EVOLUCIÓN DE LAS ESTRUCTURAS ASOCIADAS A LA ECOLOCALIZACIÓN EN DELFINES DE RÍO Y MARINOS (CETACEA, ODONTOCETI) DE AMÉRICA DEL SUR.

Tesis
Entregada a la
Universidad de Chile
En cumplimiento parcial de los requisitos
Para optar al Grado de

Doctor en Ciencias con Mención en Ecología y Biología Evolutiva

Facultad de Ciencias

Por
CAROLINA SIMON GUTSTEIN

Abril, 2013
Director de Tesis: Mauricio Canals L.
Co-director de Tesis: Mario A. Cozzuol

FACULTAD DE CIENCIAS

UNIVERSIDAD DE CHILE

INFORME DE APROBACION

TESIS DE DOCTORADO

Se informa a la Escuela de Postgrado de la Facultad de Ciencias que la Tesis de Doctorado presentada por la candidata.

CAROLINA SIMON GUTSTEIN

Ha sido aprobada por la comisión de Evaluación de la tesis como requisito para optar al grado de Doctor en Ciencias con mención en Ecologia y Biología Evolutiva, en el examen de Defensa Privada de Tesis rendido el día 17 de diciembre de 2012.

Director de Tesis:
Dr. Mauricio Canals L. ....

Co-Director de Tesis
Dr. Mario A. Cozzuol

Comisión de Evaluación de la Tesis
Dr. Alberto Veloso ....

Dr. Marco Mendes ....

Dr. Mario Penna ....

Dedico esta tesis a mi familia,
brasileira y chilena.
Esta tesis y mucho mas no seria posible,
o no tendría gracia, sin uds.

Carolina S. Gutstein nació en 1981 en Florianópolis, Brasil. Se graduó en Ciencias Biológicas en la Universidade Federal de Santa Catarina en 2003. Obtuvo el grado de magíster en Geociencias mención Paleontología en la Universidade Federal de Rio Grande do Sul en 2006. Ha desarrollado terrenos paleontológicos en diversas regiones de Chile, en especial en la Región de Atacama, en la Antártica y en el Amazonas (Brasil). También ha realizado pasantías en varias de las colecciones mas importantes de America del Sur (Argentina, Brasil, Chile y Peru), Estados Unidos, Francia e Inglaterra. Su línea de investigación abarca la evolución, registro fósil y morfología de mamíferos marinos, en especial cetáceos odontocetos. Sus resultados han sido publicado en revistas peer review tales como Journal of Mammalogy, Journal of Vertebrate Paleontology y Journal of South American Earth Sciences. Es socia fundadora y parte del primer directorio de la Asociación Paleontológica de Chile (desde 2008), socia y miembro de la directiva en la Sociedad Latino Americana de Mamíferos Acuáticos (desde 2002) y socia de la Society of Vertebrate Paleontology (desde 2006) y Society of Marine Mammalogy (desde 2010).

Agradecimientos

Esta tesis fue posible gracias al apoyo incondicional de muchas personas. En primer lugar agradezco a mi co-tutor, Mario Cozzuol, quien me motivó en el estudio de los cetáceos fósiles desde el pregrado. A mi tutor Mauricio Canals, por haberme apoyado en todas las etapas de esta tesis, por su disposición y confianza. A la comisión de tesis compuesta por Alberto Veloso, Marco Méndez y Mario Pena por importantes críticas y sugerencias a mi trabajo de tesis. Constanza Figueroa-Bravo fue de gran ayuda en el procesamiento de imágenes de tomografía, además de discusiones acerca de la evolución de los cetáceos. Agradezco también a Ana Valenzuela-Toro, Maria Jose Pérez y Roberto Yury-Yañez por la ayuda prestada en diversas etapas de esta tesis además de su amistad.

Agradezco a todas las personas encargadas de las colecciones científicas consultadas: Chile, David Rubilar-Rogers (MNHN en Santiago); Brasil, Miriam Marmontel (Instituto Mamirauá en Tefé, Amazonas), Paulo C. Simoes-Lopes en UFSC y Danilo Saraiva del Museo de Ciencias Naturais (Pontificia Universidade Católica) en Belo Horizonte; Argentina, Alejandro Kramarz del MACN en Buenos Aires y Marcelo Reguero del MLP en La Plata; Francia, Christine Argot del MNHN en Paris; Inglaterra, Richard Sabin del Natural History Museum, London; U.S.A., David Bohaska (Paleobiology) y Charley Potter (Vertebrate Zoology) del

Smithsonian Institution NMNH, en Washington D.C., y Stephen Godfrey del Calvert Marine Museum, en Maryland. Deseo agradecer a Rodrigo Passoni (Cefalo-X Florianópolis, Brasil) por el permiso y la realización de la tomografía cone-beam en su clínica.

Agradezco a Conicyt por la beca de doctorado y beca de apoyo a la realización de tesis. Becas Chile, Departamento de Postgrado y Postítulo de la Vicerrectoría de Asuntos Académicos de la Universidad de Chile y Remington Kellogg Fund de la Institución Smithsoniana.

Finalmente quiero agradecer especialmente a mi familia (Vani, Angelo, Daniela, William, Luis, Giulia, Danusa, Vinicius y mi compañero querido David) por su apoyo incondicional, tanto en mi adaptación a esta nueva vida en Chile, como en mi recuperación, desde una crisis de salud muy severa durante la realización de esta tesis. Gracias también a la familia Rubilar Rogers por su alegría y apoyo. A los amigos Michelle, Dani E., Maca, Chico, Carol Loch, Dani Laura, Paulo S.L., Jorge, Mauricio, Paulo B., Gabiroba, Pauli, Natalia, Alex, Jim, Jorge y Nick por las horas de relax tan necesarias en este proceso. Como no podría faltar los audiobooks e historias (I.K., S.F. y T.H.) por mantener me enfocada durante las madrugadas.

Gracias a todos!!!

ÍNDICE DE MATERIAS

XII. **APENDICE I**

INDICE DE TABLAS

Capitulo 1

Capitulo 2

Capitulo 3

INDICE DE FIGURAS

I. Introducción

V. Capitulo 1

VI. Capitulo 2

VII. Capitulo 3

VIII. Capitulo 4

VIII. Conclusiones

XII. Apéndice I

RESUMEN

La evolución de la ecolocalización en los odontocetos ha sido ampliamente estudiada y consiste en la emisión de un haz de sonido de alta frecuencia, recepción de ecos del sonido emitido y su procesamiento neurológico. La ecolocalización, común a todos los odontocetos actuales, se diferencia en las propiedades acústicas entre los taxones y tal vez en la preferencia de hábitat. Se ha estudiado la emisión de sonidos de alta frecuencia y la formación del haz de sonido, tanto con modelos computacionales como en experimentos conductuales. Sin embargo, trabajos que integren los distintos requerimientos para la ecolocalización en un amplio muestreo y en un contexto evolutivo, son escasos. Esto se debe, en gran parte, a que no existe consenso entre las relaciones filogenéticas de los odontocetos modernos, hecho que es generado por un muestreo taxonómico pobre en las hipótesis publicadas, pero sobre todo por la exclusión de taxa sudamericanos. Por ejemplo, los Delphinida (Inioidea+Lipotidae+Delphinoidea), grupo que presenta la transición mar-río en América del Sur y, en particular los Inioidea, tienen su historia biogeográfica marcada por la ingresión de los grandes cuerpos de agua epicontinentales durante los periodos de transgresión marina del Mioceno Tardío en la cuenca amazónica y el mar paranaense, lo que es evidenciado por cinco géneros fósiles sudamericanos, distribuidos en dos

familias: Iniidae y Pontoporiidae. Actualmente los Iniidae están restrictos a las cuencas Amazónicas y de la Orinoquía (Colombia) y están representados por un género *Inia*. Pontoporiidae en cambio está restricto al Sur del océano Atlántico (Sur de Argentina a Sureste de Brasil) con apenas una especie, *Pontoporia blainvllei*. Un evento similar ocurrió más recientemente (Plioceno-Pleistoceno) en los Delphinoidea, consistiendo en la entrada a la cuenca Amazónica del género *Sotalia*, diferenciándose en dos especies, *S. fluviatilis* y *S. guianensis*. La presencia de dos eventos de transición mar-río en dos grupos distintos y con diferentes tiempos de divergencia (entrada en el sistema fluvial) es un modelo interesante para evaluar la importancia del efecto ambiental en la evolución de la ecolocalización del grupo.

Para esto, se realizó análisis morfométricos del cráneo y perióticos. Basado en la una matriz morfológica de caracteres publicada previamente ampliamente revisada y re-codificada. Se utilizaran 248 caracteres y 35 taxones seleccionados para realizar análisis filogenéticos. Con el árbol resultante se pudieron mapear distintos caracteres como los marcadores óseos de estructuras con función conocida, las propiedades acústicas de haz de ecolocalización, la preferencia de hábitat o el dato paleoambiental (marino, fluvial, costero) y los grupos de edades geológicas.

Otro carácter de importancia, relacionado con la morfología craneal es la forma y longitud de melón, la cual ha sido relevante para la separación grupos de edad geológica y ambiental, ya que se ha sugerido relacionado con la capacidad de filtrar y enfocar el haz de sonido producido. Una mayor capacidad de enfoque es coherente con el complejo hábitat de los delfines de río y banda estrecha de súper alta frecuencia (cochlea tipo I), junto con las observaciones de comportamiento. También se ha propuesto que la extensión del melón está relacionada con la capacidad de enfoque y con el límite de frecuencia más baja del sonido producido y que esta diferencia podría ser independiente del tamaño de la cabeza.

Los sacos aéreos tienen una distribución similar en Delphinida, aunque dentro de Inioidea son complejos, subdivididos, de textura suave, juxtapuesto a los huesos del cráneo subyacentes y estan más dorsalmente posicionados (también se observa en *Phocoena*). Mientras que en Delphinidae (Delphinoidea) los sacos vestibulares son espesos, pigmentados y arrugado. Se ha propuesto para *Platanista* y *Inia*, que los sacos aéreos expandidos que rodean el melón podrían generar un haz de sonido mas enfocado, ya que actuarían como un 'espejo' acústico cóncavo, dado el límite de aire-tejido que genera reflexión de la onda sonora. El haz de ecolocalización de banda estrecha asignado en el árbol más parsimonioso se recuperó como un rasgo primitivo, lo cual fue también sugerido por el mapeo de caracteres y la reconstrucción de los nodos ancestrales del tipo de conducto coclear.

El tipo de ecolocalización "especialista" y los cambios morfológicos asociados observados en los delfines de río, son plesiomorficos y están presentes desde la divergencia entre Delphinoidea e Inioidea, estando presentes en Delphinida (con excepciones) y *Notocetus*. Mientras que la invasión a los sistemas fluviales es apomórfica, pero convergente ocurriendo en diferentes contextos filogenéticos, geológicos y temporales. El clado formado después de la divergencia de Phocoenidae con el resto de los Delphinoidea es coherente con el medio ambiente, las propiedades acústicas de ecolocalización de haz y la morfología del oído interno (tipo de conducto coclear). Esto es parcialmente coherente con el escenario propuesto en la literatura donde habría una supervivencia diferencial de los delfines del río de los linajes antiguos, en los hábitats fluviales.

I. INTRODUCCION

La ecolocalización en delfines es acompañada de modificaciones (al patrón mamífero) en la anatomía blanda como el melón, los sacos aéreos, la bursa y los sinos aéreos (Fig. 1).

I. 1. Mecanismo de la ecolocalización

La ecolocalización es una capacidad neurosensorial presente en mamíferos que surge de la especialización de la vocalización y recepción de los ecos del ultrasonido emitido, por lo que genera profundas modificaciones en las porciones craneales involucradas. En los delfines, esa habilidad ha sido demostrada con experimentos conductuales (Norris 1961), grabación y análisis de sonidos (Au y Herzing 2003, Au et al. 1995, 2004, Madsen et al. 2004), así como utilización de técnicas radiológicas como tomografía computada y resonancia magnética de delfines actuales vivos (Au et al. 2006) y muertos (*post-morten*) (Cranford 1994, 2008). De esta manera ya se tiene comprensión acerca del funcionamiento del mecanismo, sobre todo en los delfines "nariz de botella", *Tursiops truncatus*, y en el "delfín pintado", *Stenella attenuata*, más frecuentemente mantenidos en cautiverio.

El mecanismo de la ecolocalización en los delfines puede ser resumido en las etapas de emisión y recepción del sonido, como sigue:

- Consiste en la emisión de sonidos de alta frecuencia por medio de una válvula vocal ubicado en la región facial de la cabeza y asociada a una cámara vocal y tras estructuras derivadas del pasaje nasal derecho (Fig. 1). El sonido emitido viaja por el cuerpo melón, el cual enfoca el sonido, reduciendo el espectro de frecuencias e intensidades sonoras y creando a su vez una señal más específica.
- Al traspasar el melón, el sonido viaja en el agua circundante hasta encontrar algún obstáculo. El choque de la onda de alta frecuencia, en un objeto reflectante, genera un eco que retorna al local de la emisión de la onda primaria de sonido. A mayor frecuencia, mayor será la agudeza auditiva.
- Al retornar, el sonido es captado por una porción más delgada de la mandíbula del delfín que es acústicamente transparente llegando a la almohadilla grasa mandibular. Esta es altamente inervada y está conectada directamente a la placa timpánica que en los cetáceos hace las veces del tímpano (Fig. 2).
- La placa timpánica se articula con el hueso martillo (*malleus*) y tiene una contra-parte paquiostótica llamada *involucrum*, lo que otorga mayor rigidez al conjunto disminuyendo la intensidad del sonido recibido en el oído medio a través de la articulación cuerpo graso-placa timpánica-

martillo (Fig. 2).

- Considerando que la impedancia del agua y de los tejidos es muy similar, se genera otro problema que es la detección de la dirección del sonido recibido, fundamental para ubicarse y ubicar a la presa, el fondo, etc. Sin embargo, este problema es resuelto con el desarrollo de senos aéreos pterigoideos que circundan el complejo periótico-timpánico, el cual a su vez está desconectado de los demás huesos del cráneo (Fig. 3).

I. 2. Propiedades acústicas en la ecolocalización

Estudios de las frecuencias emitidas en cautiverio y en la naturaleza han mostrado, sobre todo para los Delphinidae como el delfín nariz de botella *Tursiops truncatus* y delfines hawaianos del género *Stenella*, que las frecuencias son altas (hasta 200 kHz, con un pico en 100-150 kHz; Norris et al. 1961, Au y Herzing 2003) y que pueden ser manipuladas por ellos, cambiando la frecuencia e incluso la amplitud (en tres especies de Delphinidae; Au y Benoit-Bird 2003). También se ha observado que la emisión del pulso es bimodal, teniendo un pico a frecuencias bajas (en torno de 50 kHz) y otro a frecuencias altas (en torno de 120 kHz) como en *Stenella frontalis* (Au y Herzing 2003). Tempranamente en los estudios de ecolocalización ya había sido propuesto que las capacidades auditivas y de emisión de sonido podrían tener patrones diferentes de frecuencias preferenciales, espectro de la frecuencia y volumen en diferentes especies. Particularmente, Jacobs y Hall (1972) observaron que el buffeo rosado del amazonas, *Inia geoffrensis*, se diferenciaba en todas estas características del conocido *T. truncatus* y otras especies de delfines marinos.

El tamaño corporal fue relacionado con las diferencias de tamaño de las estructuras productoras de sonido y la frecuencia preferida de los pulsos o "clicks", en *Tursiops, Pseudorca crassidens y Grampus griseus.* Sin embargo cuando se incorpora a esta comparación al monodontido *Delphinapterus leucas* (beluga) la relación no se sostiene (Watkins 1980, Madsen et al. 2004). Los parámetros de la fuente emisora en la ecolocalización en *Pseudorca* y *Grampus* no pudieron ser relacionadas a las preferencias alimenticias lo que sugiere que el tamaño promedio de la especie, su ambiente de forrajeo y uso del hábitat podrían ser las variables responsables por las diferencias observadas entre estas especies y demás. Los mismos autores señalan una gran diferencia en frecuencia e intensidad de los pulsos emitidos por la beluga, lo que debería estar influenciado por su hábitat altamente reflector (casquetes de hielo) (Madsen et al., 2004).

I. 3. Anatomía funcional de la ecolocalización

Como fue mencionado anteriormente, existen modificaciones extremas en la anatomía de los odontocetos que están relacionadas con la ecolocalización. Entre estas podemos mencionar la adquisición de estructuras únicas en comparación a los mamíferos terrestres, como la válvula vocal, los sacos vestibulares, las bursas y el melón. Adicionalmente, según Fordyce (1994), en el caso de la anatomía facial de los odontocetos las estructuras blandas dictan la forma de la contra-parte ósea, ya que esta se forma más tardíamente en el desarrollo. En todas las modificaciones que pueden ser observadas, tres procesos son cruciales para el entendimiento de la complicada anatomía craneana de los delfines: telescopaje, asimetría y paquiostosis.

I. 3. 1. *Telescopaje*

La extraordinaria modificación del cráneo de los odontocetos, en los cuales la narina ósea se ubica en el vertex del cráneo y los ojos abajo del maxilar, es dada por la sobre-posición de los huesos craneales (Fig. 6). El llamado telescopaje (*telescoping*, Kelogg 1928) consiste en la sustitución de una línea de sutura entre huesos por el crecimiento sobrepuesto de los huesos de la cara y del rostro, ampliando el contacto entre estos. Esta característica aparece en Archaeoceti (orden extinto) y llega a formar una doble capa de huesos en Odontoceti. Este fenómeno esta relacionado al desarrollo del músculo del plug nasal (*maxillo-naso-labialis*) y la formación de una cuenca maxilar-premaxillar que recibe el melón (Fordyce 1994, Heynnig 1989). También en el vertex se observa un aumento de la asimetría sobre todo en los linajes modernos de Odontoceti (surgidos durante el Mioceno), tales como, los Delphinoidea: Delphinidae, Phocoenidae y Monodontidae. Es decir, el patron de telescopaje de los odontocetos modernos esta altamente relacionada al desarrollo de las estructuras que emiten (bursa) y amplifican el sonido (sacos aéreos) y que filtran y generan un haz de sonido enfocado (melón).

I. 3. 2. *Asimetría*

La asimetría craneana es común ala mayor parte de los odontocetos. Solamente *Pontoporia blainvillei*, la única especie viviente de Pontoporiidae, presenta asimetría apenas en la anatomía blanda, siendo simétrica la anatomía ósea facial (Heynnig 1989, Cranford et al. 1996); mientras que el pontopórido fósil, *Brachydelphis mazeasi* (Muizon 1988a, Capitulo 3, Fig. 9; Capitulo 4, Fig. 8), posee un vertex craneal levemente asimétrico. Los patrones de asimetría más comunes son el contacto desigual del premaxillar con el nasal y el tamaño diferente del nasal y frontal a ambos lados. Se ha propuesto que los patrones de asimetrías estarían asociados a la ecolocalización ya que las estructuras blandas como el pasaje nasal son asimétricas e incluso hay estructuras unilaterales. En *Kogia,* dos ejemplos de esta última son la estructura generadora de sonido, la válvula vocal (= *monkey lip* y *museau du singe*) presente en el lado derecho, y el saco vestibular expandido presente en el lado izquierdo (Clarke et al. 2003, Fig. 1). Cranford et al. (1996) establecieron la homología de dichas estructuras entre 19 especies de odontocetos, las características comunes a todas las especies fueron consideradas homólogas y parte de un hipotético generador de señal para el biosonar: un par de bursas grasas embebidas en tejido conectivo, un escudo cartilaginoso, un ligamento sólido y un conjunto de sacos aéreos de tejido blando (Fig. 1). La asimetría craneal probablemente es el resultado de la asimetría en las estructuras blandas emisoras de sonido (ecolocalización) y no contribuye a la audición interaural, rol que es desarrollado por los senos aéreos pterigoideos. El desarrollo de esos senos aéreos, es evidenciado por las superficies lisas de los huesos en contacto con tales estructuras y se puede verificar su presencia desde el Eoceno en la primera ballena conocida *Pakicetus inachus* Gingerich y Russel 1981.

I. 3. 3. *Paquiostosis*

La paquiostosis es otro proceso de gran importancia en la evolución de la audición en Cetacea. Se trata del aumento de rigidez y densidad de los huesos, el que incluso puede ocurrir entre dos huesos articulados, disminuyendo así su movilidad (sinostosis). Los huesos del oído (timpánico, periótico y los huesecillos: *malleus*, *incus* y *stapes*) de los cetáceos son paquiostóticos, es decir, son más densos, rígidos y voluminosos que los propios del patrón mamífero, cuya característica es tener huesos delgados y acústicamente muy sensibles (Giraud-Sauver. 1969, McCormick et al. 1970, Ketten, 1992).

Kinkel et al. (2001) observaron que el proceso de paquiostosis y rotación de la cadena de huesecillos, observada en el registro fósil (Thewissen y Hussain 1993, Nummela et al. 2004, 2007, Fig. 2), tienen un correspondiente durante el desarrollo ontogenético de embriones de delfines modernos (Delphinidae. *Delphinus delphis* y *Stenella attenuata*). Los embriones más tempranos muestran la "condición primitiva", es decir, es semejante a la de los demás mamíferos en cuanto a los procesos del *malleus* (desarrollados), la razón de largo de los procesos (*crus breve* y *longum*) y la orientación del *incus* y de la junta *incumallear.* Según Kinkel et al. (2001), la condición encontrada en los adultos es alcanzada después de la osificación, lo que se logra por medio de una rotación de 90° y por alometría de crecimiento entre los procesos (*crus breve* es más largo que *crus longum* y el *malleus* sin la cabeza desarrollada).

Como mencionado en el tópico anterior, estos cambios estructurales y de articulación en la cadena de huesecillos y la membrana timpánica (ligamento timpánico en cetáceos) son importantes ya que el medio acuático es 5 veces más denso que el aéreo y tiene una impedancia levemente mayor que la del oído interno. El equilibrio de impedancias se da de manera opuesta al patrón de mamíferos terrestres. Se verifica otro arreglo biomecánico, en vez de necesitar una amplificación de la presión (como ocurre en el oído medio de los mamíferos terrestres), los cetáceos necesitan amplificación de la velocidad (Nummela et al. 1999a, 1999b, Hemilä et al. 1999, Fig. 6). En otras palabras, los mamíferos terrestres necesitan amplificar el sonido para evitar la reflexión al pasar de un medio menos denso (oído medio relleno de aire) a uno más denso (oído interno relleno de fluido). En ese caso, el equilibrio es alcanzado por medio de una diferencia de área entre la membrana timpánica (mayor) y la ventana oval (menor), aumentando la presión del sonido, y la razón de "palanca" de la cadena de huesecillos (*malleus* tiene proceso o palanca mayor a lo del *incus*) (Sassu y Cozi 2006). Sin embargo, en los cetáceos, este mecanismo es innecesario (Ketten 1992); los cambios estructurales que definen a Cetacea van en el sentido de la reducción de la vibración por el aumento de rigidez, como por ejemplo la aparición de una articulación del *malleus* (desde Remingtonocetidae, Eoceno) con la placa timpánica (pared fina de la bula timpánica). El sonido llega por medio del contacto de la placa timpánica con la almohadilla grasa mandibular ("fat pad"), funcionando como un "tímpano" más rígido, ya que es ósea y tiene una contra-parte paquiostótica (el *involucrum*)

(Hemilä et al. 1999, Nummela et al. 1999, 2004, 2007).

I. 4. Planteamiento de la problemática

Los trabajos mencionados han generado un marco teórico robusto y necesario para futuras contribuciones en el tema. Sin prejuicio de lo anterior, la mayoría de estos trabajos aborda cada tema individualmente sin una adecuada integración enfocándose, por ejemplo, en las estructuras generadoras de sonido, o estructuras receptoras de sonido, o aislamiento acústico y audición interaural. Por ese motivo, todavía permanecen muchas dudas en relación a cómo evolucionó la ecolocalización. Puntualmente, queda en abierto el efecto del ambiente y/o de historia evolutiva de cada grupo, en la extrema variabilidad morfológica de las estructuras relacionadas, entre las familias e incluso dentro de una misma familia (como es el caso de los Delphinidae).

Muchos trabajos en los últimos 15 años se enfocaron en dilucidar la morfología asociada, el mecanismo involucrado y su evolución (Au y Benoit-Bird 2003, Marino et al. 2000, 2007, Clarke 2003, Kinkel et al. 2001, Spoor et al. 2002, Cranford et al. 2008). El estudio morfológico de las estructuras asociadas a la emisión y recepción del sonido han mostrado que existe un correlato entre las estructuras blandas y la estructura ósea de los especímenes estudiados (ver

Wever et al. 1971, Ketten 1994, Fordyce 1994, Cranford 2008). Por ejemplo, Ketten (1994) observó que existe una correspondencia entre la forma de la cóclea y la capacidad de recibir sonidos de frecuencias altas (40-80kHz) y muy altas (>100kHz) (Fig. 5), y Wever et al. (1971) lo correlaciona con el ancho de la membrana o papila basilar denotada por el ancho de separación entre las laminas óseas presentes en canal de la cóclea, donde descansa dicha membrana.

