontoporia blainvillei* visto as diferenças das proporções a partir das medidas de volume e superfícies, assim como o desenvolvimento do rostro em relação ao complexo timpano-periótico. As bulas timpânicas são as estruturas que apresentam o desenvolvimento mais precoce dentre todas as estruturas envolvidas no biosonar. Ainda, o desaparecimento da musculatura rostral logo abaixo da porção anterior do *melon* revela o quanto as modificações ontogenéticas no biosonar da toninha podem ser drásticas e marcantes à luz da anatomia funcional.

O desenvolvimento alveolar em *Pontoporia blainvillei* foi útil para descrever as modificações da mandíbula, e vieram desses resultados algumas hipóteses atreladas a recepção do som o qual foram discutidas no Capítulo II (*i. e.* recepção de sons de alta frequência pelos dentes). O fato de que a

maior mortalidade de indivíduos em redes de pesca está associado a indivíduos juvenis (menos de três anos), inevitavelmente fui a procura de estruturas que pudessem estar associadas a uma funcionalidade ineficaz. Embora todas as hipóteses de funcionamento das estruturas anatômicas nunca serão científicas até que se teste cada uma delas, elas são importantes para instigar outros pesquisadores a comprová-las, como, por exemplo, o histórico do conhecimento à respeito da ecolocalização em cetáceos com as suspeitas do fenômeno na década de 50, e a posterior comprovação em 1961 pelo professor Dr. Kenneth Norris e seu grupo de pesquisa (Kellogg et al., 1953; McBride, 1956; Schevill and Lawrence, 1956; Norris et al., 1961).

Coincidências ou não, quatro motivos me limitam a não acreditar que os dentes estão envolvidos no sistema de ecolocalização em odontocetos: (1) o registro fóssil que demonstra as marcantes especializações no crânio para portar uma complexa região facial possivelmente envolvida na ecolocalização já apresenta uma certa "especialização" nos dentes, em que desaparecem as suas especializações para trituração mecânica do alimento (heterodontia) e os dentes torna-se todos iguais, padronizados (homodontia) (Fordyce, 2003), com exceção do boto-cor-de-rosa (*Inia geoffrensis*) que possui molares; (2) a alta variação morfológica encontrada no *melon* (a "lente" que modula o som e vai caracterizar o tipo de som produzido) ao longo das espécies de odontocetos não condiz com a baixa variação encontrada para a possível porção "receptora" do som na mandíbula (janela acústica) (Barroso et al., 2012), ao contrário da porção posterior, ou aparato alimentar; (3) em geral, odontocetos que se alimentam no fundo e a noite possuem maior número de dentes (*i. e. Delphinus delphis, Stenella attenuata, Stenella longirostris*) e o fato pode estar relacionado ao hábito e utilização do biosonar em ambientes com pouca visibilidade, como em águas turvas (*Platanista gangetica, Lipotes vexillifer, Pontoporia blainvillei*); (4) o nervo trigeminal em cetáceos.

Se comprovada a hipótese de recepção de sons de alta frequência pelos dentes, um novo conceito de receptor biológico será conhecido. A mudança mais drástica será em relação à funcionalidade do complexo timpano-periótico. As bulas timpânicas não estão envolvidas no sistema de ecolocalização, pois a inervação dos dentes faz parte do grande nervo trigeminal que, do cérebro, inerva a mandíbula inteira; diferentemente do nervo vestibulo-cochlear que liga a bula timpânica ao cérebro. São dois caminhos de nervos sensoriais que podem ter evoluído independentemente nesse grande grupo, de diferentes maneiras em mysticetos e odontocetos. Recentemente, Pyenson *et al.* (2012) descobriram um órgão sensorial na ponta da mandíbula de uma baleia jubarte (*Megaptera novaeanglie*), e dizem que deve estar associada aos movimentos da mandíbula no comportamento de captura de alimento por engolfamento de grandes quantidades de água krill. Em odontocetos, a porção anterior da inervação do nervo trigeminal evoluiu de diversas formas. Eu imagino um grande grupo que, em uma maneira humanizada de pensar, evoluiu com "dor de