De esta manera, la evolución de la ecolocalización en delfines es acompañada de modificaciones en la anatomía blanda que a su vez se asocia a la anatomía ósea. Además, se ha observado que existe una amplia variedad de morfologías asociada a la ecolocalización en los diferentes grupos de delfines que se acompaña de una variación en el patrón de "clicks" emitidos y su frecuencia preferencial. Dicha variabilidad todavía no puede ser completamente explicada por correlaciones con el tamaño o tipo de presas preferidas, quedando abierta la posibilidad de que esta variación sea producto de la variedad de ambientes en el que viven los delfines como por ejemplo ríos, zonas de estuarios y mar abierto); de su conducta (acoplada al ambiente).

Por otro lado, el hecho de que dos linajes, de orígenes filogenéticos distintos (dos súper-familias distintas) hallan ingresado en un mismo sistema fluvial en tiempos diferentes hace de las familias Iniidae-Delphinidae un buen modelo para probar la hipótesis de que cambios en el ambiente, generan cambios en la manera de ecolocalizar dada las nuevas requisiciones acústicas. Por su parte, el sistema fluvial amazónico tiene una historia geológica interesante: en el Mioceno Medio a Tardío hubieron dos grandes transgresiones marinas que cubrieron buena parte de América del Sur. Se tiene consenso de que dos cuerpos de agua estaban presentes (Latrubesse et al. 2007): el mar Paranaense (en la región de entre Ríos, Argentina) y las cuencas de Amazonas y del Orinoco inundadas (Tethys water spot, según Donoso 2003) (Fig. 10). A partir de esto y del registro fósil del grupo, se estima que la entrada de delfines marinos a ambientes de río, ocurrió hace 12-8 millones de años, como el caso de los Inioidea (Cozzuol 1996, Latrubesse *et al.* 2007). Sin embargo otro linaje diferente (i.e. *Sotalia*) invade el ambiente fluvial más recientemente (Cunha *et al.* 2005). Ambos constituyen dos eventos de transición mar-río en dos grupos distintos y con diferentes tiempos de divergencia (entrada en el sistema fluvial) siendo un interesante modelo para testear la importancia del efecto ambiental en la evolución de la ecolocalización del grupo, permitiendo conocer el orden de aparición de estructuras óseas asociadas a la ecolocalización en ambientes de río en formas "transicionales".

Preguntas tales como: ¿Es posible identificar diferencias morfológicas en las estructuras relacionadas con la ecolocalización entre delfines de río y marinos? ¿La variación de formas de las estructuras asociadas a la ecolocalización está más correlacionada con el grupo filogenético al cual pertenece un taxón o al ambiente en que vive cada taxón? De existir estas diferencias ¿podrían estos rasgos servir como indicadores del hábitat en especímenes fósiles de delfines? No han sido abordadas por la literatura y constituyen el objetivo central de este proyecto.

A partir de la estandarización de los indicadores óseos de la mayoría de los componentes que participa en el proceso acústico (emisión/recepción) se podrá inferir la presencia y grado de desarrollo/forma de dichas estructuras en especímenes vivientes de colecciones y en especímenes fósiles. Además, la posibilidad de realizar esas inferencias en taxa fósiles, proporcionará la contra-parte histórica, la que desvela una diversidad de formas más abundante que la actual.

De esta manera, se pretende abordar esta problemática desde una perspectiva integradora, utilizando técnicas diferenciadas, como tomografía computada de delfines vivientes, morfometría y variación individual, una perspectiva evolutiva a través de la comparación de la ontogenia y de las especies fósiles además de acercamientos filogenéticos cladísticos, se espera aportar en el entendimiento de la evolución de la ecolocalización en los odontocetos desde el Neógeno.

II. Hipótesis de trabajo

Las diferencias morfológicas relacionadas con la ecolocalización, entre las familias de Delphina resultan de la especialización de los taxa a su modo particular de vida.

Predicciones:

- Se podrá evidenciar un patrón de aparición de caracteres morfológicos relacionados a la ecolocalización. Este patrón mostrará características básicas en común también presentes en los grupos externos, es decir, características conservadas asociadas a los requerimientos mínimos para ecolocalizar.
- Se espera encontrar en términos generales una alta correlación entre las medidas y caracteres merísticos relacionados a la ecolocalización y el ambiente particular que habitan o habitaron.
- Se podrá evidenciar un patrón de aparición de caracteres morfológicos relacionados a la ecolocalización. Este patrón mostrará características básicas en común también presentes en los grupos externos, es decir, características conservadas asociadas a los requerimientos mínimos para ecolocalizar.
- Por otro lado, se observará una distribución consistente entre la aparición de las estructuras especializadas con el ambiente en el cual habitan o

habitaron los taxa en cuestión, lo que no estará dado por la relación de ancestría-descendencia entre los mismos.

- Para el caso particular de las especies, *Inia geoffrensis* (Inioidea: Iniidae) y *S. fluviatilis* (Delphinoidea: Delphinidae), de distinto origen filogenético y con diferentes tiempos de incursión al sistema fluvial amazónico, que cohabitan actualmente, se espera que presenten: i) especializaciones en distintos grados, relacionadas a este ambiente, respecto de sus ancestros marinos, *Pontoporia blainvillei* y *S. guianensis*, respectivamente; ii) cambios en la morfología del oído interno asociada a diferencias en frecuencias de emisión, ya que los ambientes marinos son abiertos permitiendo el uso de frecuencias preferenciales emitidas /recibidas "bajas" y presentando un haz de ecolocalización bimodal, mientras que los ambientes fluviales, más cerrados y con obstáculos, obligarían el uso de frecuencias "muy altas", de alta definición pero baja penetración, presentando un haz de ecolocalización de banda estrecha; iii) estructuras faciales y de aislamiento acústico especializadas morfológicamente distintas en los taxa de río y de mar; iv) las formas ancestrales fósiles (ej.: *Brachydelphis, Ischyrorhynchus*) a *Inia* presenten morfologías que estimen capacidades auditivas (ej.: forma de la cóclea) acorde al ambiente de depositación (marino y fluvial, respectivamente) de donde provienen dichos fósiles.

III. Objetivos

III. 1. Objetivo general

Caracterizar morfo-funcionalmente las estructuras asociadas a la ecolocalización en Delphina, y relacionadas con la diversidad de tipos de ecolocalización: proximidad filogenética, ambiente en que habitan (río o mar).

III. 2. Objetivos específicos

- Determinar la correspondencia ósea de "estructuras blandas" relacionadas a la ecolocalización en los taxa actuales de interés, creando estimadores de estas estructuras.
- Utilizar los estimadores óseos ya descritos en la literatura y los propuestos, en el punto anterior, para inferir la presencia/ausencia de dichas estructuras en especímenes de colecciones (actuales y fósiles) y categorizar morfo-funcionalmente las estructuras en cada taxa.
- Realizar un análisis filogenético, basado en matrices ya publicadas incorporando los taxa fósil sudamericanos con el propósito de establecer las relaciones filogenéticas de los Delphina.
- Como un punto focal se verificará específicamente, a través de comparaciones ancestro-descendiente, cómo evolucionó la ecolocalización en dos diferentes linajes: Inioidea (delfines de río sudamericanos) y Delphinoidea (delfines marinos costeros y oceánicos), de ambiente fluvial y marino respectivamente.

IV. Estructura de la tesis

Esta tesis esta dividida en 5 capítulos:

1. El primer capítulo, "Cetáceos fósiles de Chile: contexto evolutivo y paleobiogeográfico" introduce al origen y diversificación de los cetáceos y da cuenta del estudio realizado en cetáceos fósiles en Chile. Además se resalta la importancia del registro de odontocetos fósiles del Mioceno tardío, como es el caso de la Fm. Bahía Inglesa, que presenta abundancia de especímenes y buena conservación, permitiendo la realización de estudios morfométricos y de variación como los propuestos aquí. Además la asamblea de la Fm. Bahía Inglesa es rica en delfines Inioidea, y por lo tanto grupo-hermano de los delfines de río del Amazonas (Inia).
2. El segundo capitulo "High frequency echolocation, ear morphology, and the marine-freshwater transition: a comparative study of extant and extinct dolphins (Odontoceti)" analiza la morfología coclear (con el uso de imágenes de tomografía volumétrica del cone-beam) y de los perióticos en general (medidas) con los datos disponibles en la literatura respecto al rango de frecuencias y forma del haz de sonido de ecolocalización, medidas en la naturaleza y en cautiverio en trabajos previos. Además se realizó una comparación entre grupos ambientales (según preferencia de

hábitat o paleoambiente asignado para el local de colecta), de edades geológicas, y taxonómicos (a nivel de familia y súper-familia).

3. El tercer capitulo "Facial soft tissue and bony morphology, implications to the evolution of echolocation on marine and freshwater Delphinida (Cetacea, Odontoceti)" analiza la morfología blanda (con el uso de imágenes de tomografía volumétrica del cone-beam) y osea (medidas) de la región facial y ventral del cráneo. Estos fueron comparadas con los datos disponibles en la literatura respecto al rango de frecuencias y forma del haz de sonido de ecolocalización, medidas en la naturaleza y en cautiverio en trabajos previos. Además, como el el capítulo anterior, se realizó una comparación entre grupos ambientales (según preferencia de hábitat o paleoambiente asignado para el local de colecta), de edades geológicas, y taxonómicos (a nivel de familia y súper-familia) y se comparó con los resultados obtenidos en los perióticos.
4. El cuarto capítulo "New Toothed Whales (Inioidea, Odontoceti) from the Neogene of the South-East Pacific (Atacama Region, Chile) and North Atlantic (North Carolina, U.S.A.): implications to river dolphins distribution and facial morphology.", se describe un nuevo género de Inioidea. En este capítulo se discute la validad del grupo Inioidea, basada en un nuevo análisis de la matriz de Geisler et al. 2012 que incorpora además

la muy aumentada diversidad morfológica del grupo, considerando los taxa aquí descritos. En esta nueva propuesta, se corrobora la asignación de *Ischyrorhynchus* a Inioidea y no al grupo asiático (Platanistoidea) como ha sido propuesto por algunos autores.

5. Por ultimo se enuncian las conclusiones generales de la tesis y se analizan directamente las hipótesis de trabajo, integrando los capítulos anteriores.

Anexo 1— Figuras referidas en el texto.

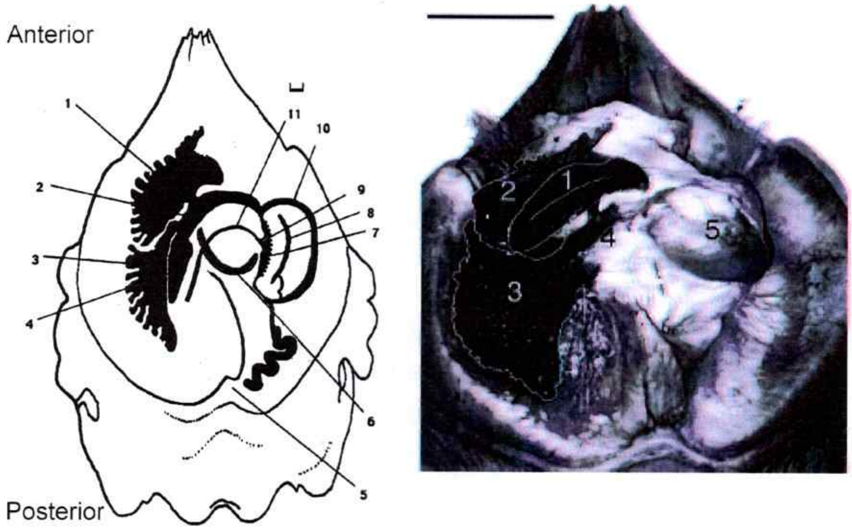


Figura 1. Vista dorsal del cráneo de *Kogia breviceps*. Nótese la acentuada asimetría de los pasajes nasales y bolsas asociadas. **Izquierda.** Esquema. 1, saco izquierdo del pasaje vestibular derecho; 2, pasaje vestibular derecho; 3, pasaje vestibular izquierdo; 4, pasaje nasal izquierdo; 5, septum sagital dorsal; 6, saco nasofrontal; 7, cámara vocal; 8, ramas de las bolsas (pouches) dentro del cojín (cushion); 9, válvula vocal; 10, ramas que se extienden por la porción externa del cojín; 11, pasaje nasal derecho o 'tubo vocal'. Escala = 1 cm. **Derecha.** Cráneo con algunos tejidos. Los sacos de los pasajes vestibulares están rellenos con resina. 1, contorno del orificio respiratorio; 2, saco izquierdo del pasaje vestibular derecho; 3, saco vestibular izquierdo; 4, pasaje vestibular derecho; 5, tejido conectivo blanco que envuelve el complejo del órgano espermaceti y la porción posterior del melón. Escala = 5 cm. Tomado de Clarke (2006).

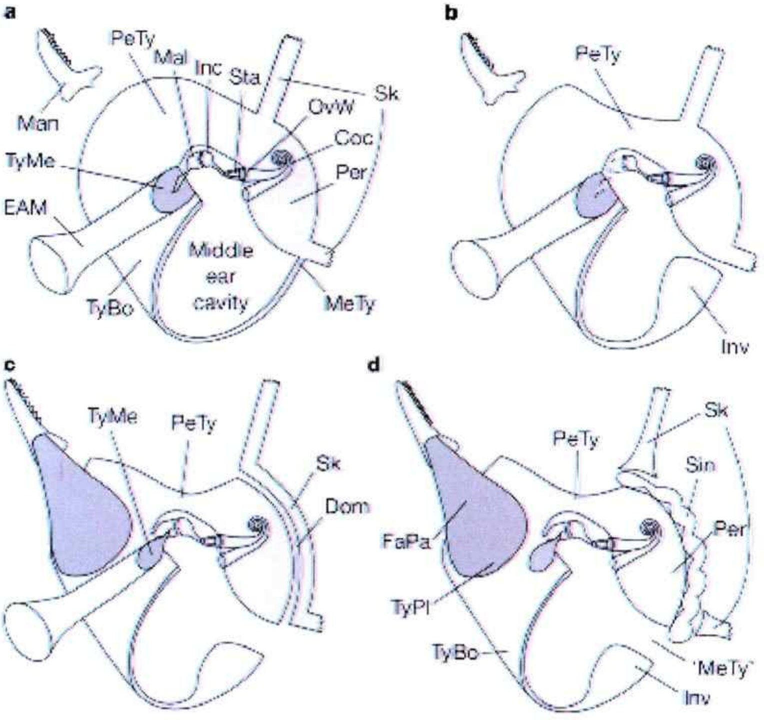


Figura 2. Diagrama del oído de un mamíferos terrestre generalizado (a), un pakicetídeo (b), un remingtonocetídeo/ protocetídeo (c) y un odontoceto moderno (d) mostrando las diferentes configuraciones de articulación entre la cadena de huesecillos y el tímpano(a)/placa timpánica(c,d).

Abrev.: Coc, cóclea; Dom, depresión en forma de domo para recibir al periótico; EAM, meato auditivo externo; FaPa, almohadilla grasa; Inc, *incus*; Inv, *involucrum*; Mal, *malleus*; Man, mandíbula; MeTy, Synostosis medial entre el hueso periótico y timpánico, en cetáceos esta synostosis es ausente y es homóloga al "gap" entre esto huesos ('MeTy'); OvW, ventana oval; Per, hueso periótico; PeTy, junta entre periótico y timpánico; Sin, sinos rellenos de aire; Sk, cráneo; Sta, *stapes*; TyBo, hueso timpánico; TyMe, membrana timpánica; TyPl, placa timpánica. Tomado de Nummela et al. (2007).

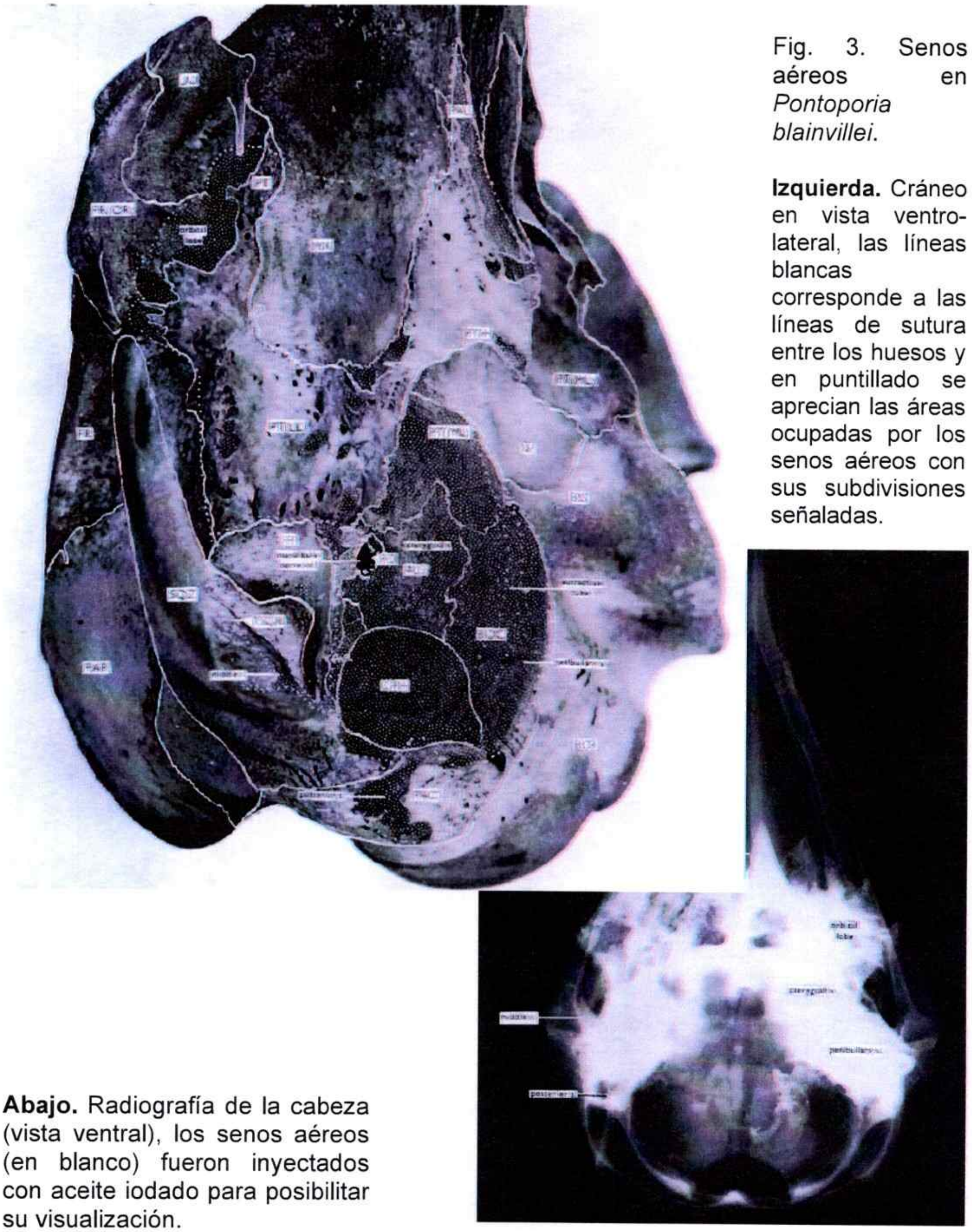


Fig. 3. Senos aéreos en *Pontoporia blainvillei*.

Izquierda. Cráneo en vista ventro-lateral, las líneas blancas corresponde a las líneas de sutura entre los huesos y en puntillado se aprecian las áreas ocupadas por los senos aéreos con sus subdivisiones señaladas.

Abajo. Radiografía de la cabeza (vista ventral), los senos aéreos (en blanco) fueron inyectados con aceite iodado para posibilitar su visualización.

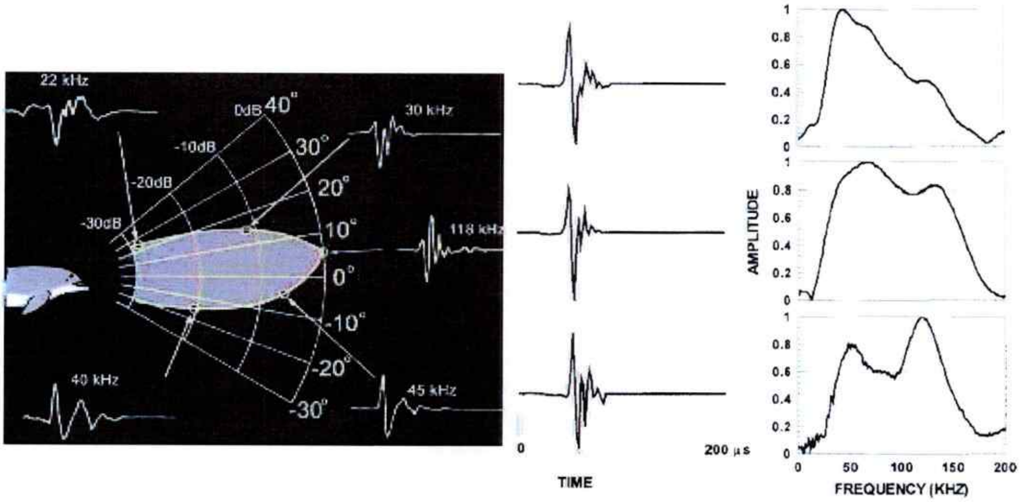


Fig. 4. Rango de frecuencias preferenciales emitidas en odontocetos. Nótese la direccionalidad de las frecuencias máximas emitidas (izquierda). Tomado de Au et al 2002 y modificado de Au et al. 2006.

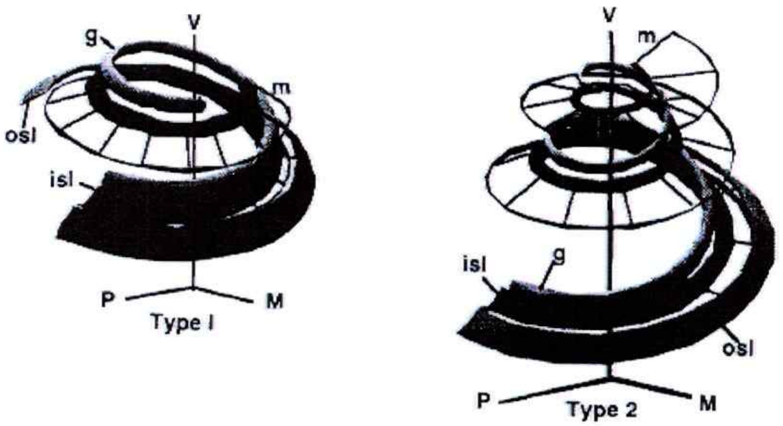


Fig. 5. Tipos de cóclea de odontocetos asociados a frecuencias preferenciales altas (Tipo I, menor a 100kHz) y muy altas (Tipo II, mayor a 100kHz). El esquema muestra las principales estructuras de la cóclea de los odontocetos tales como: membrana basilar (m); lamina espiral ósea interna (isl); la lamina espiral ósea externa (osl); ganglio espiral (g); lateral (l); posterior (P); ventral (v).

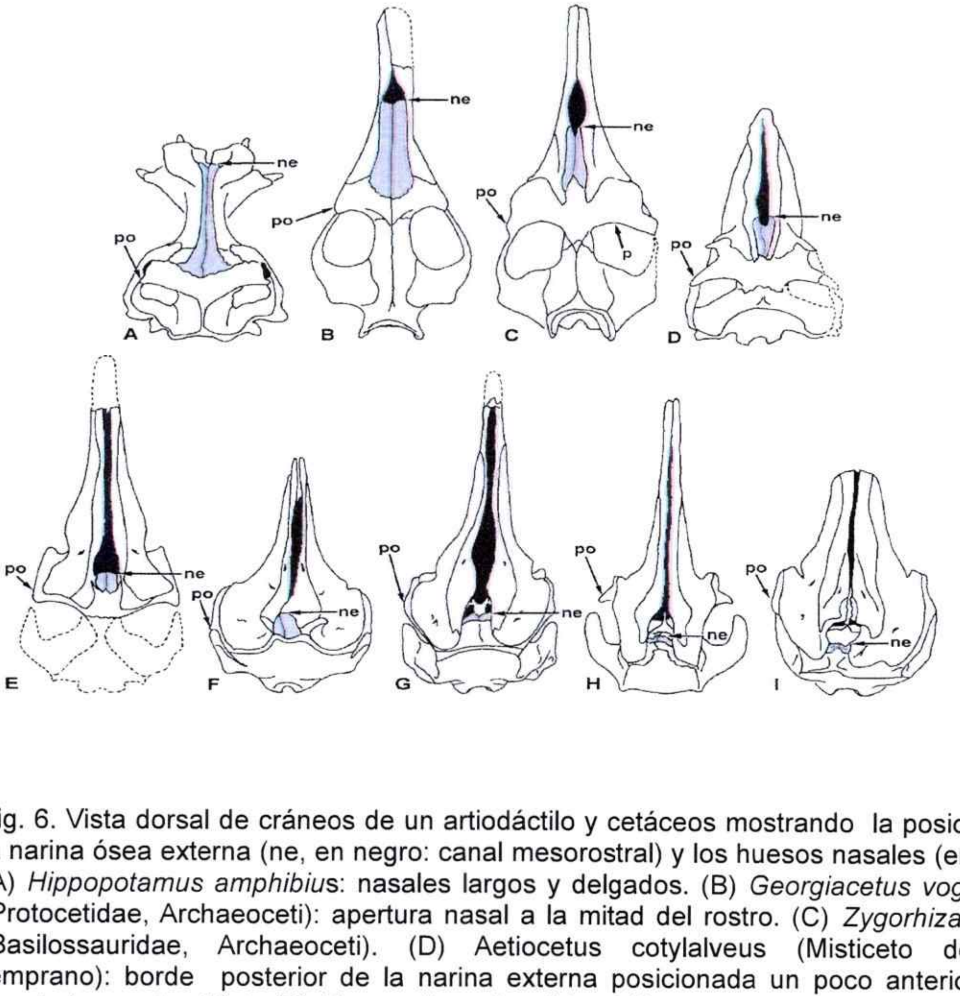


Fig. 6. Vista dorsal de cráneos de un artiodáctilo y cetáceos mostrando la posición de la narina ósea externa (ne, en negro: canal mesorostral) y los huesos nasales (en gris). (A) *Hippopotamus amphibius*: nasales largos y delgados. (B) *Georgiacetus vogtlensis* (Protocetidae, Archaeoceti): apertura nasal a la mitad del rostro. (C) *Zygorhiza kochii* (Basilossauridae, Archaeoceti). (D) Aetiocetus cotylalveus (Misticeto dentado temprano): borde posterior de la narina externa posicionada un poco anterior a la escotadura anteorbital. (E) *Xenorophus sloanii* (porción posterior reconstruida): borde anterior de los nasales en línea con la porción media de la órbita. (F) *Ziphius cavirostris*: borde anterior de los nasales en línea con la mitad posterior del proceso supraorbital del frontal. (G) *Waipatia maerewhenua* (Squalodontidae): nasales en línea con el gap entre el proceso postorbital y el proceso zigomático del ecamoso. (H) *Inia geoffrensis:* nasales en linea con el borde anterior de la fosa del escamoso (fossa temporal). (I) *Delphinapterus leucas*: nasales posteriores al borde anterior de la fossa del escamoso. Tomado de Geisler y Sanders (2003).

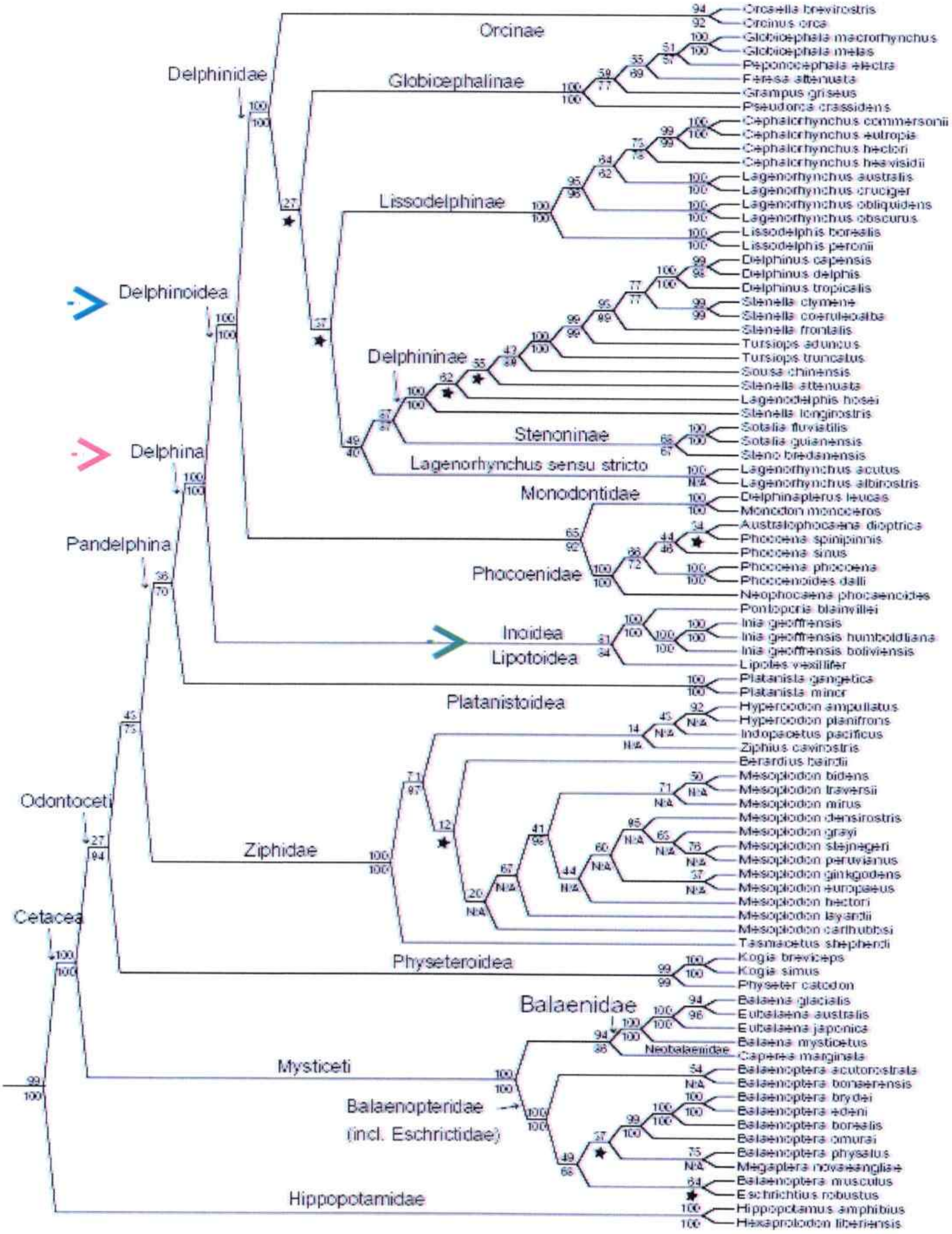

Orcinae
Delphinidae
Globicephalinae
Lissodelphinae
Delphinoidea
Delphininae
Delphina
Stenoninae
Lagenorhynchus sensu stricto
Monodontidae
Pandelphina
Phocoenidae
Inoidea
Lipotoidea
Platanistoidea
Odontoceti
Ziphidae
Cetacea
Physeteroidea
Balaenidae
Neobalaenidae
Mysticeti
Balaenopteridae
(incl. Eschrictidae)
Hippopotamidae
Orcaella brevirostris
Orcinus orca
Globicephala macrorhynchus
Globicephala melas
Peponocephala electra
Feresa attenuata
Grampus griseus
Pseudorca crassidens
Cephalorhynchus commersonii
Cephalorhynchus eutropia
Cephalorhynchus hectori
Cephalorhynchus heavisidii
Lagenorhynchus australis
Lagenorhynchus cruciger
Lagenorhynchus obliquidens
Lagenorhynchus obscurus
Lissodelphis borealis
Lissodelphis peronii
Delphinus capensis
Delphinus delphis
Delphinus tropicalis
Stenella clymene
Stenella coeruleoalba
Stenella frontalis
Tursiops aduncus
Tursiops truncatus
Sousa chinensis
Stenella attenuata
Lagenodelphis hosei
Stenella longirostris
Sotalia fluviatilis
Sotalia guianensis
Steno bredanensis
Lagenorhynchus acutus
Lagenorhynchus albirostris
Delphinapterus leucas
Monodon monoceros
Australophocaena dioptrica
Phocoena spinipinnis
Phocoena sinus
Phocoena phocoena
Phocoenoides dalli
Neophocaena phocaenoides
Pontoporia blainvillei
Inia geoffrensis
Inia geoffrensis humboldtiana
Inia geoffrensis boliviensis
Lipotes vexillifer
Platanista gangetica
Platanista minor
Hyperoodon ampullatus
Hyperoodon planifrons
Indopacetus pacificus
Ziphius cavirostris
Berardius bairdii
Mesoplodon bidens
Mesoplodon traversii
Mesoplodon mirus
Mesoplodon densirostris
Mesoplodon grayi
Mesoplodon stejnegeri
Mesoplodon peruvianus
Mesoplodon ginkgodens
Mesoplodon europaeus
Mesoplodon hectori
Mesoplodon layardii
Mesoplodon carlhubbsi
Tasmacetus shepherdi
Kogia breviceps
Kogia simus
Physeter catodon
Balaena glacialis
Eubalaena australis
Eubalaena japonica
Balaena mysticetus
Caperea marginata
Balaenoptera acutorostrata
Balaenoptera bonaerensis
Balaenoptera brydei
Balaenoptera edeni
Balaenoptera borealis
Balaenoptera omurai
Balaenoptera physalus
Megaptera novaeangliae
Balaenoptera musculus
Eschrichtius robustus
Hippopotamus amphibius
Hexaprotodon liberiensis

Fig. 7. Filogenia molecular publicada por Arnason y May-Collado (2008) indicando los grupos de Cetacea. Incluyendo los Delphina (flecha roja), grupo en el que se enfoca el presente trabajo, subdividido en dos linajes principales Delphinoidea y Inioidea (flechas azul y verde, respectivamente). Inioidea esta aquí propuesto conjuntamente con Lipotoidea (*Lipotes vexillifer*).

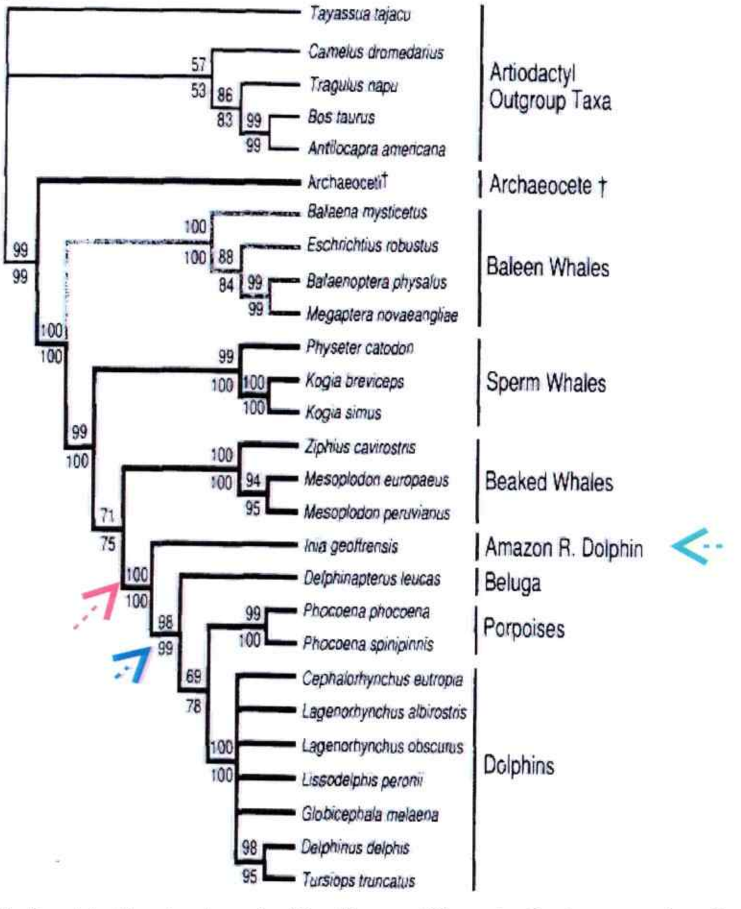
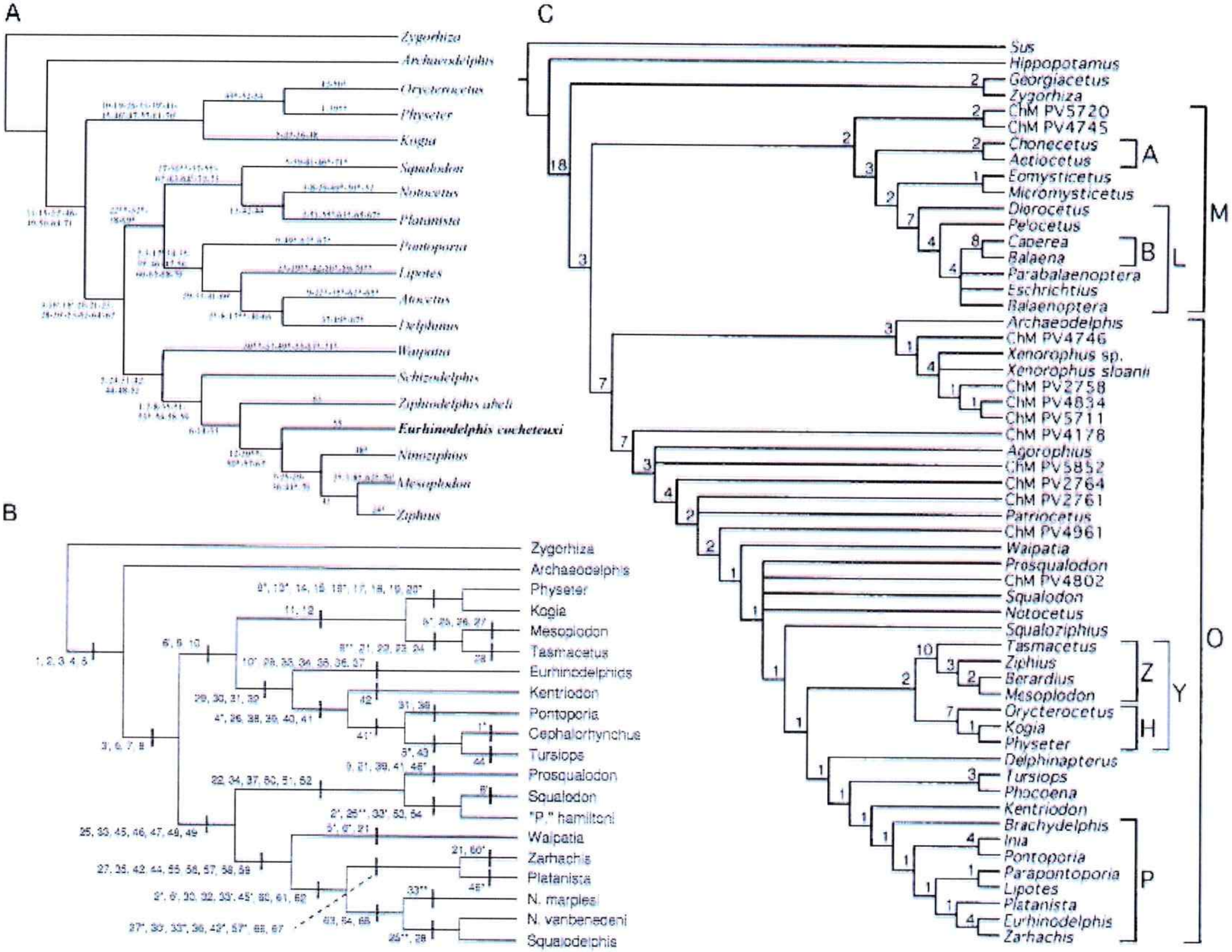


Fig. 8. Consenso estricto de las hipótesis de relación filogenética de Cetacea sobre la base de 360 caracteres morfológicos + Secuencia de ADN (los caracteres morfológicos fueron pesados como transversiones y o transiciones). Transiciones - Largo del árbol = 1.950, CI (sin caracteres no informativos) = 0.675, RI = 0.889, and RC = 0.649. Transversiones – LA= 2,508, CI (sin caracteres no informativos) = 0.699, RI = 0.904, and RC = 0.666. Los valores de bootstrap están arriba (transiciones) y abajo (transversiones) en cada nodo. (Tomado de Messenger y Mcguire, 1998). Los nodos que definen grupos equivalentes a los nombrados por May-Collado et al. (2008, ver fig. 7) están indicados por las flechas: Delphina (flecha roja), Delphinoidea (flechas azul) y Inioidea (flecha verde).

Figura 9– **(página siguiente)** Diferentes análisis filogenéticos, basados en caracteres morfológicos. A) árbol mas parsimonioso (AMP=1; LA=162; IC=0,53; IR=0,73) obtenido por Lambert (2005) diseñada para indagar a cerca de las relaciones filogenéticas de Eurhinodelphis (números corresponden a los caracteres que soportan los respectivos nodos).. B) árbol de consenso estricto obtenido por Fordyce (1994) diseñada para establecer las relaciones filogenéticas de Waipatia (números corresponden a los caracteres que soportan los respectivos nodos). C) Árbol de consenso de 21 AMPs obtenido por Geisler y Sanders (2003; LA=2539; IC e IR no informados) para la matriz de 56 taxa (actuales y extintos) codificados para 304 caracteres morfológicos (los números corresponden al suporte de Bremmer). Abreviaciones de Taxa: A, Aetiocetidae; B, Balaenoidea; H, Physeteridae; L, Balaenomorpha taxon nuevo; M, Mysticeti; O, Odontoceti; P, Platanistoidea; Y, Physeteroidea; Z, Ziphiidae.


A
Zygorhiza
Archaeodelphis
Orycterocetus
Physeter
Kogia
Squalodon
Notocetus
Platanista
Pontoporia
Lipotes
Atocetus
Delphinus
Waipatia
Schizodelphis
Ziphiodelphis abeli
Eurhinodelphis cocheteuxi
Ninoziphius
Mesoplodon
Ziphius
B
Zygorhiza
Archaeodelphis
Physeter
Kogia
Mesoplodon
Tasmacetus
Eurhinodelphids
Kentriodon
Pontoporia
Cephalorhynchus
Tursiops
Prosqualodon
Squalodon
"P." hamiltoni
Waipatia
Zarhachis
Platanista
N. marplesi
N. vanbenedeni
Squalodelphis
C
Sus
Hippopotamus
Georgiacetus
Zygorhiza
ChM PV5720
ChM PV4745
Chonecetus
Aetiocetus
Eomysticetus
Micromysticetus
Diorocetus
Pelocetus
Caperea
Balaena
Parabalaenoptera
Eschrichtius
Balaenoptera
Archaeodelphis
ChM PV4746
Xenorophus sp.
Xenorophus sloanii
ChM PV2758
ChM PV4834
ChM PV5711
ChM PV4178
Agorophius
ChM PV5852
ChM PV2764
ChM PV2761
Patriocetus
ChM PV4961
Waipatia
Prosqualodon
ChM PV4802
Squalodon
Notocetus
Squaloziphius
Tasmacetus
Ziphius
Berardius
Mesoplodon
Orycterocetus
Kogia
Physeter
Delphinapterus
Tursiops
Phocoena
Kentriodon
Brachydelphis
Inia
Pontoporia
Parapontoporia
Lipotes
Platanista
Eurhinodelphis
Zarhachis
A
B
L
M
Z
H
Y
P
O

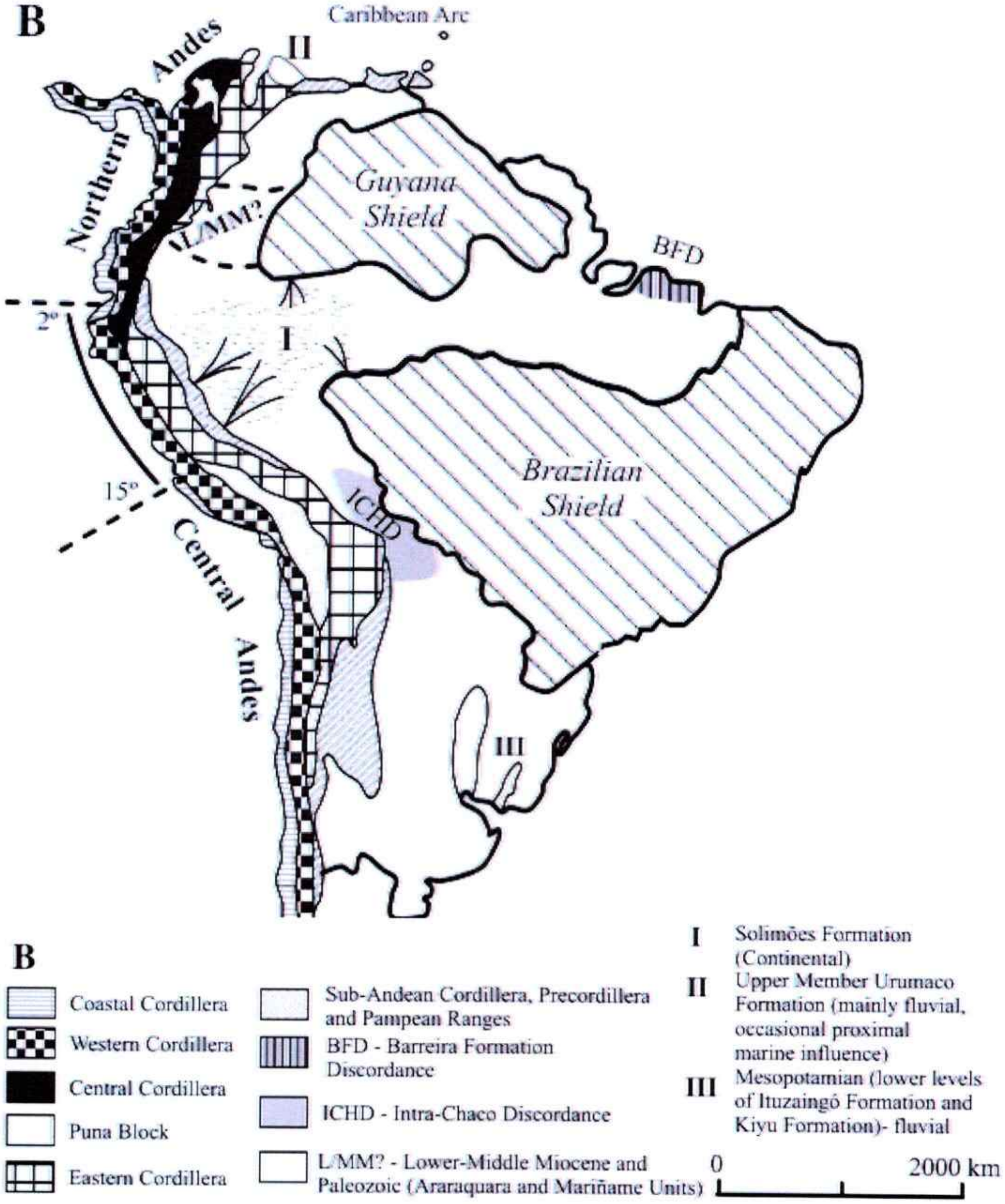


Fig. 10. Mapa de reconstrucción paleogeográfica de America del Sur extraído de Latrubesse et al. 2007. Nótese las regiones que estuvieron sumergidas en el Mioceno Tardío: I y III, correspondientes a la Fm. Solimoes y la Fm. Ituzaingó de donde provienen especímenes de delfines utilizados en este trabajo.

V. Capitulo 1

CETÁCEOS FÓSILES DE CHILE: CONTEXTO EVOLUTIVO Y PALEOBIOGEOGRÁFICO

Carolina S. Gutstein[a,b]

Ana M. Valenzuela-Toro[a]

V. Capitulo 1

CETÁCEOS FÓSILES DE CHILE: CONTEXTO EVOLUTIVO Y PALEOBIOGEOGRÁFICO

Carolina S. Gutstein[a,b]

Ana M. Valenzuela-Toro[a]

[a]Laboratorio de Ecofisiología, Facultad de Ciencias, Universidad de Chile, Las Palmeras 3425, Ñuñoa, Santiago, Chile, sgcarolina@gmail.com, avalenzuela.toro@gmail.com

[b]Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, Washington DC, 20013-7012, U.S.A.

V. 1. Resumen

El registro geológico marino de Chile es extenso, ya que en muchos períodos la mayor parte de su territorio, estuvo cubierto por océanos o mares epicontinentales someros. De esta manera, los taxa de vertebrados marinos (ej.: cocodrilos marinos, plesiosaurios, elasmobranquios, pinnípedos, cetáceos) son parte importante del patrimonio paleontológico de Chile, siendo muy abundantes, tanto en número como en diversidad de formas, aportando valiosa información estratigráfica y paleobiogeográfica.