dente". Talvez não uma dor, mas uma alta sensibilidade que assume a porção anterior da mandíbula a região do biosonar que mais associa a característica do som recebida com a anatomia do organismo. A toninha possui o melon mais alongado de todos odontocetos, devido a extrema assimetria do lado direito. Essa lente conduz o som em uma forma de feixe estreito capaz de atingir 148 KHZ em pulsos ultrasônicos. Uma mandíbula com maior superfície de contato seria, e é, o melhor receptor para um sonar com essa característica, a toninha é um dos cetáceos que mais tem dentes (cerca de 200). Outros grupos possuem um ou nenhum par de dentes, os zífideos (Odontoceti: Ziphiidae). Acredito que o nervo trigeminal evoluiu diferentemente nas diferentes linhagens dos cetáceos ecolocalizadores. Entre elas, o nervo pode ter evoluído de tal sensibilidade que não foram necessários os dentes para realizar a ecolocalização. Esses animais vivem somente em águas muito profundas onde se alimentam preferencialmente de grandes lulas por sucção (Johnson et al., 2004). Nesses grupos, como em *Ziphius cavirostris* (Evans and England, 2001; Cranford et al., 2008b), o nervo trigeminal pode ser tão sensível e adaptado a um ambiente sem muitos ruídos que uma bomba sonora pode provocar um colapso no cérebro e eventos em massa, como reportado na literatura.

Os assobios ("*whistles*"), os quais são sons utilizados por odontocetos para socialização, são percebidos pela bula timpânica. Isso explica porque mysticetos e odontocetos possuem a bula timpânica isolada do crânio por um *sinus* de ar, mesmo a estrutura não fazendo parte do sistema de ecolocalização. Na minha concepção, apenas os sons (pulsos sonoros) atrelados à ecolocalização estão associados à hipótese proposta.

Embora alguns autores afirmem que a toninha não realiza sons de socialização (assobios) (May-Collado et al., 2007), eu acredito que ninguém nunca conseguiu gravá-los e é possível que os 148 KHz possam estar atrelados à esses tipos de som. Talvez, com o advento de hidrofones mais especializados poderemos desvendar ainda mais capacidade dessa espécie (Cranford et al., 2008a).

Acredito cada pesquisador que dedica a vida em tentar entender como funciona o biosonar dos odontocetos sempre ilustra em sua mente sempre tenta imaginar como um mamífero (nós) que "aprendeu" a se comunicar e se orientar através do som no ambiente aquático. Tentar compreender como um animal se torna consciente do ambiente em sua volta (e consegue agarrar uma presa que ou nada muito rápido ou só aparece à noite) com a mesma estrutura do sistema nervoso que na espécie humana evoluiu simplesmente para sentir dor, é impossível. Impossível também, é imaginar como não só o animal aprende a utilizar esse sistema, mas como a mãe aprende a ensinar o filhote. Provavelmente, a mãe golfinho deve utilizar um sistema de aprendizado por um certo tipo de condicionamento (Pavlov, 1927), por isso o longo acompanhamento materno (Hendry, 2002).

Por fim, acredito que as novas ferramentas de investigação do biosonar em odontocetos como a tomografia computadorizada e ressonância magnética podem trazer resultados importantes para a educação ambiental, no sentido de chamar a atenção da problemática da toninha de uma forma que seja atrativo ao público em geral. Embora a toninha seja conhecida a anos por muitos pesquisadores que vêem a problemática crescer, o problema parece aumentar. O maior resultado desse trabalho é que juvenis possuem muita debilidade nas primeiras fases da vida; e que onde houver rede de emalhe, provavelmente haverá morte de toninhas. A exclusão da pesca em algumas áreas prioritárias é, possivelmente, a única forma de proteger a espécie da extinção. Salve a toninha!

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