Debido a esa abundancia, el registro fósil de cetáceos ha sido documentado en la literatura desde de la última parte del siglo XIX por el naturalista Rodulfo A.

Philippi quien describió taxa nuevos como *Neobalaena simpsoni*, (Ancud, Región de Los Lagos; Mysticeti) y *Delphinus domeykoi* (costa central, La Cueva; Odontoceti), aunque estos no sean válidos actualmente. La casi totalidad de los registros formales en la literatura provienen de la Formación Bahía Inglesa (Mioceno medio-Plioceno tardío, Región de Atacama) con 17 taxa de misticetos y odontocetos. Dentro de los odontocetos, se destaca la super-familia Inioidea (grupo que incluye atualmente al bufeo del Amazonas, *Inia* spp.) representada por cráneos, dientes y perióticos. También están presentes cráneos de la familia Phocoenidae, dientes de Physeteridae, Ziphiidae y Delphinidae. La Formación Coquimbo (Mioceno tardío-Plioceno, Región de Coquimbo, Le Roux *et al.* 2006) presenta mayormente registros de Mysticeti y un espécimen de Pontoporiidae, familia estrechamente relacionada a los bufeos amazónicos y que actualmente esta restringida a una especie que habita aguas costeras y estuarinas del Atlántico Sur). En el área de Navidad (VI Región), la Formación Rapel (=Fm. Navidad para algunos autores) presenta un fragmento de rostro articulado con dientes asignado a Physeteridae. Hasta el presente momento no hay registros, en la literatura, de cetáceos en el Neógeno marino de las Formaciones Ranquil y Lincai, aunque probablemente se necesitan campañas de prospección y estudios sistematicos. En resumen, la Región de Atacama presenta el 85% de los registros de Chile. Lo que en términos del registro sudamericano corresponde a 50% de las familias registradas en la última revisión (1996).

V. 2. Introducción

El Orden Cetacea Brisson, 1762 incluye los Subordenes Archaeoceti (ballenas extintas y formas anfibias), Mysticeti (ballenas con barbas) y Odontoceti (delfines, marsopas y cachalotes; Van Valen, 1968).

Los arqueocetos empezaron su notable incursión al ambiente acuático en el mar de Tethys durante el Eoceno temprano (aprox. 50 MA). En años recientes se ha incrementado notablemente el registro fósil de este grupo mostrando, de manera evidente, la transformación de artiodáctilos terrestres (mamíferos con número par de dedos en las extremidades) en "ballenas" completamente acuáticas, siendo considerado uno de los casos de macroevolución mejor representados en el registro fósil (Thewissen y Bajpai, 2001). A través del Eoceno, existían muchas formas de arqueocetos que empezaron a extender su restringida distribución inicial hasta alcanzar todos los océanos del planeta. La diversidad de formas es notable, desde animales grandes y cuadrúpedos, como *Ambulocetus natans* Thewissen, Madar y Hussain (1996) hasta los gráciles remingtonocetidos (Eoceno medio), como *Remingtonocetus harudiensis* (Kumar y Sahni, 1986). Esta diversidad de formas debió reflejar diferentes "modos de vida": los primeros probablemente cazaban vertebrados terrestres que se acercaran a cuerpos de agua como bahías y estuarios, similar a la manera de caza de los cocodrilos en los márgenes de ambientes marinos y dulce-acuícolas; mientras que los últimos eran de pequeño tamaño, poseedores de un hocico largo y delgado, que habitaron mares someros sobre el actual territorio de Pakistán, constituyendo un linaje que es muy distinto al plan corporal de las cetáceos modernos siendo un ejemplo de la diversificación y recambio taxonómico en la evolución de los arqueocetos durante el Eoceno, no formando parte de la rama que da origen a las ballenas y delfines modernos.

Los Pakicetidae fueron considerados las primeras ballenas debido a que fueron encontrados en sedimentos marinos eocénicos y presentan marcas del desarrollo de senos aéreos del pterigóides, en los huesos de basicráneo[68], esto permite inferir que en los taxones fósiles debieron poseer cierto aislamiento acústico del oído medio e interno, carácter esencial y determinante de las primeras "ballenas" (Luo y Gingerich, 1999). Sin embargo, según estudios recientes sus ancestros podrían ya ser acuáticos en conducta, como indica el estudio reciente del raoelido *Indohyus* (Thewissen et al., 2007), que poseía un engrosamiento en la bula timpánica (*involucrum*) y los huesos osteesocleróticos (con médula reducida) así como todos los mamíferos acuáticos y semi-acuáticos actuales. De esta manera, para estos autores, el origen de la modificación morfológica que se dio en el linaje de los cetáceos, fue el reflejo del cambio a una dieta acuática y depredatoria, y no el cambio de medio simplemente, ya que sus ancestros ya tenían el habito acuático.

---

[68] La porción ventral del cráneo, incluye los esfenóides, basiocciptal y pterigóides, y complejo periótico-timpánico. Las marcas de la expansión de los senos aéreos del pterigóides se encuentran al rededor del complejo periotico-timpánico, crestas baciocciptales y basiesfenoides. En algunos delfines modernos y marsopas se encuentran expandidos hasta el maxilar y frontal, al rededor de la cavidad ótica.

Las relaciones filogenéticas de Cetacea dentro de Mammalia, y de los clados dentro de Cetacea, son constantemente debatidas en la literatura (Agnarsson y May-Collado, 2008; Thewissen et al., 2007; Gatesy *et al.,* 1999; Geisler y Sanders, 2003; Gingerich *et al.,* 1983; Milinkovitch *et al.,* 1993, 1994 y 1995; Kellogg, 1928; Spauling *et al.*, 2009; Thewissen *et al.*, 2007; Geisler *et al.* 2011, Uhen *et al.* 2011). Entre las evidencias utilizadas, están los caracteres morfológicos y moleculares que han sido interpretados por diferentes autores sugiriendo distintas hipótesis de relación (ver Figura 1 y 2). Relaciones entre Archaeoceti (Cetacea) y Mesonychia (condilartros extintos), como grupos-hermanos relacionados al clado Artyodactyla (O'Leary y Gatesy, 2008); o entre Archaeoceti y Artyodactyla, como grupos-hermanos (Gingerich *et al.,* 1983; O'Leary y Geisler, 1999; Thewissen *et al.,* 1998; Thewissen y Madar, 1999). Gingerich (2001) y Thewissen *et al.*, (2001) consideran Cetacea como un grupo monofilético y hermano de Artyodactyla, dada la estrecha relación entre Archaeoceti y *Diacodexis* (un artiodáctilo primitivo). Por otro lado, el clado Hippopotamidae también ha sido propuesto como grupo hermano de Cetacea (Thewissen y Williams, 2002; Thewissen et al., 2007; Gatesy *et al.,* 1997, 1999; Gatesy y O´Leary, 1999; Nikaido *et al.,* 1999; Ursing y Arnason, 1998), lo que formaría el clado Cetartiodactyla y, consecuentemente, caracterizando a Artiodactyla como parafilético. Esa hipótesis fue basada principalmente en análisis filogenéticos moleculares, pero que también vienen siendo discutidas con base en caracteres morfológicos (Geisler y Uhen, 2003) y con análisis de evidencia total (Geisler *et al.* 2011). La morfología de *Indohyus* Thewissen *et al.* (2007), corrobora, al menos en parte, esta hipótesis. No obstante, independentemente de la especie ancestral señalada en los diversos análisis, el orden Cetacea ha sido considerado un grupo monofilético.

Diversos análisis cladísticos discuten la posición de Cetacea dentro de Artiodactyla, teniendo como grupo-hermano los raoelidos, hipopótamos o mesoniquidos (Spaulding *et al.*, 2009) todos artiodáctilos, entretanto, apenas los mesoniquidos son carnívoros. Uhen (2008) ha propuesto una nomenclatura taxonómica para los grupos de arqueocetos, incluyendo: Pakicetidae *Ambulocetus*, Remingtonocetidae, Protocetidae (parafiletico) y los mas derivados Pelagiceti (Basilosauridae y demás). Recientes hallazgos en Perú indican la presencia y diversidad de arqueocetos (un especimen atribuido a Protocetidae y tres géneros nuevos de Pelagiceti; Martinez et al. 2010; Uhen et al., 2011) en el Pacifico Sur en una temprana edad (Eoceno medio). Estos nuevos registros cambian una vez mas la interpretación paleobiogeografica del grupo, sobretodo en el caso de Protocetidae que era hasta entonces, considerado exclusivo del Hemisferio Norte.

Si bien la evolución temprana de los arqueocetos ha sido bastante estudiada, aspectos aún poco entendidos son la filogenia de las ballenas y de los delfines modernos, los Neoceti (Fordyce y Muizon, 2001). Neoceti, que incluye a los cetáceos modernos y sus ancestros, surge en el Oligoceno-Mioceno (35-25 millones de años aproximadamente) pero su origen filogenético aún es controvertido y las relaciones entre las diferentes familias permanece incierta en muchos casos. En su revisión de los taxa oligocenos de Cetacea, Whitmore y Sanders (1977), señalaron que existen pocos registros pero estos están ampliamente distribuidos en el mundo. En las ultimas décadas, nuevos hallazgos fósiles, principalmente de especímenes mejor preservados, posibilitaron la descripción de nuevos taxa oligoceno-miocenos (Fordyce, 1994, 2002; Muizon, 1987) que hoy son cruciales para el entendimiento de la evolución de los cetáceos modernos (grupos vivientes). En esa etapa ya se empieza a tener un panorama amplio acerca de la evolución de los Neoceti. *Simocetus rayi* Fordyce 2002, *Waipatia mauhereana* Fordyce 1994 y *Notocetus vanbenedeni* Muizon 1987 son ejemplos de especies descritas en los últimos 25 años y que cambiaron la interpretación evolutiva de los odontocetos, pasando de un grupo unido por caracteres dentales plesiomórficos, los squalodontidos, a una visión mas integradora de la morfología craneal, como el levantamiento del vertex y el desplazamiento hacia posterior de los forámenes del nervio trigémino. Características morfológicas faciales relacionadas a la capacidad de ecolocalizar, la que es observada en los cráneos de odontocetos basales, como es el caso de *S. rayi* (Fordyce, 2002).

Por otro lado, el registro fósil de cetáceos en América del Sur e islas cercanas, según la última revisión (Cozzuol, 1996) incluye a una familia de Archaeoceti (Basilosauridae) y 15 familias de Neoceti: Llanocetidae (islas antárticas), Cetotheriidae, Balaenidae, Balaenopteridae (Mysticeti), Physeteridae, Ziphiidae, Squalodelphidae, Squalodontidae, Eurhinodelphidae, Iniidae, Pontoporiidae, Kentriodontidae, Phocoenidae, Odobenocetopsidae y Delphinidae (Odontoceti). Solamente nueve familias de Neoceti están registradas en Chile (Tabla 1). Hasta la fecha no hay registro de arqueocetos en el país, grupo que, en el continente, esta restringido a formaciones eocenas de Perú (Martínez et al., 2010; Uhen et al. 2011). Adicionalmente, restos fragmentarios (mandíbula con dientes) de un arqueoceto fueron registrados en Isla Seymour (Fm. La Meseta, Antártica; Buono *et al.*, 2011), como también una serie de dientes aislados de asignación incierta (Borsuk-Bialynicka, 1988; Fostowicz-Frelik, 2003; Jadwiszczak, 2006). La diversidad encontrada en Perú y los registros de Antártica sugiere que la ausencia de registro fósil de arqueocetos en Chile es transitoria, incrementando la importancia de realizar búsquedas sistemáticas enfocadas en sedimentos marinos paleógenos tales como la Fm. Loreto (Sierra Dorotea, Region de Magallanes) en donde fueron documentados restos fósiles de aves (Yury-Yanez *et al.* 2011; ver capítulo X).

V. 2. 1. Los cetáceos fósiles en Chile

Debido al amplio registro geológico marino del país (la mayor parte de lo que hoy es el territorio nacional, estuvo cubierto por océanos o mares someros epicontinentales), los Cetáceos son parte importante del patrimonio paleontológico de Chile, estando registrados abundantemente en las cuencas sedimentarias marinas cenozoicas. Sin embargo, casi la totalidad de los especímenes de cetáceos fósiles chilenos están restringidos al Neógeno, período comprendido entre los 23 y los 1,8 millones de años antes del presente, lo que es equivalente a las épocas Mioceno y Plioceno, del más antiguo al más reciente.

En 1887, R. Philippi reportó los primeros restos fósiles de cetáceos en Chile, que corresponden a un Misticeto de Ancud, Región de Los Lagos (posiblemente Fm. Lacuí), *Balaena simpsoni* (*nomen nudum*)„ y a un odontoceto, *Delphinus domeykoi* (*nomen nudum*)„ de la localidad de La Cueva, probablemente Fm. la Cueva (Plioceno Superior – Encinas *et al.* 2006). Posteriormente, Gigoux (1899) reportó una ballena fósil que afloraba durante la marea baja en la Playa del Cable (Caldera, Región de Atacama), sin embargo, esta no fue colectada. Oliver-Schneider (1926, 1927 y 1935) hizo una serie de listados de las especies de cetáceos fósiles incluyendo las familias Balaenidae, Balaenopteridae, Cetotheridae y Delphinidae. Sin embargo, la mayor parte de los registros de esa época no fueron colectados y/o no se encuentran en museos o colecciones científicas, por lo que no es posible corroborarlos actualmente.

El estudio de los cetáceos fósiles se dio apenas de manera tangencial durante los años subsiguientes. Ya en las últimas décadas, Tavera (1979) reporta la presencia de vértebras aisladas y de un esqueleto completo (en las dependencias del MNHN, pero sin número de colección) de *Balaena*? *simpsoni* provenientes del Neógeno de la localidad de Boca del Río Rapel (Formación

Navidad). Donoso-Barros (1975) publicó una revisión sumaria de los cetáceos fósiles de Chile, Tamayo y Frassinetti (1980) registran los mamíferos fósiles y vivientes y posteriormente, Frassinetti (1982) realizó una revisión de la literatura acerca de mamíferos fósiles del país, en la cual son citados y comentados los trabajados citados aquí, pero en esta ocasion no se verifico la identificación ni la existencia de los especímenes en las colecciones.

También existe una serie de registros informales en resúmenes de congresos que intentaban dar cuenta de la gran diversidad y abundancia de los restos de vertebrados en Caldera (Fm. Bahía Inglesa, Mioceno medio-Plioceno tardío, Canto et al., 2002; Quilodrán, 2002; Domínguez y Brito 2001; entre otros). Sin embargo, en general, los especímenes asignados a diferentes taxa fueron apenas mencionados, sobre todo en el caso de los odontocetos, muchas veces sin referencia a números de colecciones o fotos, haciendo imposible la corroboración de dichos registros. Por ejemplo, en la Fm. Coquimbo (Región de Coquimbo) fueron reportados restos fósiles atribuidos a misticetos (Plioceno; Salinas, 1988; Canto y Yáñez, 1991) que habrían sido colectados e ingresados en la colección de la Universidad Católica del Norte de Coquimbo, pero no se ha reportado su número de acceso lo que nos impidió corroborar la existencia y/o asignación taxonómica de este espécimen.

La revisión mas reciente de los registros de cetáceos del país fue realizada por Donoso-Barros en 1975, sin embargo, una revisión crítica no ha sido efectuada hasta el momento, por lo que estos no han podido ser confirmados y apenas han sido referidos a los trabajos anteriores de Philippi y Oliver-Schneider (op. cit.). Por lo que se hace necesario el estudio y descripción sistemática, bien como una revisión completa de los registros existente de manera a identificar los registros todavía válidos y así conocer la real diversidad de cetáceos fósiles.

V. 2. 2. Abreviaciones Institucionales y Terminología

SGO.PV, Sección Paleontología, Museo Nacional de Historia Natural, Santiago, Chile; **MPC**, Museo Paleontológico de Caldera, Municipalidad de Caldera, Región de Atacama, Chile. **MNHN**, Museo Nacional de Historia Natural de Chile.

V. 3. Depósitos del Neógeno Marino en Chile

El Neógeno es un período de grandes transformaciones geomorfológicas y consecuentemente ambientales, especialmente en la región que es hoy el territorio de Chile. Se estima la presencia de un evento tectónico con consecuencias globales, una erosión por debajo de la placa continental que ocasionó transgresiones marinas en diversas localidades (en Nueva Zelanda, Costa rica y Guatemala) lo que podría ser atribuido como la origen de las cuencas neógenas marinas de Chile (Encinas *et al.* 2006). De manera mas local, tres grandes acontecimientos ocurrieron en el devenir de este período (~30 - 2 m.a.): los dos últimos puntos altos de la orogénesis andina, lo que produce en el Norte de Chile una altitud promedio estimada en mas de 2000m de altitud (Reich *et al.,* 2006); como consecuencia, el establecimiento de la sombra de lluvia de la cordillera de los Andes favoreciendo la expansión de la Diagonal Árida y del Desierto de Atacama. Además, de manera virtualmente sincrónica, se establece la corriente de Humboldt, la que ciertamente interfiere también en la formación y mantención de la ya mencionada Diagonal Árida. Más específicamente en el ambiente marino, ocurren una serie de transgresiones y regresiones conocidas a nivel global, sobretodo durante el Mioceno, pero con el fuerte tectonismo de la costa chilena como componente local. Esto es evidenciado por los depósitos de la Fm. Coquimbo (LeRoux *et al.,* 2006), Bahía Inglesa (Marquardt,1999; Achurra, 2004; Achurra et. al., 2009), Mejillones (Marquardt *et al.,* 2004), Ranquil y Lacuí (Finger *et al.,* 2007), que consisten en varios metros de sedimentos marinos neógenos ubicados sobre el nivel del mar actual.

Tales eventos geológicos debieron generar cambios considerables en los ambientes marinos los que pueden estar relacionados con el establecimiento, diversificación y origen de ciertos grupos de vertebrados, incluyendo los cetáceos. Específicamente, el levantamiento del Morro Copiapó en la cuenca sedimentaria de Caldera, de manera contemporánea con la deposición de sedimentos de la Fm. Bahía Inglesa, generó cambios de batimetría de la cuenca (Achurra, 2004), incrementando el aporte de sedimentos a la misma (A. Mourgues com. pers., 2009) lo que ciertamente habría facilitado el proceso de fosilización de la tanatocenosis de la cuenca, haciendola más probable y mejor preservado como indican los trabajos en evolución (Gutstein *et al.*, 2007; Rubilar-Rogers *et al.*, 2009; Pyenson *et al.*, 2010). A continuación se describe sumariamente las formaciones en que se han reportado cetáceos fósiles ordenados por ubicación geográfica de norte a sur.

En la Región de Atacama, se destaca la **Formación Bahía Inglesa** descrita por Rojo (1985) y enmendada por Marquardt (1999) y que data del Mioceno medio - Plioceno tardío (Achurra, 2004; Achurra *et al.*, 2009). La Fm. Bahía Inglesa está ubicada a lo largo del borde costero del desierto de Atacama en la región homónima y presenta una diversidad sin precedentes, que pese al apenas reciente estudio sistemático ya cuenta con cerca de 70 taxa reconocidos, entre ellos, peces, reptiles aves y mamíferos (Walsh y Suarez, 2005). Esta abundancia convierte el yacimiento en uno de los mas importantes en fauna de vertebrados marinos de Chile e incluso una de las más relevantes del continente. Esa formación presenta una fauna de cetáceos diversa con 11 géneros distintos, en su mayoría de odontocetos. En la localidad de Mina fosforita, Fm. Bahía Inglesa se han hecho muchos hallazgos recientes, perfilando este sitio como un candidato a la categoría de Parque Paleontológico, dada la relevancia del yacimiento. El "bonebed" (capa de huesos) es el nivel mejor estudiado con 66 taxa reconocidos en la última revisión (Gutstein *et al.*, 2008). Además existen nuevos sitios como "El Morro" que ofrecen acumulaciones de esqueletos parciales virtualmente completos de vertebrados (Gutstein *et al.*, 2007) y "Cerro Ballena" (Suárez *et al.*, 2010), en donde se han encontrado decenas de esqueletos completos y parcialmente completos de misticetos de la familia Balaenopteridae, pero todavía con contexto estratigrafico incierto dentro de la formación.

En el Norte chico, en el litoral de la Región de Coquimbo, la **Formación Coquimbo** (Mioceno Tardío-Plioceno, LeRoux *et al.*, 2006) ha sido poco estudiada en el contexto de los cetáceos. Aunque existen registros en la literatura de un Pontopórido asignado a *Pliopontos* sp. (Canto *et al.*, 2002), un género del Plioceno de la Fm. Pisco, y de Mysticeti (Salinas, 1988; Yañez y Canto, 1991), estos fueron hallazgos fortuitos, no habiéndose realizado prospección y/o excavación sistemática específica para recuperar restos de vertebrados. En términos geológicos, esta formación ha sido recientemente descrita a la luz de la estratigrafia de secuencias, habiéndose reconocido 13 unidades estratigráficas dentro de 5 secuencias transgresivo-regresiva, lo que además permitió caracterizar los ambientes, profundidades, cambios eustáticos y la tectónica localizada (LeRoux *et al.*, 2006).

El Plioceno en Chile Central, esta registrado en sedimentos que corresponden a los miembros o **formaciones Rapel y La Cueva,** según el autor. Los niveles atribuidos a Fm. Rapel representan un sistema deposicional diferente y que presenta discordancias con las formaciones Lincacheu (subyacente) y La Cueva (suprayacente) (Encinas *et al.*, 2006). La **Fm. o Miembro Licancheu** todavía no registra restos de cetáceos, en la literatura. La Fm. La Cueva, definida por Tavera (1979), es considerada Plioceno por la asociación de invertebrados encontrada en sus niveles. Esta Formación da la edad máxima a las Fm. Rapel y Lincancheu que no poseen evidencia bioestratigráfica o dataciones que permitan acotar sus edades.

La Formación Navidad (Mioceno tardío - Plioceno temprano) fue primeramente descrita por Darwin (1846). Dicha formación o el área de Navidad (con diversas formaciones según Encinas et al., 2006) comprende secuencias de areniscas, teniendo una edad y estratigrafía muy discutida (ver también Finger *et al.,* 2007; Nielsen y Glodny, 2009). La discrepancia entre estos autores probablemente esta dada por retrabajo y desplazamiento hacia zonas más profundas de sedimentos más antiguos todavía desconocidos (Finger *et al.,* 2007). Esos yacimientos fueron reconocidos como miembros (Licancheu, Rapel y Navidad) por Tavera (1968, 1979), entre otros ordenamientos (ver resumen en Encinas *et al.,* 2006) siendo más recientemente interpretados como una secuencia transgresiva marina depositada entre el Mioceno Tardío y el Plioceno Temprano (Encinas *et al.* 2006). Según esos autores, los miembros son elevados a formaciones geológicas independientes (Plioceno: Fm. Licancheu, Fm. Rapel y Fm. La Cueva) ya que encontraron discordancias sedimentarias entre ellos. Sin embargo, todavía no existe consenso entre los investigadores no habiendo una propuesta única de nomenclatura para dichas formaciones, los últimos trabajos parecen resaltar el hecho de que existe un importante retrabajo de los macrofósiles, los que serían de una edad y ambiente diferente al registrado por los microfósiles y sedimentos (Finger et al., 2007; Nielsen et al., 2009). Además, según los mismos autores, las formaciones Navidad (*sensu* Encinas et al., 2006), Ranquil y Lacuí se formaron por acción del mismo conjunto de eventos geológicos (tectónica, sedimentación, etc). En el área de Navidad es posible encontrar restos fósiles de una diversa fauna marina, tales como moluscos (bivalvos, pelecypodos, gastrópodos, escafópodos y cefalópodos), artrópodos (crustáceos), equinodermos, briozoos y braquiópodos. En la localidad de Punta Perro. en areniscas amarillo-café características de la unidad 2 de la sucesión sedimentaria de Suárez *et al.* (2006), se registran fósiles de vertebrados: dientes de tiburón, restos de peces óseos y restos no determinados de cetáceos.

En general, los fósiles tanto aislados como articulados de misticetos son muy numerosos en todo la porción costera del territorio nacional. Contradictoriamente, son poco representados en las colecciones institucionales, eso debido, en parte, a la complicada logística para la excavación de dichos especímenes, siendo a la vez extremadamente frágiles y de gran tamaño. A continuación se detallan algunos de estos especímenes citados en la literatura.

V. 4. Mysticeti

Como fue mencionado por Tamayo y Frassinetti (1980), Oliver (1927) habría asignado todos los restos de misticetos como pertenecientes a *N.*

simpsoni, pero posteriormente (Oliver, 1935) reconsideró esta opinión, dejando la asignación de esta especie exclusivamente a la ballena descrita anteriormente por Philippi (ver abajo). Estos materiales fueron solamente mencionados en la literatura (Tavera, 1979 Tamayo y Frassinetti, 1980), y no se encuentran en colecciones ni tampoco en fotos o dibujos en los artículos citados, por lo que no pueden ser corroborados. El holotipo de *B. simpsoni* Philippi 1887 o *N. simpsoni* (Oliver, 1927, 1935), proveniente de la localidad de Ancud (Isla de Chiloé, Región de los Lagos), consistía en una placa occipital, fragmento de la mandíbula, seis vértebras y apófisis dorsales todavía en la matriz. La asignación a un nuevo táxon ya había sido cuestionada por Cabrera (1926), quien señaló que podrían, incluso, no corresponder a la familia Balaenidae. Además, del holotipo (SGO.PV S/N) apenas perduran en las colecciones del MNHN un fragmento de cráneo que incluye el occipital, lo que no permite diagnosis precisa, ya que las características diagnósticas se encuentran en la región facial del cráneo (morfología y relación entre los huesos nasal, frontal, parietal, maxilla y premaxilla en la porción facial) entre otros. El cóndilo occipital presenta un alto grado de porosidad, lo que junto con el tamaño, permite clasificar el material como Mysticeti. La morfología lateromedialmente comprimida del escudo occipital, es similar al observado en el género actual *Caperea*, lo que probablemente (aunque no mencionado) fue utilizado para asignar el especimen, en Tamayo y Frassineti (1980), al genero actual *Caperea*, asignándolo a la nueva combinación *C. simpsoni*. Sin embargo, estas asignaciones necesitan ser revisadas y más material debe ser analizado antes que se pueda confirmar su asignación taxonómica, por lo que preliminarmente se considerara como un misticeto indeterminado. De la misma manera, los otros materiales citados, como vértebras aisladas (Tavera, 1979) y un ejemplar virtualmente completo de *Neobalaena simpsoni* (Oliver 1927, 1935) de las Formaciones Licancheo y Navidad (Tavera, 1979, p. 32 y 75), Área de Navidad, también permanecen indeterminados.

Aún en el registro de Misticetos, fueron reportados por Salinas (1988) el hallazgo de dos esqueletos articulados con exposición de cráneo, columna vertebral casi completa y porciones de lo miembros anteriores. Los cuales fueron ilustrados (fotografías y dibujos) pero sin referencias a su local de resguardo o número de colección y/o terreno. Los esqueletos reportados por Salinas (1988) no fueron colectados en esta ocasión. La misma autora asignó dichos esqueletos a Balaenopteriidae por la separación entre las vértebras cervicales. Según Yáñez y Canto (1991) esta diagnosis fue equivocada ya que el cráneo que figura en ambos artículos posee el arqueamiento del rostro característico de Balaenidae. Además los autores señalan que el carácter de las vértebras cervicales no puede ser corroborado ya que el fósil no fue recolectado. Sin embargo, la falta de material colectado también es un problema para corroborar el carácter señalado por estos autores (arqueamiento del rostro) lo que no puede ser confirmado por las imágenes disponibles, pudiéndose tratar de una deformación por diagénesis, un artefacto producto de la paralaxia (las fotos están tomadas en vista dorso-lateral). A ese último factor se suma el hecho de que esa característica es distinta en el dibujo y en la foto, y que además difiere entre los dos esqueletos reportados. Además el carácter señalado por Salinas (1988) "separación de las vértebras cervicales" excluye la asignación a Balaenidae pero podría ser atribuido a un Cetotheridae (familia de misticetos extinta). Por la ausencia de evidencias craneales diagnósticas (forma del maxillar, nasal, parietal, entre otros), que al parecer no fueron observadas, y con la imposibilidad de revisar los materiales, aquí se considerará la asignación a Mysticeti *indet.* proveniente de los niveles pliocenos de la Formación Coquimbo.

Adicionalmente, existe el registro de Misticetos indeterminados de la Fm. Bahía Inglesa (Gutstein et al., 2006, 2008). Domínguez y Brito (2002) habían asignado los restos de MPC0001 (Fig. 3) a un Balaenidae. Una descripcion formal es necesaria para concluir la asignación taxonómica, ya que el especimen consiste en un cráneo completo y fue atribuido a una edad antigua para la familia (Mioceno medio). Sin embargo, la forma del rostro es ensanchada y no estrecha como en los Balaenidae, sugiriendo mas bien una afinidad con Balaenopteriidae o Cetotheridae. Existen registros mas antiguos de misticetos modernos (*crown-group*; ej.: *Morenocetus* un Balaenidae del Mioceno temprano de Argentina, Fm. Gayman; Cabrera, 1926, Cione et al., 2011; Churchill et al., 2011), sin embargo de tratarse de un taxón de los Balaenopteriidae modernos (*crown group*) podría indicar una edad más antigua para este (Pyenson, comunicación personal, nov. 2009). Desde luego, la descripción formal y estudio acabado de este material se hace necesario.

El registro de Mysticeti en Chile es amplio, abundante y aparentemente diverso, presentando a lo menos diferentes clases de tamaño. Sin embargo, esto no se condice con los especímenes conservados en las colecciones, debido en parte por el desafío logístico que representa la excavación y extracción de una ballena completa. Pero tal vez un argumento más importante es la falta de estudios sistemáticos en paleontología y en especial en misticetos, no habiendo ningún ejemplo de estudio sistemático del grupo en el país. Tal situación debiese motivar a jóvenes científicos en el estudio de este grupo tan ampliamente registrado en Chile, sobretodo en el neógeno tardío.

V. 5. Odontoceti

El más antiguo registro de un odontoceto fósil (en la literatura) en Chile es el de Phillippi (1887), quien describió dos huesos fragmentarios de la aleta pectoral, nombrando una nueva especie, *Delphinus domeykoi* (Fig. 4). Los materiales asignados al holotipo (SGO.PV 6018) consisten en dos huesos que según el mismo autor corresponderían al cúbito (ulna) y el radio de la mano derecha, ambos provenientes de la localidad de La Cueva, Colchagua, Región del Libertador Bernardo O'Higgins (Fm. La Cueva, Plioceno; Encinas et al. 2006). Este material fue reportado posteriormente por Tamayo y Frassinetti (1980) que señalan lo fragmentario del registro. Debido a la escasez de materiales y de la poca información diagnóstica que estos restos fragmentarios ofrecen se asignan estos restos a Odontoceti *indet.*, ya que, además, por su gran tamaño se puede descartar la pertenencia al género *Delphinus.* Adicionalmente, el especímen SGO.PV 6018b identificado como cúbito derecho (=ulna) por Philippi (1887) es en verdad correspondiente a un húmero izquierdo, ya que presenta la articulación bipartida para la ulna y el radio, además del oleacranon muy poco desarrollado en el borde superior. El ejemplar SGO.PV 6018a si corresponde a la porción distal del radio, pero izquierdo, ya que presenta la faceta de contacto distal con la ulna en el borde medial, en forma triangular, y el borde externo más afilado en forma de quilla. De todas maneras es dificil asegurar a que ambos especimenes pertanezcan a un mismo individuo, ya que tampoco se cuentan con datos de colecta. La textura del hueso (poco porosos) permite descartar la asignacion a Mysticeti y asignar provisoriamente a Odontoceti, aunque su tamaño, grande y alargado (sobretodo del radio) descartan la pertenencia a Delphinidae, haciendo que *Delphinus domeykoi* sea considerado aquí *nomen nudum.*

V. 5. 1. Delphinida

Definido por Muizon (1988), Delphinida es considerado monofilético hasta hoy día, con apenas algunas modificaciones. Análisis moleculares lo emplazan un poco más basalmente, incluyendo a *Platanista* y bautizándolo con un nuevo nombre, Pandelphinida (May-Collado et al., 2007). Utilizaremos el término Delphinida (Pandelphinida es definido en base a análisis moleculares que no incluyen especies fósiles) para referirnos al grupo que comprende los Inioidea ("delfines de río sudamericanos") y Delphinoidea (delfines y marsopas modernos). Este grupo surge en el Mioceno temprano, con registros cosmopolitas de Kentriodontidae (Muizon y Fordyce, 2001). Luego esta familia se diversifica, aunque cabe la duda si no se trata de un grupo parafilético o incluso polifilético, dado que análisis filogenéticos que testeen su monofilia no han sido realizados. Y posteriormente, en el Mioceno medio-tardío las demás familias están todas representadas y diversificadas, habiendo un recambio faunístico con la desaparición de los Kentriodontidae en el registro fósil, origen y diversificación los demás Delphinoidea. Por otro lado, su grupo hermano, los Inioidea, alcanzan su máxima diversificación durante el Mioceno Tardío y Plioceno, habiendo actualmente apenas dos especies. Aparentemente este grupo también fue sustituido con la creciente diversificación ocurrida en Delphinidae sobretodo en el Plioceno, lo que es visible hoy en día, ya que los Delphinidae son la familia mas común, bien distribuida y diversa en nuestros litorales (Shirihai y Jarrett, 2009).

V. 5. 2. Inioidea

Los Inioidea son tradicionalmente conocidos como los delfines de río de América del Sur, aunque al analizar el registro fósil esta definición ya no tiene cabida. Se compone de dos o tres familias, dependiendo del autor, siendo

Pontoporiidae y Iniidae siempre presentes, ambos restringidos a los sistemas fluviales y costeros de la porción atlántica de Sudamérica en la actualidad, sin embargo, en el Neógeno tardío, estas dos familias se encuentran en localidades tan lejanas como la costa atlántica de los EE.UU., *Goniodelphis hudsoni* Allen 1941 de los estratos del Mioceno tardío-Plioceno temprano de la Fm. Bone Valley (Hemphiliano, NALMA; Sellards, 1915; Morgan, 1994) en Florida. En el mar del Norte también se encuentran restos comúnmente atribuidos a Pontoporiidae, como especimenes de cf. *Pontistes* y aff. *Brachydelphis* (Pyenson y Hoch, 2007) y *Protophocoena minima* (Lambert y Post, 2005). Aunque representadas por material fragmentario, son registros marinos que sugieren una distribución más bien cosmopolita que endémica a un continente, cambiando radicalmente la visión evolutiva y biogeográfica del grupo. En el caso de *Goniodelphis* la Fm. Bone Valley (Florida, E.E.U.U.) está marcada por una fuerte mezcla de ambientes a juzgar por los taxa de vertebrados, siendo posible el hábito fluvial o marino para la especie.

En Chile, en los niveles de la Fm. Bahía Inglesa (Mioceno tardío), se destaca la presencia masiva de restos de Inioidea, como es el caso del género *Brachydelphis* (Cozzuol 2010, Geisler *et al.*, 2011). Este genero posee relevancia sistemática generando controversia entre los distintos autores, siendo asignado a Pontoporiidae (*sensu* Muizon, 1988), Platanistoidea (*sensu* Geisler y Sanders, 2003), Brachydelphidae (Cozzuol, 2010) e Inioidea (Geisler *et al.*, 2011), dependiendo del autor. Así como también son comunes los especímenes asignados a los géneros *Pliopontos* sp. y *Pontistes* sp., asignados a Pontoporiidae (Muizon, 1988), aunque ambos fueron apenas mencionados, sin una descripción formal (Gutstein et al., 2006, 2008).

El género *Brachydelphis* fue descrito como un Pontporiidae derivado, fundador de la Subfamilia Brachydelphininae (Muizon 1988a,b) pero revisiones recientes (Gutstein *et al.,* 2009; Cozzuol, 2010) lo sugieren como taxón basal de Inioidea (*sensu* Muizon, 1988b) o a lo menos no dentro de Pontoporiidae (Geisler *et al.,* 2011). Además, se ha descrito una nueva forma para la Fm. Bahía Inglesa, también presente en la Fm. Pisco (Perú), hasta el momento apenas descrita como una nueva forma del género *Brachydelphis,* dada la semejanza con la especie tipo del género, pero sin ser nombrada como nueva especie dada la falta de materiales más completos y también debido a la gran variación presente en *Brachydelphis mazeasi* y en la especie actual *Pontoporia blainvillei* (Gutstein *et al.,* 2009). La nueva forma se caracteriza por presentar un rostro largo, polidontia (en comparación a *Brachydelphis mazeasi*, pero no en relación a *P. blainvilei*), de mayor tamaño en general y con un surco entre los nasales. Además presenta una excavación en la porción lateral del nasal, caracteres considerados diagnósticos para *Stenasodelphis russelae* Godfrey y Barnes, 2008 del Mioceno tardío de la Fm. St. Marys (Maryland, E.E.U.U.). Mas estudios son necesarios pero al parecer *Brachydelphis* n. form. (Fm. Bahia Inglesa y Fm. Pisco) y *S. russelae* (Fm. St. Marys) podrían corresponder al mismo taxón, estando presente en el Pacifico Sur y Norte, similar la distribución antitropical observada en los Phocoenidae (Barnes, 1985b). Otra situación de posible sinonimia y distribucion en ambos hemisferios, ocurre con *Auroracetus bakerae* Gibson y Geisler 2009 (Plioceno de Carolina del Norte, E.E.U.U.) que es una especie basada en un especimen juvenil, y probablemente un neonato, dado la ausencia de fusion en la mayor parte de los huesos craneales. Esto hace que los caracteres diagnosticos sean dudosos, ya que por ejemplo el premaxillar reducido mencionado en su diagnosis (Gibson y Geisler 2009) es un carácter observado en especimenes juveniles de Brachydelphis y Pontoporia (Gutstein et al. 2009).

Restos craneales fueron identificados como *Pliopontos* sp. (SGO.PV 967, ver Figura 6) por presentar el proceso premaxilar posterolateral mas desarrollado que el proceso medial, característica observada apenas en *Pliopontos littoralis* dentro de todos los demás Pontoporiidae. También posee crestas maxilares como en *Pliopontos* y *Pontoporia* pero menos desarrolladas que en *Brachydelphis*. Cráneo plano, con vertex poco prominente y cuenca prenarial poco desarrollada, similar a los demás Pontoporiidae. El género monoespecífico, *Pliopontos*, fue creado por Muizon (1983) para describir especímenes (craneos) del Plioceno de la Fm. Pisco y fue considerado un táxon guía para niveles pliocenos de esta formación. Su presencia en el Mioceno tardío de Chile aumenta su rango de distribución espacial y temporal.

Canto *et al.* (2002) asigna restos postcraneales (secuencia vertebral) provenientes de niveles pliocenos de la Fm. Coquimbo al género *Pliopontos* sp.

Sin embargo, el especímen no está asociado o articulado a restos craneales por lo que no se pueden reconocer los caracteres diagnósticos del género. La determinación desempeñada por Canto *et al.* (2000) no pudo ser corroborada en el presente análisis ya que carecía de caracteres diagnósticos (los que son apenas craneales en *P. littoralis*) y el análisis morfométrico y estadístico llevado a cabo por los autores mencionados presentan problemas conceptuales (e.g.: atribuyen los ejes X e Y al holotipo de *Pliopontos littoralis* y SGO.PV 305, respectivamente; ver fig. 1 en Canto *et al.,* 2002). Es decir, los autores consideran los especímenes como variables en vez de las medidas tomadas, lo que viola los supuestos de una regresión lineal (Zar, 1996). Al parecer los autores trataron de realizar un análisis multivariado (considerando todas las medidas) con apenas dos especimenes y utilizando una herramienta de análisis bivariada, como la regresión lineal. Por lo tanto, el resultado estadísticamente significativo es un artefacto del mal uso del coeficiente de determinación de Pearson (r^2).

Sin embargo, aunque Muizon (1988) no cita caracteres postcraneales en la definición de Pontoporiidae, *P. blainvillei* presenta una morfología vertebral peculiar y única, con los procesos transversos achatados dorsoventralmente y ensanchados latero-medialmente (observación personal) muy semejantes al especimen de la Fm. Coquimbo, permitiendo la asignacion preliminar a Pontoporiidae.

Este registro reafirma, junto con los depósitos de la Fm. B. Inglesa, la importancia del grupo Inioidea como un componente de la fauna de cetáceos de Chile, ya señalada en la Formación Pisco (Perú; Muizon 1983, 1988). Esto es interesante ya que esta familia no esta presente en el Pacífico en la actualidad y, sin embargo, en el Neógeno eran cetáceos relativamente comunes.

Por otro lado, especimenes craneales preservados en vista dorsal (MPC 3052, SGO.PV 964, ver Figura 5), de la localidad de Mina fosforita de la Fm. Bahía Inglesa fueron previamente mencionados y referidos a cf. *Pontistes* por Gutstein *et al.* (2008). El género *Pontistes* fue creado por Burmeister (1885) cuando describió la especie *P. rectifrons*, proveniente de sedimentos del Mioceno tardío marino de la Fm. Ituzaingó en el Noreste de Argentina. El holotipo es un cráneo parcial, donde se observa los premaxilares con un proceso posterolateral y uno posteromedial a la diferencia de los otros generos (*Brachydelphis*, apenas posteromedial; *Pontoporia* y *Pliopontos*, apenas posterolateral). Rasgo que presenta el especimen de Bahía Inglesa, así como la ausencia de crestas maxilares; placa premaxillar (fossa premaxillar en los demás odontocetos) elavada, plana y recta. El registro de *Pontistes* sp. amplia la distribucion del género para el Océano Pacifico. Siendo anteriormente conocido en el Atlántico Norte (Pyenson and Hoch, 2007) y Sur (Burmeister, 1885; Cozzuol, 1996).

V. 5. 3. Delphinoidea

Delphinoidea, como definido por Muizon (1988b), agrupa a las familias relacionadas a los delfines actuales, que se tornaron dominantes en las asociaciones marinas de odontocetos, sobretodo después del Neógeno tardío. Su origen es muy debatido, habiéndose considerado por mucho tiempo que una familia primitiva habría dado origen a la super familia, la familia Kentriodontidae, como definida por Barnes (1985a). En su sentido tradicional (Muizon 1988b) los Delphinoidea incluyen a las familias: Kentriodontidae, Phocoenidae, Delphinidae y Monodontidae. De las cuales la familia Phocoenidae esta mejor representada en Chile. Kentriodontidae y Monodontidae no se encuentra en la literatura, y Delphinidae esta pobremente mencionada en resúmenes de congreso (Gutstein *et al.*, 2006). En general, especimenes atribuibles a cualquier grupo dentro de Delphinoidea son escasamente registrados para las formaciones neógenas de Chile. Esfuerzos de colecta y estudio sistemáticos en diversas localidad de de la Fm. Bahía Inglesa vienen siendo realizados desde el año 2009, ya siendo posible apreciar un incremento de especimenes de Delphinoidea modernos e incluso de Kentriodontidae (Delphinoidea basal, Rubilar-Rogers *et al.*, 2009, Pyenson *et al.*, 2011a y b) respecto de la última revisión (Gutstein *et al.*, 2008), sugiriendo que este hecho este más relacionado a la falta de esfuerzos sistemáticos que a la ausencia o poca representatividad de este grupo en los depósitos neógenos del país.

Los Phocoenidae son una familia de Delphinoidea que se diversifica junto con los Delphinidae en el Mioceno tardío (*crown-group*). Se ha postulado que la historia evolutiva de los phocenidos (marsopas) estaría ligada al Hemisfério Norte (Fordyce, 2009), sin embargo, esto no puede ser asegurado debido a la falta de estudios en diversas formaciones del neógeno tardío, destacándose las formaciones sudamericanas e incluso de Chile. Gutstein *et al.* (2008) listaron la familia Phocoenidae en los registros del "bonebed" de la Fm. Bahia Inglesa, con base en un cráneo parcial en vista dorsal (MPC 0004). Además de un cráneo preservado apenas en vista ventral (MPC), siendo muy similar a *Lomacetus* y *Piscolithax* (Gutstein *et al.*, 2008), ambos géneros fueron descritos para la Fm. Pisco, siendo el primero del Mioceno tardío y el segundo del intervalo Mioceno-Plioceno (Muizon, 1988, 1984). Fordyce (2009) hace referencia a que el registro de los Phocoenidae empieza en el Mioceno tardío, sin embargo, los registros de Phocoenidae modernos (*crown-group*) no se separan temporalmente de los Phocoenidae basales (*stem-group*) no aportando para acotar el origen y la diversificación de la familia. El registro más antiguo de Phocoenidae basal es de la Fm. Monterey (Mioceno tardío), *Salumniphocoena stocktoni* Wilson 1973.

La distribución de los registros de Phocoenidae están usualmente restringidos en la zona tropical del Pacifico Norte y Este (Fordyce, 2009), sin embargo, los registros de Chile (Gutstein *et al.*, 2008), amplían su rango a la zona subtropical durante el Neógeno.

Existe un registro (Yañez *et al.*, 1994) de una especie actual de la familia que habita la costa de Chile, *Phocoena spinipinnis,* basado en un espécimen que se encuentra en exhibición en el Museo de Historia Natural de Concepción (s/n), sin embargo, no es posible descartar que sea mas bien un registro histórico (Holoceno) dada la falta de información de procedencia y la información entregada respecto de los foraminíferos del sedimento colectado del espécimen. En efecto, la presencia de un foraminífero con rango de distribución exclusivamente actual, hace mas probable que este corresponda a un espécimen del fondo marino actual. Dichos restos históricos son comúnes y muchas veces se encuentran mineralizados (no en este caso), siendo en algunos casos confundidos con registro fósil.

V. 5. 4. Ziphioidea

Las ballenas picudas o los zifios son odontocetos que perdieron sus dientes (a excepción de un par en los machos) y desarrollaron una gran diversidad de formas en el vértex craneal, siendo la asimetría en la cresta premaxillar[69] una característica conspicua y variada en la familia (Bianucci et al., 2007: Fig. 33-3), y un hocico alargado, producto de su especialización alimenticia conocida como "suction feeding" (alimentación por succión). La familia tiene registros entre el Mioceno y el Plioceno temprano, *Squaloziphis*

---

[69] Cresta formada por el engruesamiento en el proceso nasal del premaxilar (*sensu* Mead y Fordyce 2009) la sutura con el nasal y el frontal, es considerada diagnostica para la familia (Lambert 2005, Bianucci et al. 2007).

emlongi Muizon 1991, fue descrito como el zifio mas antiguo (Mioceno inferior), sin embargo, existe discusión acerca de la validez de su asignación a Ziphidae (Lambert, 2005).

Los registros de zifios fósiles del hemisferio Norte suman 8 géneros y 12 especies y los mas recientemente estudiados fósiles de Sudáfrica registrando 8 géneros y 10 especies. En América del Sur, existen 3 especies descritas para la Fm. Pisco (Peru; Bianucci *et al.,* 2009, Lambert *et al.,* 2010), donde se encuentra además una gran concentración de zifios (8 esqueletos asociados. Bianucci *et al.,* 2010).

En contraste, los zifios son escasos en el registro de cetáceos de Chile pudiéndose encontrar apenas una mención de un diente (MPC 227) del bonebed de la Fm. Bahia inglesa (Gutstein *et al.,* 2008). El especimen consiste en un diente con la base robusta y de forma rectangular, como observado en zifios como *Ninoziphius platyrostris* Muizon 1983 o *Ziphiorostrum marginatun* (Lambert, 2005).

V. 5. 5. Physeteroidea

Physeteroidea compreende las familias Kogiidae y Physeteriidae y fue originada en el Oligoceno con *Ferecetotherium* Mchelidze, 1970. Al igual que la mayor parte de los grupos de odontocetos, alcanzó su maxima diversificación durante el Mioceno (Kazár, 2002; Fordyce, 2009). Ejemplos de registros en el Mioceno temprano son *Idiorophus patagonicus* Lydeker 1894 y *Diaphorocetus* de Argentina.

La familia Physeteridae es reconocida principalmente por la modificación de los huesos faciales. La familia es caracterizada por presentar una región cóncava que ocupa toda la porción facial y parte del rostro, la cuenca supracranial dorsal (Heyning, 1989). Esta estructura ósea esta relacionada principalmente al órgano exclusivo de la superfamilia (Physeteroidea) el espermaceti, como observado en fisetéridos vivientes (cachalotes).

aff. *Idiorophus* Kellogg 1925

Existe registro de una porción mediana del rostro, con porción mandibular, maxilar y dientes articulados (SGO.PV 250) provenientes de la localidad de Sur de Rio Rapel (desembocadura), equivalente al Mioceno tardío según Encinas et al. (2006) y Nielsen y Glodny (2009). Covacevich y Frassinetti (1986) hacen alusión a la edad y locación de estos materiales como Mioceno medio-tardío, aunque los restos no fueron encontrados *in situ*, pero los estudios anteriores los sitúan a nivel de la Fm. Licancheu.

SGO.PV 250 fue mencionado como Odontoceti indet. (Tamayo y

Frassinetti, 1980) y como Physeteriidae indet. (Canto, 2007). Aquí se asigna a Physeteriidae con afinidad al género *Idiorophus* Kellogg 1925 por presentar dientes cónicos con esmalte con líneas longitudinales en la corona, dientes alargados y afilados en la extremidad distal, que también es curvada hacia posterior. El rostro es afilado, con los maxilares no visibles en vista dorsal, posicionados abajo de los premaxilares, siendo este un carácter plástico también observado en otros taxa de rostros largos como en *Pontoporia*, *Inia*, *Platanista*. El espécimen presenta sínfisis mandibular fusionada en toda la porción preservada concordante con lo observado en los Physeteriidae. Estos poseen una sínfisis alargada, extendiéndose mas de la mitad del largo de la mandíbula. No obstante, presenta dientes mandibulares y maxilares /premaxilares, lo que no ocurre en los Physeteridae modernos, pero si en las especies fósiles (Hampe, 2006). El género *Idiorophus* viene siendo utilizado (Uhen et al., 2008), después de ser validado, sinonimizando varios otros géneros como *Apenophyseter* (ahora *nomen dubium*) creados durante el último siglo, la mayoría de ellos basados en material bastante fragmentario. La morfología de la mandíbula en sección transversal se asemeja mucho a la observada en *Idiorophus*, por presentar los alveolos inclinados muy profundos, bien como un canal meckelianno expandido y dispuestos separadamente. Además la forma ventral de la unión de las hemi-mandibulas no es dividida como en *Physeter* y *Aulophyseter* (como ilustrado en Cozzuol, 1988).

Por otro lado, la morfología de los dientes también se asemeja a la de

Idiorophus, siendo alargados, sin embargo, la morfología dentaria así como la mandibular puede ser muy variable y en muchos casos convergente, por lo que no podemos hacer una asignación taxonómica mas precisa, por lo incompleto del fósil. De todas maneras, este especimen representa el primer registro de Physeteriidae en la Fm. Navidad.

aff. *Scaldicetus* Du Bus 1867

La validez del genero *Scaldicetus* ha sido cuestionada ya que se basa en especímenes fragmentarios y existe un gran numero de especímenes reconocidos casi exclusivamente por caracteres dentales, los cuales suelen ser homoplásicos (convergentes o simplemente plesiomórficos) (Hampe, 2006). Sin embargo, si se tiene en cuenta que se tratan de morfotipos, pueden ser usados con fines prácticos. Los especímenes reportados en Gutstein et al. (2008) corresponden a dientes de diferentes rangos de tamaño, por lo que corresponden a diferentes morfotipos. De esta manera, los dientes aislados mencionados en Gutstein *et al.* (2008; MPC 0008-20, 0057-60, 0070-78, 0214, 0215) corresponden a una serie bastante grande de dientes de cf. *Scaldicetus*. Estos se diferencian de los dientes de Hoplocetinae por no presentar la corona separada por un "cuello" alargado (Hampe, 2006). Al margen de la discusión de la validez de este taxón, los dientes ilustrados (Figura 7) son semejantes a los comúnmente atribuidos a este género.

Dentro de los grandes odontocetos están los nuevos registros de Physeteriidae de la Fm. Bahía Inglesa, siendo además una nueva forma de Hoplocetinae, *Livyathan melvillei* Lambert *et al.* 2010 que presenta dientes desproporcionadamente grandes para su tamaño corporal e incluso de cabeza, siendo la proporción de la cabeza con el resto del cuerpo menor que en *Physeter macrocephalus*. El tamaño del diente es al menos el doble del tamaño del diente de un cachalote actual, midiendo 12 cm de diámetro y 36 cm de largo. Pyenson et al. (2011) mencionan la presencia de *Livyathan* en Chile (en la Fm. Bahía Inglesa) aunque el especimen se encuentre todavía en estudio.

Kogiidae *indet.*

Se registra un periótico aislado (SGO.PV 1117) de la localidad de Mina fosforita, Fm. Bahía Inglesa asignado al primer registro de Kogiidae para la Formación (Canto, 2007). Sin embargo, dicha comunicación no presenta una descripción anatómica o un análisis de los caracteres diagnósticos para respaldar su asignación. Al parecer, no se trata de una publicación científica (*peer reviewed*), en razón del mal uso de términos estadísticos y anatómicos básicos (e.g.,"vista exterior" en lugar de vista dorsal), literatura desactualizada e imprecisa, como es el caso de la edad de las capas fosfáticas (Mioceno tardío; Marquardt et al., 2000) citada con la edad general de todo el paquete sedimentario de la Fm. Bahía Inglesa (Mioceno medio a Plioceno; Marquardt et al., 2000).

Los caracteres diagnósticos que permiten asignar a Physeteroidea son: presencia de un osículo accesorio fusionado con la foveafovea epitubaria del proceso anterior del periótico (ver Mead y Fordyce, 2009). El proceso anterior esta incompleto, sin embargo, las proporciones de la cóclea *vs* procesos son compatibles con la de la forma general de la familia, así como la inclinación de los procesos entre si, y el pequeño tamaño sumado a la reducción del proceso posterior del periótico permiten identificarlo como Kogiidae a diferencia de Physeteriidae.

V. 6. Contexto paleobiogeográfico del registro de odontocetos neógenos de Chile

Como ya fue mencionado anteriormente el registro geológico marino de Chile es extenso, ya que en muchos períodos (Jurásico, Cretácico, Paleógeno, Neógeno) la mayor parte de su territorio, fue cubierto por océanos o mares someros epi-continentales Por esa razón los cetáceos son un componente abundante e importante del patrimonio paleontológico de Chile, estando registrados abundantemente en las formaciones marinas neógenas. Los más antiguos registros de cetáceos fósiles en la literatura datan de 1887 con los trabajos del famoso naturalista Rodulfo A. Philippi que describió *Neobalaena* *simpsoni*, (Sur, Ancud; Mysticeti) y *Delphinus domeykoi* (costa central, La Cueva, Odontoceti) aunque no son taxa válidos actualmente.

La casi totalidad de los registros provienen de la Fm. Bahía Inglesa que presenta 17 taxa en su mayoría provenientes de capas de arenisca a conglomerado fosfóricos, conocidas como "bonebed" (cama de huesos) y de limolitas supra-yacentes que contiene gran proporción de esqueletos articulados a asociados (Gutstein *et al.*, 2007). Los taxa presentes en dicha formación incluyen restos craneales de Inioidea (*Brachydelphis mazeasi*, *Brachydelphis* n. forma, *Pliopontos* sp., *Pontistes* sp., nueva especie no descrita), así como dientes y perióticos aislados (Pontoporiidae indet.), restos craneanos de Delphinoidea, como Phocoenidae (aff. *Lomacetus* y Phocoeninae indet.); y Physeteroidea, correspondiendo a dientes de diferentes formas de Physeteridae (cf. *Scaldicetus*, *Livyathan*), además de Ziphiidae indet. La Fm. Coquimbo registra restos de Mysticeti *indet.*, Pontoporiidae *indet.* (SGO-PV 305). El Área de Navidad (Fm. Rapel) con un fragmento de rostro articulado con dientes asignado a Physeteridae.

De las familias de odontocetos fósiles que ocurren en América del Sur durante el Neógeno (Physeteriidae, Kogiidae, Ziphiidae, Delphinidae, Pontoporiidae, Monodontidae, Kentriodontidae, Phocoenidae, Odobenocetopsidae) el 80% están registradas en las formaciones de Chile, con la excepción de Odobenocetopsidae y Monodontidae. Sin embargo, apenas 55% de estas están al menos mencionadas en resúmenes de congresos y existe apenas una publicación indexada (ISI) registrando odontocetos para la Fm. Bahía Inglesa (Gutstein *et al.*, 2009). Esta disparidad entre registro y publicaciones muestra la necesidad de continuar e incrementar el estudio de este grupo. Tratándose de cetáceos, los estratos neógenos más importantes de Chile son el Área de Navidad (diversas formaciones *sensu* Encinas *et al.* 2006), la Fm. Coquimbo y destacadamente la Fm. Bahía Inglesa. Estas formaciones tienen cierto grado de contemporaneidad, sobretodo llevando en consideración la reasignación temporal del área de Navidad para el Mioceno tardío-Plioceno inferior y habiendo facies sedimentarias similares entre la base de la Fm. Coquimbo (Plioceno) y buena parte de la Fm. Bahía Inglesa (Mioceno medio-Plioceno superior), sobretodo las capas fosilíferas que corresponden predominantemente al Mioceno tardío-Plioceno inferior en esta última (Encinas et al 2006; Achurra 2004, Achurra *et al.* 2009).

V. 7. Paleobiología y paleobiogeografía de Inioidea a la luz de los hallazgos de la Fm. Bahía Inglesa.

Es conocido a nivel mundial que ocurre un reemplazo en las familias dominantes en términos de diversidad taxonómica a través del Neógeno en mamíferos marinos (pinnípedos, Valenzuela-Toro et al., 2013; odontocetos, Fordyce, 1980; Steeman et al., 2009; Cozzuol,1996; Cione et al., 2005a,b). Por ejemplo, en el registro mundial de odontocetos se observa un cambio de las formas dominante de Kentriodontidae a Delphinidae del Mioceno medio-Mioceno tardío, además de la presencia de otros grupos (Fordyce y Muizon, 2001). Se observa también una disparidad morfológica entre las formas del Mioceno medio en relación a los del Mioceno tardío, en donde las formas del Mioceno tardío se parecen mas a los grupos hoy existentes, con algunas excepciones (Gutstein et al., aceptado; Fordyce, 1980; Steeman et al., 2009; Cozzuol, 1996; Cione et al., 2005a,b). Algunas publicaciones recientes documentan una gran diversidad de inioides en ambos hemisferios (Pyenson y Hoch, 2007; Barnes y Godfrey, 2008; Geisler et al., 2012) destacándose lo observado en la Fm. Bahía Inglesa, en donde co-ocurren 4 generos (5 especies) del grupo, además estos restos son abundantes, tanto en terreno como en colecciones científicas (MPC y SGO.PV).

En una perspectiva mas general, las familias de odontocetos presentes en Neógeno de la Región de Atacama son las mismas encontradas en Perú (Ica, Fm. Pisco, Mioceno medio-Plioceno; DeVries y Muizon, 1985). En términos de especies existen nuevas formas como *Pliopontos*, de la familia Pontoporiidae, de la cual la única especie viviente habita el Océano Atlántico (*Pontoporia blainvillei*), pero que en el registro fósil se encuentra bien representada en el Océano Pacífico (Mioceno tardío de la Fm. Bahía Inglesa). Además, dentro de la misma familia, se extiende el registro del género

Pontistes que, hasta recientemente era considerado exclusivo del Océano Atlántico (Burmeister, 1885; Pyenson y Hoch, 2007). Estos nuevos registros se suman a la reciente redescripción de *Brachydelphis mazeasi* (Gutstein et al., 2009) y el reconocimiento de una nueva forma con rostro largo, ampliando el conocimiento de los Inioidea en América del Sur, grupo que esta representado apenas por dos géneros en la actualidad y por registros aislados de géneros neógenos, siempre restringidos temporalmente y en su distribución. Se destaca la ocurrencia de al menos cuatro formas en la Fm. Bahía Inglesa, hecho que convierte dicha formación en la más diversa en cuanto a registros de Inioidea y que amplia la distribución de los géneros antes conocidos por registros puntuales. Por otro lado, a pesar de la predominancia de registros de la familia en América del Sur, registros más recientes y nuevas interpretaciones, aunque sobre la base de especímenes fragmentarios, vienen siendo reportados para el Atlántico Norte como es el caso de algunos perióticos asignados a aff. *Pontoporia* (Whitmore, 1994), cráneos de *Protophocoena minima* (Lambert, 2005), cf. *Pontistes* y Pontoporiidae indet. (Pyenson and Hoch, 2007), *Stenasodelphis* Barnes y Godfrey 2008, *Auroracetus* Gibson y Geisler 2009 , *Meherrinia* Geisler *et al.* 2012.

Estos registros y su interpretación paleobiogeográfica son interesantes, dado que el registro fósil es significativamente similar al registro de varamientos de las costas (tanatocenosis) y es además fidedigno a la real población que habita el área marina colindante (Pyenson et al., 2011). Además las diferentes abundancias de taxa de mamíferos marinos en una tanatocenosis, y por ende en su tafocenosis, esta correlacionada a la real población: una población residente de una área marina cercana (una cuenca o un estuario, por ejemplo) será mas abundante en la tanatocenosis que una especie que vive en aguas oceánicas o áreas relativamente mas lejanas (Liebic et al., 2003). Por lo tanto, en el caso de la Fm. Bahía Inglesa se puede afirmar que los inioides eran parte importante de la comunidad de la cuenca de caldera, durante el Mioceno tardío. En contraposición en el Plioceno de la misma formación el grupo no está representado, encontrándose apenas delfines (Delphinidae) hasta la fecha.

De hecho el registro de Pyenson y Hoch (2007), ahora visto desde la perspectiva de la revisión morfológica de *Brachydelphis* (Gutstein *et al.* 2009), que caracteriza la variación morfológica del género, nos permite determinar ese especimen como cf. *Brachydelphis* sp. (en lugar de Pontoporiidae indet.) lo que tiene implicancias mayores para la interpretación paleobiológica del taxón y también del origen de los Inioidea y de los Pontoporiidae dependiendo del marco sistemático al que uno se atiene. Por ejemplo, la distribución en dos océanos en una variedad de ambientes durante el Mioceno medio a tardío hace difícil la comparación con los Inioidea vivientes, restringidos a "pequeñas" áreas con hábitats mas bien homogéneos: someros y con aporte continental.

Como un hito especial en la biogeografía y evolución de los delfines de América del Sur dos eventos de invasión del ambiente fluvial ocurrieron en tiempo y grupos distintos: Delphinidae e Iniidae. En el primer grupo, el género *Sotalia*, de origen estimado en el océano Atlántico (*Sotalia guianensis*), habría invadido la cuenca amazónica (*S. fluviatilis*) entre 5 y 2,5 millones de años durante el Plioceno (Cunha et al., 2005). Sin embargo, el registro fósil del género es inexistente y esta divergencia fue estimada utilizando la tasa de mutación de mamíferos en general, por lo que esta fecha podría estar sobre-estimada. Sobretodo considerando que la población dulce-acuícola estaría más sujeta a cambios en el número poblacional (i.e. durante el descenso del nivel del mar del Pleistoceno) pudiendo provocar efecto fundador y fijación de alelos raros. Por otro lado, la entrada de los Inioidea es estimada por Banguera-Hinestroza et al. (2005) para el Mioceno Medio-Tardío, basándose en género fósil más antiguo y basal, *Brachydelphis mazeasi* (Perú y Chile). Interesantemente este segundo grupo ha sido recientemente incrementado en número de especies, especímenes, rango biogeográfico y de edad (Gutstein et al., aceptado; Pyenson y Hoch, 2007; Godfrey y Barnes, 2008; Lambert y Post, 2005; Ribeiro et al., 1998; Whitmore et al., 1994), tornando más compleja la historia evolutiva del grupo.

Por su parte, el sistema fluvial amazónico tiene una historia geológica interesante: en el Mioceno medio a tardío hubo dos grandes transgresiones marinas que cubrieron buena parte de América del Sur. Se tiene consenso de que dos cuerpos de agua estaban presentes (Latrubesse et al., 2007): el mar Paranaense (en la región de entre Ríos, Argentina) y las cuencas de

Amazonas y del Orinoco inundadas (*Tethys water spot*, según Donato, 2003).

V. 8. Conclusiones

En resumen la Región de Atacama posee 85% de los registros de Chile. Lo que en términos del registro sudamericano corresponde a 50% de las familias registradas hace 10 años, en la última revisión (Cozzuol 1996).

Hasta el presente momento no hay registros, en la literatura, de cetáceos en el neógeno marino de las Formaciones Ranquil, Lincai y Mejillones, aún que probablemente se necesitan campañas de prospección y estudio de los materiales, ya que restos vertebrales han sido observados informalmente (exposición del museo de la Universidad de Antofagasta), provenientes de la Fm. Mejillones.

La fauna de cetáceos de la Fm. Bahía Inglesa es similar a la registrada en niveles miocenos de la Formación Pisco (Suárez et al., 2005), e incluye un significativo componente de cetáceos fósiles, como: *P. littoralis* (Plioceno inferior, Fm. Pisco), *B. mazeasi* (Mioceno medio, Fm. Pisco) y *P. rectifrons* (Mioceno tardío, Fm. Ituzaingó, Argentina). Los registros chilenos amplían el rango crono-estratigráfico y paleobiogeográfico de las especies mencionadas, haciendo más compleja la historia evolutiva de la familia. Sin embargo, también deja en evidencia que los 'niveles de vertebrados' descritos para la Fm. Pisco (Muizon y DeVries, 1985) no tienen su correspondencia en los estratos de la Formación Bahía Inglesa, que presenta retrabajo pero no con niveles pliocenos.

Tanto en el caso de los tiburones (*C. carcharias* y *C. hastalis*) ampliamente utilizado como indicador crono-estratigráfico, como en el caso de los taxa de odontocetos (ej. Pontoporiidae, Phocoenidae) utilizado en la Fm. Pisco (Muizon y Devries, 1985) parece no ser exacto, ya que taxa propuestos como guías del Mioceno tardío y Plioceno en la Fm. Pisco (sensu Muizon y Devries, 1985) se encuentran juntos en el "bonebed" (Mioceno Tardío; Achurra 2004, Suárez y Marquardt, 2003; Walsh y Suárez, 2005).

La Fm. Bahía Inglesa cuenta con capas bien expuestas con tal aglomeración de restos que fueron llamadas "capa de huesos" (bonebeds) de edad Mesiniano-Tortoniano (Mioceno Tardío). El estudio de la fauna de cetáceos, bien como la fauna y flora general, tiene potenciales como el de ampliar el entendimiento en los tiempos de formación de la corriente de Humboldt (e.g. Rubilar-Rogers et al., 2009) y por ende en la expansión hasta estas latitudes del desierto de Atacama. Como estas capas condensan la diversidad de estas edades con un registro diverso y abundante, su ensamble debería reflejar las modificaciones macro-climáticas como el establecimiento de la corriente de Humboldt y la expansión del deserto de Atacama.

Se destacan los nuevos registros que amplían el rango crono-estratigráfico de *Pliopontos littoralis*, que se consideraba un especie tipo del Plioceno y aquí aparece en capas del Mioceno tardío. Además de la presencia de *Pontistes rectifrons*, como primer registro en el Océano Pacífico. Estos hallazgos refuerzan la importancia de la Fm. Bahía Inglesa en el entendimiento de la biodiversidad del final del Neógeno y especialmente de la evolución y biogeografía de los Inioidea, grupo hasta ahora enigmático y muy interesante dado su cambio morfológico y ambiental correlacionados (ver Capitulo 2).

Tabla 1. Restos fósiles asignados a Cetacea provenientes de diversas formaciones geológicas chilenas.

Taxa	**Número colección**	**Asignación taxonómica válida**	**Localidad/Fm.**	**Edad/ Época/ Período**
Mysticeti				
Mysticeti *indet.*	MPC 001	Gutstein *et al.* 2008	Punta Cachos, Fm. Bahía Inglesa	Mioceno medio-tardío
Mysticeti *indet.*	MPC 3012, 3014-3033	Gutstein *et al.* 2008	Mina fosforita, Fm. Bahía Inglesa	Mioceno tardío
Mysticeti *indet.*	SGO.PV S/N	este trabajo	Ancud (Isla de Chiloé, Región de los Lagos) Fm. indeterminada	indet.
Odontoceti				
Odontoceti indet.	SGO.PV 6018	este trabajo	La Cueva, Colchagua, Región del Lib. Bernardo O'Higgins, Fm. La Cueva	Plioceno
Inioidea				
Pontoporiidae *indet.*	SGO.PV 305	este trabajo	Caleta Herradura, Fm. Coquimbo	Mioceno tardío-Plioceno
cf. *Pliopontos littoralis*	SGO.PV 967, MPC 0003, 3034	Gutstein *et al.* 2008	Mina Fosforita, Fm. Bahía Inglesa	Mioceno tardío
cf. *Pontistes*	SGO.PV 964, MPC 3052	Gutstein *et al.* 2008	Mina Fosforita, Fm. Bahía Inglesa	Mioceno tardío
Brachydelphis	SGO.PV	Gutstein *et al.*,	Mina Fosforita, Fm.	Mioceno

mazeasi	746, 748-750, 966, MPC 202, 377s	2009	Bahía Inglesa	tardío
cf. *Brachydelphis* n. forma	SGO.PV 759, 972, 1109	Gutstein *et al.*, 2009	Mina Fosforita, Fm. Bahía Inglesa	Mioceno tardío
Delphinoidea				
Phocoenidae indet.	MPC 0004	Gutstein *et al.* 2008	Mina Fosforita, Fm. Bahía Inglesa	Mioceno tardío
Physeteroidea				
cf. *Scaldicetus*	MPC 0008-20, 0057-60, 0070-78, 0214, 0215	Gutstein *et al.* 2008	Mina Fosforita, Fm. Bahía Inglesa	Mioceno tardío
aff. *Idiorophus*	SGO-PV 250	este trabajo	Sur de Río Rapel, Fm. Licancheu	Mioceno Tardío
Kogiidae indet.	SGO-PV 1117	este trabajo	Mina Fosforita, Fm. Bahía Inglesa	Mioceno tardío
Ziphioidea				
Ziphiidae indet.	MPC 227	Gutstein *et al.* 2008	Mina Fosforita, Fm. Bahía Inglesa	Mioceno tardío

V. 9. Referencias bibliográficas

Achurra, L., 2004. Cambios del nivel del mar y evolución tectónica de la cuenca Neógena de Caldera, III Región. [tesis Magíster]: Santiago, Chile, Departamento de Geología de la Universidad de Chile, 138 p.

Achurra, L. E., J. P. Lacassie, J. P. Le Roux, C. Marquardt, M. Belmar, J. Ruiz-del-Solar, and S. E. Ishman. 2009. Manganese nodules in the Miocene Bahía Inglesa Formation, north-central Chile: petrography, geochemistry, genesis and palaeoceanographic significance. Sedimentary Geology 217:128–139.

Banguera-Hinestroza E, Cárdenas H, Ruiz-García M, Marmontel M, Gaitán E, Vázquez R, García-Vallejo F. 2002. Molecular Identification of Evolutionarily Significant Units in the Amazon River Dolphin *Inia* sp. (Cetacea: Iniidae). Journal Hered 93:312-322.

Barnes, L.G. 1985a. Fossil pontoporiid dolphin (Cetacea: Mammalia) from the Pacific coast of North America. Contributions in Science, Natural History Museum of Los Angeles County 363: 1-34.

Barnes, L.G. 1985b. Evolution, taxonomy and antitropical distributions of the porpoises (Phocoenidae, Mammalia). Marine Mammal Science 1:149–165.

Bianucci, G., O. Lambert, and K. Post. 2007. A high diversity in fossil beaked whales (Mammalia, Odontoceti, Ziphiidae) recovered by trawling from the sea floor off South Africa. Geodiversitas 29:561-618.

Bianucci, G., S. C. Vaiani, and S. Casati. 2009. A new delphinid record (Odontoceti, Cetacea) from the Early Pliocene of Tuscany (Central Italy): systematics and biostratigraphic considerations. Neus Jahrbuch fur Geologie und Palaontologie Abhandlungen 254:275-292.

Bianucci, G., O. Lambert, and K. Post. 2010. High concentration of long-snouted beaked whales (Genus Messapicetus) from the Miocene of Peru. Palaeontology 53:1077-1098.

Borsuk-Bialynicka, M. 1988. New remains of Archaeoceti from the Paleogene of Antarctica. Polish Polar Research 9(4):437-445

Burmeister, G. 1885. Examen crítico de los mamíferos y reptiles fósiles denominados por D. Augusto Bravard y mencionados en su obra precedente. Anales del Museo Nacional de Buenos Aires 97-174 + 2 plates.

Cabrera A. 1926. Cetáceos fósiles del Museo de La Plata. Revista del Museo de La Plata 29: 363-411.

Canto, J., Cozzuol, M.A. & Yañez, J. 2002. Mamíferos marinos neógenos de la Formación Bahía Inglesa, Caldera1, III Región, Chile. I Congreso Latinoamericano de Paleontología de Vertebrados. p. 22-23.

Canto, J.H., Crovetto, A. & Covacechi, V. 2002 . Hallazgo de Pliopontos sp. (Cetacea: Pontoporiidae) en el Neógeno de Chile. Noticiario Mensual del Museo Nacional de Historia Natural de Santiago de Chile 350:28-37.

Canto, J. 2007. Physetetoidea (Cetacea: Odontoceti) fósiles en el neógeno de Chile. Noticiario Mensual, Museo Nacional de Historia Natural 359: 9-22.

Cione, A.L., J. Mennucci, F. Santalucita y C.Acosta Hospitaleche. 2005. Local extinction of genus Carcharias (Elasmobranchii, Odontaspididae) in the eastern Pacific Ocean. Revista Geológica de Chile.

Cozzuol M. 1988. Una nueva especie de Saurodelphis Burmeister, 1891 (Cetacea: Iniidae) del "Mesopotamiense" (Mioceno Tardio-Plioceno Temprano) de la Provincia de Entre Rios, Argentina. Ameghiniana 25:39-45

Cozzuol, M.A. 1996. The records of the aquatic mammals in Southern South America. Münchner Geowiss. Abhandlungen 30: 321-342.

Cozzuol, M. A. 2010. Fossil record and the evolutionary history of Iniodea. In M. Ruiz-Garcia, J. Shotsell (editors), Biology, Evolution, and Conservation of River Dolphins within South America and Asia 193-217.

Covacevich, V.; Frassinetti, D. 1986. El género *Cancellaria* en el Mioceno de Chile con descripción de cuatro especies nuevas (Gastropoda: Cancellariidae). Revista Geológica de Chile 28-29: 33-67.

Cunha HA, da Silva VMF, Lailson-Brito J, Santos MCO, Flores PAC, et al. (2005) Riverine and marine ecotypes of Sotalia dolphins are different species. Marine Biology 148: 449–457.

Darwin, C. 1846. Geological observations on South America. *Smith, Elder and Co.*: 279 p. London.

Donato, M., P. Posadas, D. R. Miranda-esquivel, E. O. Jaureguizar, and G. Cladera. 2003. Historical biogeography of the Andean region : evidence from Listroderina (Coleoptera : Curculionidae : Rhytirrhinini) in the context of the South American geobiotic scenario. Society 339-352.

Donoso-Barros, R. 1975. Contribución al conocimiento de los cetáceos vivientes y fósiles del territorio de Chile. Gayana, Zoología, 36, 127 pp.

Emslie, S. y Guerra-Correa, C. 2003. A new species of pinguin (Spheniscidae: spheniscus) and other birds from the Late Pliocene of Chile. Proceedings of the biological society of Washington 116(2): 308-316.

Encinas, A., Le Roux, J.P. , Buatois, L.A., Nielsen, S.N., Finger, K.L. , Fourtanier, E. y Lavenu, A. 2006. Nuevo esquema estratigráfico para los depósitos mio-pliocenos del área de Navidad (33°00'-34°30'S), Chile central. Revista Geológica de Chile 33, No. 2: 221-246.

Finger, K. L., S. N. Nielsen, T. J. Devries, A. Encinas, and D. E. Peterson. 2007. Paleontologic evidence for sedimentary displacement in Neogene forearc basins of central Chile. Palaios 22:3-16.

Frassinetti, D.C. 1982. Bibliografía escogida y comentada sobre mamífros fósiles de Chile. Publicacoión ocasional n° 37. Museo Nacional de Historia natural, Santiago de Chile. 3-24.

Fordyce, R. E. 1980. The Fossil Cetacea of New Zealand. New Zealand Geological Survey Report 90:1-60.

Fordyce, R.E. 1994. *Waipatia maerewhenua*, new genus and species (Waipatiidae, New Family), an archaic Late Oligocene dolphin (Cetacea: Odontoceti: Platanistoidea) from New Zealand. Pp. 147-176 in Contributions in Marine Mammal Paleontology honoring Frank C. Whitmore, Jr. (A. Berta and T. Deméré, eds.). Proceedings of the San Diego Society of Natural History 29.

Fordyce, R. E. 2002. *Simocetus rayi* (Odontoceti: Simocetidae, New Family): A bizarre new archaic Oligocene dolphin from the Eastern Pacific. In: Cenozoic Mammals of Land and Sea, Tributes to the Career of Clayton E. Ray, R. E. Emry, ed., pp. 185–222, Smithsonian Contribution. Paleobiology 93.

Fordyce, R.E. & Barnes, L.G. 1994. The evolutionary history of whales and dolphins. Annual Review of Earth Planetary Sciences 22:419-455.

Fordyce, R.E. & Muizon, C., 2001. Evolutionary history of Cetaceans: a review. Pp. 163–233 in Secondary Adaptation to Life in the Water (deBuVrenil, V. and J.M. Mazin, eds.). Pfeil Verlag, Munich.

Fordyce, R. E. 2002. Simocetus rayi (Odontoceti, Simocetidae, new family); a bizarre new archaic Oligocene dolphin from the eastern North Pacific. Smithsonian Contributions to Paleobiology 93:185-222.

Fordyce, R. E. 2009. Cetacean Evolution; pp. 201-207 in (Eds.) Perrin, W. F., B. G. Wursig, and J. G. M. Thewissen. Encyclopedia of Marine Mammals. Academic Press, 1414 pp.

Fostowicz-Frelik, L. 2003. An enigmatic whale tooth from the Upper Eocene of Seymour Island, Antarctica. Polish Polar Research 24(1):13-28.

Gatesy, J. 1997. More DNA support for a Cetacea/Hippopotamidae clade: the blood-clotting protein gene Y-Fibrinogen. Molecular Biology and Evolution 14:537-543.

Gatesy, J. 1999. Stability of cladistic relatioshps between Cetacea and higher Artiodactyla taxa. Systematic Biology 48(1):6-20.

Gatesy, J., O'Leary, M.A., 2001. Deciphering whale origins with molecules and fossils. Trends Ecology Evolution 16: 562–570.

Geisler, J.H., & Sanders, A.E. 2003. Morphological evidence for the phylogeny of Cetacea. J. Mamm. Evol. 10, 23–129.

Geisler, J.H. & Uhen, M. D. 2003. Morphological Support for a close relantioship between Hippos and Whales. Journal of Vertebrate Paleontology 23:991–996.

Geisler, J. H., M. R. McGowen, G. Yang, and J. Gatesy. 2011. A supermatrix analysis of genomic, morphological, and paleontological data from crown Cetacea. BMC Evolutionary Biology 11:112.

Geisler J. H., S. J. Godfrey, and O. Lambert. 2012. A new genus and species of late Miocene inioid (Cetacea, Odontoceti) from the Meherrin River, North Carolina, U.S.A. Journal of Vertebrate Paleontology 32:198-211.

Gibson, M. L. and J. H. Geisler. 2009. A new Pliocene dolphin (Cetacea: Pontoporiidae), from the Lee Creek Mine, North Carolina. Journal of Vertebrate Paleontology 29:966-971.

Gingerich, P.D., Wells, N. A., Russell, D. E. & Shah, S. M. I. 1983. Origin of whales in epicontinental remmant seas: new evidances from the early eocene of Pakistan. Science. 220:403-406.

Gingerich, P.D. 2001. Origin of whales form early Artiodactyls: hands and feet of Eocen Protocetid from Pakistan. Science. 293:2239-2242.

Gigoux, E. 1899. Un fósil más en Caldera. Revista Chilena de Historia Natural, 3(9): 129-131.

Godfrey S. J. and L. G. Barnes. 2008. A new genus and species of late Miocene pontoporiid dolphin (Cetacea: Odontoceti) from the St. Marys Formation in Maryland. Journal of Vertebrate Paleontology 28:520-528.

Gutstein, C.S., Cozzuol, M.A., Suárez, M. 2006. The cetaceans from Bahía Inglesa Formation (Atacama, Chile): Taphonomic approach and paleogeographical implications. Journal of Vertebrate Paleontology 26: 71A.

Gutstein, C.S, Rubilar-Rogers, D. y Suárez, M. 2007. Nuevo yacimiento con vertebrados fósiles del Neógeno del desierto de Atacama (Formación Bahía Inglesa). Actas GEOSUR.

Gutstein, C.S., Yuri, R.Y., Soto, S., Suárez, M.E., Rubilar-Rogers, D.E. 2008. La fauna de vertebrados fósiles del "bonebed" de la Formación Bahía Inglesa y aspectos taxonómicos. Actas del I Simposio – Paleontología en Chile, MNHN, pp. 102-108.

Gutstein, C.S., Cozzuol, M.A., Vargas, A.O.; Suárez, M., Schultz, C.L. 2009. Patterns of skull variation of Brachydelphis (Cetacea, Odontoceti, Pontoporiidae) from South-Easthern Pacific Neogene. Journal of Mammalogy 90: 504-519.

Gutstein, C.S., Figueroa-Bravo, C.P., Pyenson, N.D., Yury-Yañez, R.E. , Cozzuol, M.A., Canals, M.L. (aceptado). High frequency echolocation, ear morphology, and the marine-freshwater transition: a comparative study of extant and extinct dolphins (Odontoceti). Palaeogeography, Palaeoclimatology, Palaeoecology.

Hampe, O. 2006. Middle/late Miocene hoplocetine sperm whale remains (Odontoceti: Physeteridae) of North Germany with an emended classification of the Hoplocetinae. Fossil Record – Mitteilungen Aus Dem Museum Für Naturkunde 9:61-86.

Heyning, J.E. 1989. Comparative facial anatomy of beaked whales (Ziphiidae) and a systematic revision among the families of extant Odontoceti. Contributions in Science Natural History Museum of Los Angeles County 405: 1-64.

Jadwiszczak, P. 2006. Eocene penguins of Seymour Island, Antarctica: The earliest record, taxonomic problems and some evolutionary considerations. Polish Polar Research 27(4):287-302.

Kazar, E. 2002. Revised phylogeny of the Physeteridae (Mammalia: Cetacea) in light of Placoziphius Van Beneden, 1869 and Aulophyseter Kellogg, 1927. Bulletin de l'Institute Royal des Sciences Naturelles de Belgique, Sciences de la

Terre 72:151-17.

Kellogg, R. 1928. The history of whales - their adaptation to life in the water. Quarterly Review of Biology 3:29-76.

Kumar K. and A. Sahni. 1986. Remingtonocetus harudiensis, new combination, a middle Eocene archaeocete (Mammalia, Cetacea) from western Kutch, India. Journal of Vertebrate Paleontology 6(4):326-349

Lambert O. 2005. Systematics and Phylogeny of the fossil beaked whales *Ziphirostrum* du Bus, 1868 and *Choneziphius* Duvernoy, 1851 (Mammalia, Cetacea, Odontoceti), from the Neogene of Antwerp (North of Belgium). Geodiversitas 27(3): 443-497.

Lambert, O., and K. Post. 2005. First European pontoporiid dolphins (Mammalia: Cetacea, Odontoceti) from the Miocene of Belgium and The Netherlands. Deinsea 11:7-20.

Lambert O., Bianucci G. and Post K. 2010. Tusk-bearing beaked whales from the Miocene of Peru: sexual dimorphism in fossil ziphiids? Journal of Mammalogy 91: 19-26.

Lambert O., G. Bianucci, K. Post, C. de Muizon, R. Salas-Gismondi, M. Urbina, and J. Reumer. 2010. The giant bite of a new raptorial sperm whale from the Miocene epoch of Peru. Nature 466:105-8.

Latrubesse, E., Silva, S.F., Cozzuol, M., Absy, M.L., 2007. Late Miocene continental sedimentation in the southwestern Amazonia and its regional significance: Biotic and geological evidence. Journal of South American Earth Science 23, 61–80.

Le Roux, J.P.; Olivares, D.M.; Nielsen, S.N.; Smith, N.D.; Middleton, H.; Fenner, J.; Ishman, S.E. 2006. Miocene-Pliocene bay sedimentation as controlled by regional crustal behaviour, local tectonics and eustatic sea-level changes in the Coquimbo Formation at the Bay of Tongoy, central Chile. Sedimentary Geology, 184 (1-2): 133-153.

Liebig, P. M., T.-S. a. Taylor, and K. W. Flessa. 2003. Bones on the Beach: Marine Mammal Taphonomy of the Colorado Delta, Mexico. Palaios 18:168-175.

Luo, Z., and Gingerich, P.D. Terrestrial Mesonychia to aquatic Cetacea: transformation of the basicranium and evolution of hearing in whales. University of Michigan Papers on Paleontology 31: 1–98.

Marquardt, C., 1999. Neotectónica de la franja costera y aportes a la geología regional entre Caldera y Caleta Pajonal (278009–278459S), III Región de Atacama. Tesis, Universidad de Chile, Santiago. 297 pp.

Marquardt, C., Blanco, N., Godoy, E., Lavenu, A., Ortlieb, L., Marchant, M. & Guzmán, N. 2000. Estratigrafía del Cenozoico Superior en el área de Caldera (26°45'-28°S). In: Actas IX Congreso Geológico Chileno No. 9, Vol. 2, p. 504 - 508.

Marquardt, C.; Lavenu, A.; Ortlieb, L.; Godoy, E.; Comte, D. 2004. Coastal neotectonics in Southern Central Andes: uplift and deformation of marine terraces in Northern Chile (27°S). Tectonophysics 394: 193-219.

Martínez-Cáceres, M. y de Muizon, C. 2011. A new basilosaurid (Cetacea, Pelagiceti) from the Late Eocene to Early Oligocene Otuma Formation of Peru. Comptes Rendus Palevol 10:517-526.

May-Collado L, Agnarsson I, 2006. Cytochrome b and Bayesian inference of whale phylogeny. Molecular Phylogenetics and Evolution 38: 344-354.

Milinkovitch, M. C., Orti, G., & Meyer, A. 1993. Revised phylogeny of whales suggested by mitochondrial ribosomal DNA sequences. Science 12: 346–348.

Milinkovitch, M. C., Meyer, A., & Powell, J. R. 1994. Phylogeny of all major groups of cetaceans based on DNA sequences from three mitochondrial genes. Mol. Biol. Evol. 11: 939–948.

Milinkovitch, M. C., Orti, G., & Meyer, A. 1995. Novel phylogeny of whales revisited but not revised. Mol. Biol. Evol. 12: 518–520.

Morgan GS. 1994. Miocene and Pliocene marine mammal faunas from the Bone Valley Formation of Central Florida. Proceedings of San Diego Society of Natural History 29: 239-268.

Muizon, C. de.1983. Pliopontos littoralis un nouveau Platanistidae Cetacea du Pliocéne de la côte péruvienne. Comptes Rendus de l'Academie de Sciences de Paris. Sér. II. 296:1203-1206.

Muizon, C. de.1984. Les vertébrés fossiles de la Formation Pisco (Pérou) II. Les odontocètes (Cetacea, Mammalia) du Pliocène inférieur de Sud-Sacaco. Travaux de l'Institut Français d'Études Andines 27: 1-188.

Muizon, C. 1987. The affinites of *Notocetus vanbenedeni*, an early Miocene Platanistoid (Cetacea, Mammalia) from Patagonia, Southern Argentina. American Museum Novitates 2904:1-20.

Muizon, C. de.1988a. Vertebrés fossiles de la Formation Pisco (Pérou) III: Les Odontocètes (Cetacea: Mammalia) du Miocène. Recherche sur les Civilizations, Institut Français d'Étudies Andines, Memoire. 78:1- 244.

Muizon, C. de.1988b. Les relations phylogenétiques dea Delphinida (Cetacea; Mammalia). Annales de Paleontologie (Vert.-Invert.), 74(4):159-227.

Muizon, C. de.1991. A new ziphiid (Odontoceti, Mammalia) from the Early Miocene of Washington state (USA) and a phylogenetical analysis of the major groups of odontocetes. Bulletin du Muséum national d'Histoire naturelle, 4e sér.,Sect. C 12: 279–326.

DeVries, T. J. and C. de Muizon. 1985. Geology and paleontology of late Cenozoic marine deposits in the Sacaco area (Peru). Geologische Rundschau 74(3), 547-563.

Nielsen, S. N.; Glodny, J. (2009): Early Miocene subtropical water temperatures in the southeast Pacific. Palaeogeography Palaeoclimatology Palaeoecology, 280, 3-4, 480-488.

Nielsen, S.N., K. Bandel & B. Kröger. 2009. Palaeobiogeographical provenance, taphonomy, and mode of life of *Aturia cubaensis* (Lea, 1841) (Cephalopoda, Nautiloidea) from Cainozoic deposits of Chile. Geobios 42: 73-88.

Nikaido, M., A. P. Rooney , and N. Okada. 1999. Phylogenetic relationships among cetartiodactyls based on insertions of short and long interspersed elements: hippopotamuses are the closest extant relatives of whales. Proceedings of the National Academy of Sciences of the United States of America 96:10261–10266.

O'Leary, M. A., and J. H. Geisler. 1999. The position of Cetacea within mammalia: phylogenetic analysis of morphological data from extinct and extant taxa. Systematic Biology 48:455-490.

O'Leary, M.A. y Gatesy, J. 2008. Impact of increased character sampling on the phylogeny of Cetartiodactyla (Mammalia): combined analysis including fossils. Cladistics 24 397–442

Oliver-Schneider, C. 1926. Lista preliminar de los mamíferos fósiles de Chile. Revista Chilena de Historia Natural 30: 144-156. 1 mapa.

Oliver-Schneider, C. 1927. Las condiciones biológicas de la fauna vertebrada en Chile en la era Cenozoica. Boletín de la Sociedad Biológica de Concepción 1(1-2): 68-79.

Oliver-Schneider, C. 1935. Mamíferos fósiles de Chile. Adiciones y correciones a una lista preliminar. Revista Chilena de Historia Natural 39: 297-304.

O'Leary, M. A. & Geisler, J. H. 1999. The position of Cetacea within Mammalia: phylogenetic analysis of morphological data from extinct and extant taxa. Systematic Biology 48(3): 455-490.

Philippi, R.A.1887. Los fósiles terciários i cuartarios de Chile. 256pp. 58 lams. Imprenta Brockhaus, Leipzig.

Pyenson, N. D. and E. Hoch. 2007. Tortonian pontoporiid odontocetes from the eastern North Sea. Journal of Vertebrate Paleontology 27(3):757-762.

Pyenson, N.D., R.B. Irmis, and J.H. Lipps. 2010. Comment on "Climate, Critters, and Cetaceans: Cenozoic Drivers of the Evolution of Modern Whales." *Science*, 330: 178-a.

Quilodrán, P. V. 2002. Una nueva especie de marsopa fósil (Phocoeninae, Phocoenidae, Odontoceti, Cetacea) para el Neógeno de la Formación Bahía Inglesa, III Región, Noerte de Chile. I Congreso Latinoamericano de Paleontología de Vertebrados. p. 46-47.

Rech, J. a., B. S. Currie, G. Michalski, and A. M. Cowan. 2006. Neogene climate change and uplift in the Atacama Desert, Chile. Geology 34:761.

Ribeiro, A.M., Drehmer, C.J., Buchmann, F.S.C. & Simões-Lopes, P.C. 1998. Pleistocene skull remains of Pontoporia blainvillei (Cetacea, Pontoporiidae) from the coastal plain of Rio Grande do Sul State, Brazil, and the relationships of pontoporids. *Revista da Universidade de Guarulhos.* 3(6):71 – 77.

Rojo, M. A. 1985. Un aporte al conocimiento del Terciario marino: Formación Bahía Inglesa. Actas IV Congreso Geologico Chileno 1.514-1.533.

Salinas, P. 1988. Hallazgo de cetáceos fósiles (Mysticeti, Balaenopteridae) en la ciudad de Coquimbo, Chile. Revista Geológica de Chile. 15(1):89-94.

Sellards, E. H. 1915. The pebble phosphates of Florida. Florida Geological Survey, Annual Report 7:25–116.

Shirihai, H., Jarret, B., 2009. Whales, Dolphins and Seals. A Guide to the Marine Mammals of the World. A&C Black Publishers, London. 384pp.

Spaulding, M., O'Leary, M.A., Gatesy, J. 2009. Relationships of Cetacea (Artiodactyla) among mammals: increased taxon sampling alters interpretations of key fossils and character evolution . PLoS ONE 4(9) e7062:1-14.

Steeman, M. E., M. B. Hebsgaard, R. E. Fordyce, S. Y. W. Ho, D. L. Rabosky, R. Nielsen, C. Rahbek et al. 2009. Radiation of extant cetaceans driven by restructuring of the oceans. Systematic Biology 58:573-585.

Suárez, M. E. & Marquardt, C. 2003. Revisión preliminar de las faunas de peces elasmobranquios del Mesozoico y Cenozoico de Chile: Su valor como indicadores cronoestratigráficos. In: Actas X Congreso Geológico Chileno, Concepción.

Suárez, M.E.; Encinas, A.; Ward, D. 2006. An Early Miocene elasmobranch fauna from the Navidad Formation, Central Chile, South America. Cainozoic Research 4: 3-18.

Suárez M., Yury-Yáñez R., Valenzuela-Toro A. 2010. Primer sitio con vertebrados marinos de edad pleistoceno en Chile, Caldera, Región de Atacama. In libro de resúmenes II Simposio de Paleontología en Chile.

Tamayo, M. y D. Frassinetti. 1980. Catalógo de los mamíferos fósiles y vivientes de Chile. Boletín Museo Nacional Historia Natural, 37: 323-399.

Tavera, J. 1968. Estudio de la formación Navidad en el Provincia de Santiago con referencia especial a las localidades tipos de Navidad, Matanza, Boca Rapel y Topocalma. Sociedad Geológica de Chile, Resúmenes: 59-60.

Tavera, J.J. 1979. Estratigrafía y paleontología de la Formación Navidad, Provincia de Colchaga, Chile (LAT 30°50' – 34°S). Boletin del Museo Nacional Historia Natural de Chile. 36: 5-176, laminas 1-21.

Thewissen, J. G. M., S. I. Madar, and S. T. Hussain. 1996. Ambulocetus natans, an Eocene cetacean (Mammalia) from Pakistan. Courier Forschungsinstitut Senckenberg 191:1-81.

Thewissen, J.G.M., Madar, S.I. & Hussain, S.T. 1998. Whales ankles and evolutionary relationships. Nature. 395:452.

Thewissen, J.G.M. & Madar, S.I. 1999. Ankle morphology of the earliest cetaceans and its implications for the phylogenetic relations among Ungulates. Systematic Biology 48(1): 21-30.

Thewissen, J. G. M., and S. Bajpai. 2001. Dental Morphology of Remingtonocetidae (Cetacea, Mammalia). Journal of Paleontology 75:463-465.

Thewissen, J.G.M.; Williams, E. M.; Roe, L.J. & Hussain, S.T. 2001. Skeletons of terrestrial cetaceans and the relationship of whales and artiodactyls. Nature 413:277-281.

Thewissen, J. G. M., and E. M. Williams. 2002. The early radiations of Cetacea (Mammalis): Evolutionary Pattern and Developmental Correlations. Annual Review of Ecology and Systematics 33:73-90.

Thewissen, J.G.M, Cooper LN, Clementz MT, Bajpai S, Tiwari BN. 2007. Whales originated from aquatic artiodactyls in the Eocene epoch of India. Nature 450:1190-1194.

Uhen, M. D. 2008b. New protocetid whales from Alabama and Mississippi, and a new cetacean clade, Pelagiceti. Journal of Vertebrate Paleontology, 28:589–593.

Uhen, M. D., N. D. Pyenson, T. J. Devries, M. Urbina, and P. R. Renne. 2011. New Middle Eocene Whales from the Pisco Basin of Peru. Society 85:955-969.

Ursing, B. M. & Arnason, U. 1998 The complete mitochondrial DNA sequence of the pig (*Sus scrofa*). Journal Molecular Evolution 47:302-306.

Valenzuela-Toro, A. M., C. S. Gutstein, R. M. Varas-Malca, M. E. Suárez, and N. D. Pyenson. 2013. Pinniped turnover in the South Pacific Ocean: New evidence from the Plio-Pleistocene of the Atacama desert, Chile. Journal of Vertebrate Paleontology

Van Valen, Leigh M. 1968. Monophyly or diphyly in the origin of whales. Evolution. 22(1):37-41

Zar, J. H. 1996. Biostatistical Analysis. Third Edition. Prentice-Hall, Inc., Englewood Cliffs, N.J., New Jersey. USA.

Walsh, S.A. & Suárez, M. 2005. First post–Mesozoic record of Crocodyliformes from Chile. Acta Palaeontologica Polonica 50 (3): 595–600.

Whitmore F. C. and A. E. Sanders. 1977. Review of the Oligocene Cetacea. *Systematic Zoology* 25:304-320.

Whitmore, F.C. 1994. Neogene climatic changes and the emergence the modern whale fauna of the North Atlantic Ocean. Pp. 221-227 in Contributions in Marine Mammal Paleontology honoring Frank C. Whitmore, Jr. (A. Berta and T. Deméré, eds.). Proceedings of the San Diego Society of Natural History 29.

Wilson, L.E. 1973. A delphinid (Mammalia, Cetacea) from the Miocene of Palos Verdes Hills, California. University of California Publications in Geological Sciences 103:1-34.

Yáñez J & J. Canto. 1991. Rectificación de cetáceos fósiles de Coquimbo, Chile. Revista Geológica de Chile 18: 181-182.

Yáñez J., J. Canto & J.C. Reyes. 1994. Cráneo fósil de Phocoena spinipinnis (Cetacea: Phocoenidae). Noticiario Mensual del Museo de Historia Natural (Chile) 324: 24-29.

Yury-Yáñez R., R. Otero, S. Soto-Acuña, M. E. Suárez, D. Rubilar-Rogers, M. Sallaberry. In press. First bird remains from the Eocene of Algarrobo, central Chile. Andean Geology.

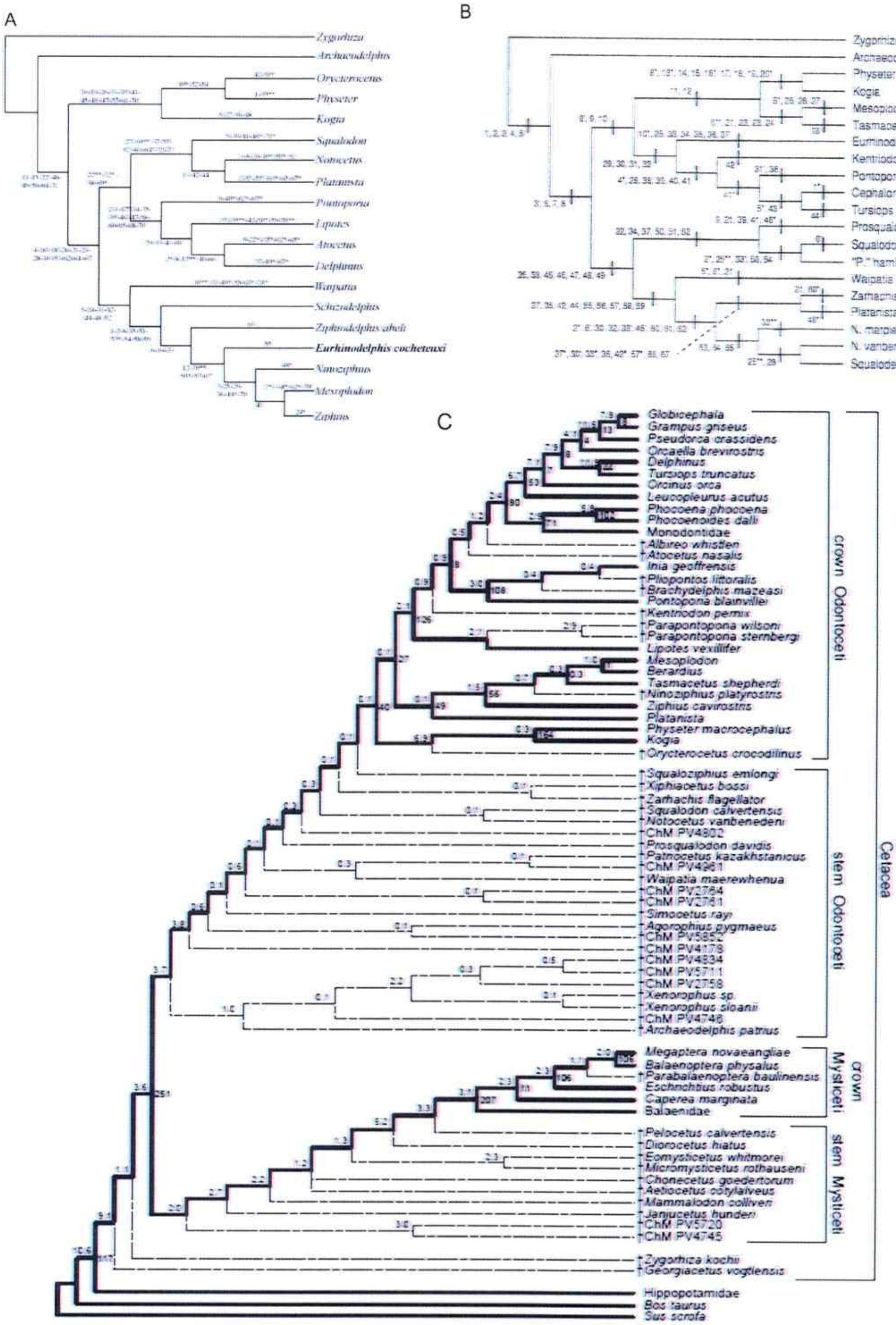

A
Zygorhiza
Archaeodelphis
Orycterocetus
Physeter
Kogia
Squalodon
Notocetus
Platanista
Pontoporia
Lipotes
Atocetus
Delphinus
Waipatia
Schizodelphis
Ziphiodelphus abeli
Eurhinodelphis cocheteuxi
Ninoziphius
Mesoplodon
Ziphius
B
Zygorhiza
Archaeodelphis
Physeter
Kogia
Mesoplodon
Tasmacetus
Eurhinodelphids
Kentriodon
Pontoporia
Cephalorhynchus
Tursiops
Prosqualodon
Squalodon
"P." hamiltoni
Waipatia
Zarhachis
Platanista
N. marples
N. vanbenedeni
Squalodelphis
C
Globicephala
Grampus griseus
Pseudorca crassidens
Orcaella brevirostris
Delphinus
Tursiops truncatus
Orcinus orca
Leucopleurus acutus
Phocoena phocoena
Phocoenoides dalli
Monodontidae
†Albireo whistleri
†Atocetus nasalis
Inia geoffrensis
†Pliopontos littoralis
†Brachydelphis mazeasi
Pontoporia blainvillei
†Kentriodon pernix
†Parapontoporia wilsoni
†Parapontoporia sternbergi
Lipotes vexillifer
Mesoplodon
Berardius
Tasmacetus shepherdi
†Ninoziphius platyrostris
Ziphius cavirostris
Platanista
Physeter macrocephalus
Kogia
†Orycterocetus crocodilinus
†Squaloziphius emlongi
†Xiphiacetus bossi
†Zarhachis flagellator
†Squalodon calvertensis
†Notocetus vanbenedeni
†ChM PV4802
†Prosqualodon davidis
†Patriocetus kazakhstanicus
†ChM PV4961
†Waipatia maerewhenua
†ChM PV2764
†ChM PV2761
†Simocetus rayi
†Agorophius pygmaeus
†ChM PV5852
†ChM PV4178
†ChM PV4834
†ChM PV5711
†ChM PV2758
†Xenorophus sp.
†Xenorophus sloanii
†ChM PV4746
†Archaeodelphis patrius
Megaptera novaeangliae
Balaenoptera physalus
†Parabalaenoptera baulinensis
Eschrichtius robustus
Caperea marginata
Balaenidae
†Pelocetus calvertensis
†Diorocetus hiatus
†Eomysticetus whitmorei
†Micromysticetus rothauseni
†Chonecetus goedertorum
†Aetiocetus cotylalveus
†Mammalodon colliveri
†Janjucetus hunderi
†ChM PV5720
†ChM PV4745
†Zygorhiza kochii
†Georgiacetus vogtlensis
Hippopotamidae
Bos taurus
Sus scrofa
crown Odontoceti
stem Odontoceti
crown Mysticeti
stem Mysticeti
Cetacea

Figura 1. Hipótesis de relación en Cetacea: A) Lambert, 2005; B) Fordyce, 1994; C) Geisler et al., 2011.

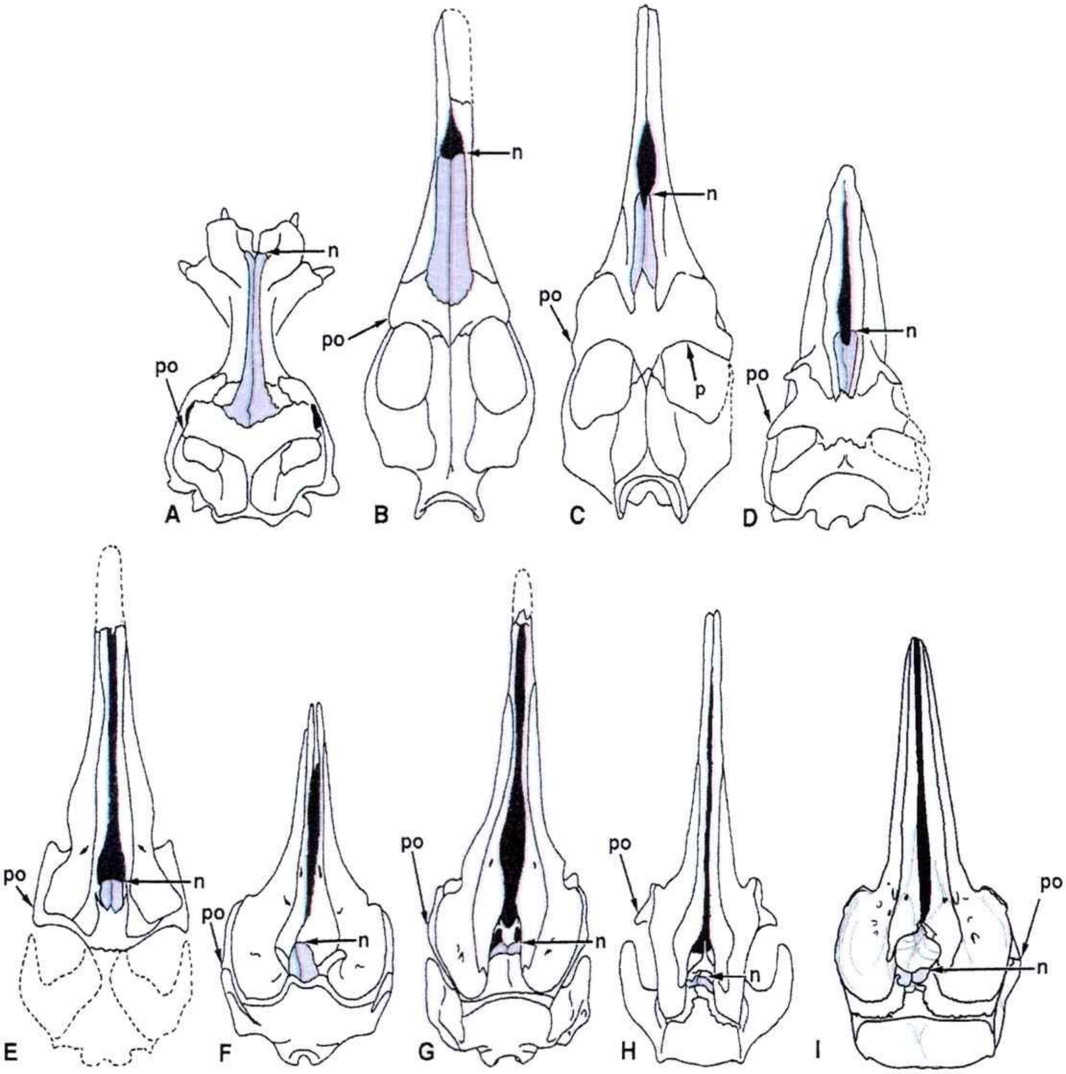


Figura 2. Vista dorsal de cráneos de artiodáctilos y cetáceos mostrando la posición de la narina ósea externa (ne, en negro: canal mesorostral) y los huesos nasales (en gris). (A) *Hippopotamus amphibius*: nasales largos y delgados. (B) *Georgiacetus votglensis* (Protocetidae, Archaeoceti): apertura nasal a la mitad del rostro. (C) *Zygorhiza kochii* (Basilossauridae, Archaeoceti). (D) *Aetiocetus cotylalveus* (Misticeto dentado temprano): borde posterior de la narina externa posicionada un poco anterior a la reentrancia anteorbital. (E) *Xenorophus sloanii* (porción posterior reconstruida): borde anterior de los nasales en línea con la porción media de la órbita. (F) *Ziphius*

cavirostris: borde anterior de los nasales en línea con la mitad posterior del proceso supraorbital del frontal. (G) *Waipatia maerewhenua* (Squalodontidae): nasales en línea con el gap entre el proceso postorbital y el proceso zigomático del ecamoso. (H) *Inia geoffrensis:* nasales en linea con el borde anterior de la fossa del escamoso (fossa temporal). (I) *Delphinapterus leucas*: nasales posteriores al borde anterior de la fossa del escamoso. Modificado de Geisler y Sanders (2003).

Figura 3. Cráneo de misticeto indeterminado (Cetacea, Mysticeti) que se encuentra en exhibición y como pieza fundacional (MPC 0001) del Museo Paleontológico de Caldera.

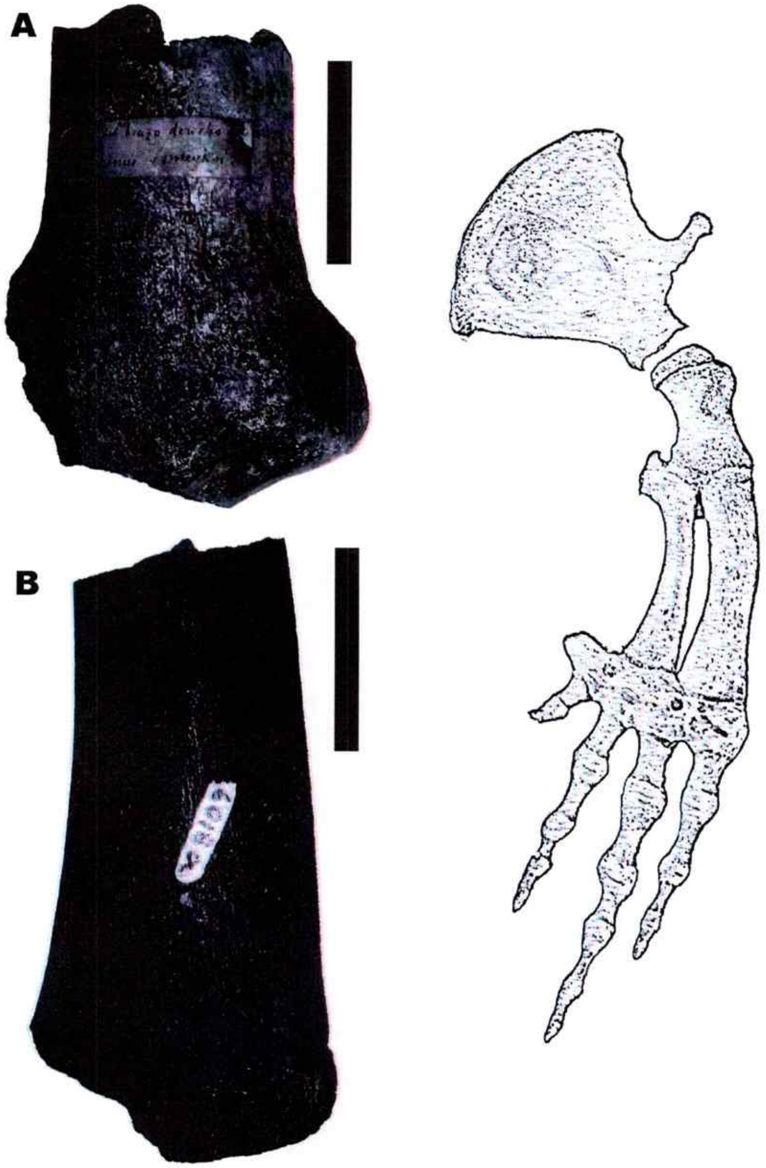


Figura 4. Restos de *Delphinus domeykoi nomen dubium* SGO.PV 6018. A) humero parcial y B) ulna parcial. Al lado derecho se aprecia una reconstruccion de una aleta de odontoceto.

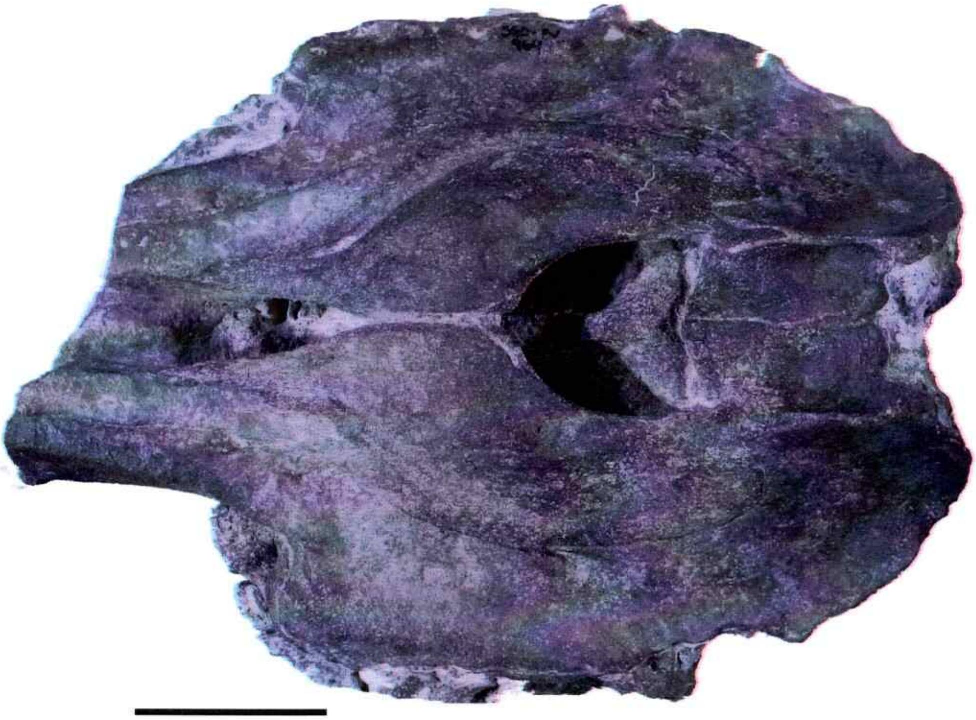


Figura 5. Cráneo de *Pontistes* sp. (Inioidea, Pontoporiidae) proveniente de Formación Bahía Inglesa.

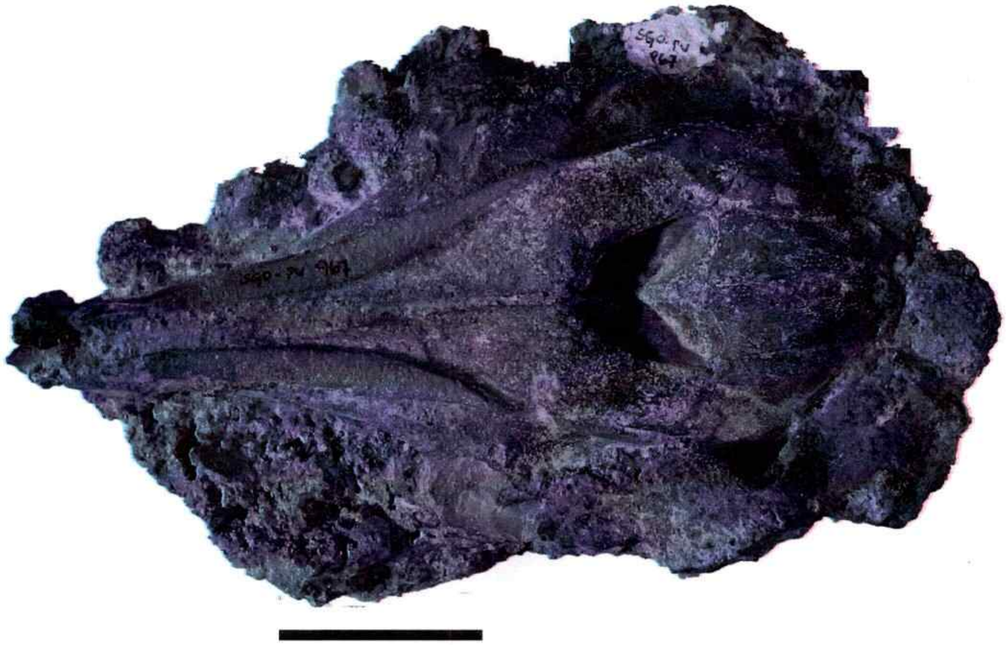


Figura 6. Cráneo de *Pliopontos* sp. (Inioidea, Pontoporiidae) proveniente de Formación Bahía Inglesa.

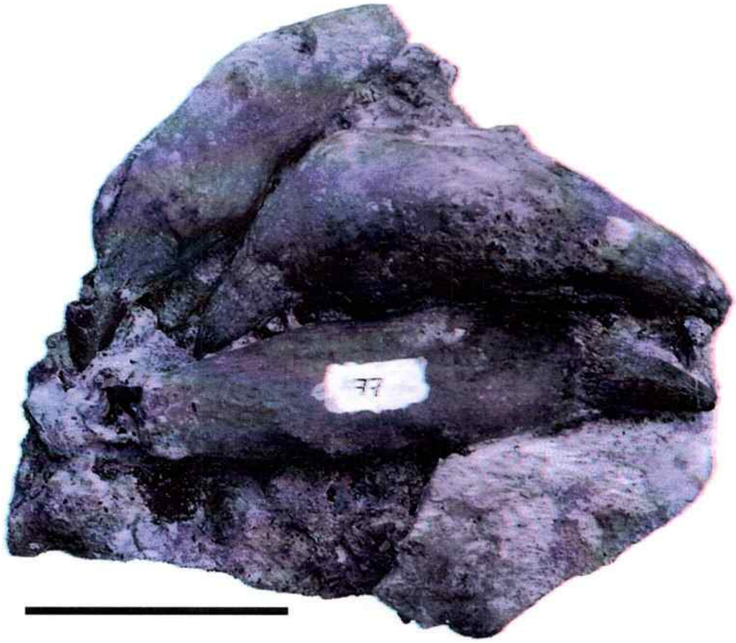


Figura 7. Dientes de *Scaldicetus* sp. (Pyseteroidea) proveniente de Formación Bahía Inglesa.

Capitulo 2

High frequency echolocation, ear morphology, and the marine-freshwater transition: a comparative study of extant and extinct dolphins (Odontoceti)

CAROLINA S. GUTSTEIN

CONSTANZA P. FIGUEROA-BRAVO

NICHOLAS D. PYENSON

MARIO A. COZZUOL

ROBERTO E. YURY-YAÑEZ

MAURICIO CANALS

VI. Capítulo 2

High frequency echolocation, ear morphology, and the marine-freshwater transition: a comparative study of extant and extinct dolphins (Odontoceti)

C.S. Gutstein[a,b,*], C.P. Figueroa-Bravo[a,e], N.D. Pyenson[b], R.E. Yury-Yañez[c], M.A. Cozzuol[d], M. Canals[a,f]

[a]Laboratorio de Ecofisiología, Facultad de Ciencias, Universidad de Chile, Las Palmeras 3425, Ñuñoa, Santiago, Chile. Phone/fax (+56) 2 8958513. sgcarolina@gmail.com

[b]Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, Washington DC, 20013-7012, USA. pyensonn@si.edu

[c]Laboratorio de Zoología de Vertebrados, Facultad de Ciencias, Universidad de Chile, Las Palmeras 3425, Ñuñoa, Santiago, Chile. robyury@ug.uchile.cl

[d]Departamento de Zoologia, Instiuto Ciências Biológicas, Universidade Federal de Minas Gerais, Av. Antônio Carlos, 6627, Pampulha, 31270-910, Belo Horizonte, MG, Brasil. cozzuol@icb.ufmg.br

[e]fbconstanza@gmail.com

[f]mcanals@uchile.cl

[*]To whom correspondence should be addressed: sgcarolina@gmail.com

V.1. ABSTRACT

Odontocetes are unique among marine mammals in several ways, although two notable traits stand out: first, they are the only marine mammals known to use echolocation; and second, several of their lineages have independently evolved obligate freshwater habits from marine ancestries. These lineages, which are represented by the paraphyletic extant "river dolphins", show dramatic external morphological convergences, relative to oceanic dolphins (Delphinoidea). Also, different acoustic signatures parallel these morphological differences, with oceanic dolphins ranging from 40 to 140 kHz with two peak (or bimodal) frequencies and "river dolphins" with only one peak (or narrow-band), around 100 kHz. These differences in echolocation abilities suggest that the sensory systems responsible for detecting these different sound frequencies should also differ, although quantitative assessments of the cetacean hearing system, especially with the tympanoperiotics of odontocetes, remain understudied and taxonomically undersampled. To test if ear bone morphology reflects underlying environmentally driven differences in echolocation ability, we assembled a dataset of odontocete periotics (n = 114) from extant and fossil species. Specifically, we examined 21 periotic measurements, including 18 external and 3 internal linear measurements, the latter of which were examined using cone-beam scanning tomography. Results from multivariate canonical ordination analyses show that periotic height, periotic thickness and pars cochlearis width each explain the largest amount of interspecific variation in our dataset.

Because these measurements correspond structurally to the acoustic hearing ranges, we propose that they are also proxies for environmental preference (i.e., marine, freshwater and intermediate habitats). One of the implications of these correlations is that periotic morphology may be useful for deciphering environmental preferences of extinct odontocetes.

Keywords: river dolphins, Inioidea, Delphinoidea, periotic, ecomorphology, evolution

VI.2. Introduction

Echolocation is a sophisticated biosonar system that has evolved several times in distantly related mammals (tenrecs, toothed whales, microchiropteran bats and Egyptian fruit bats). Toothed whales (Odontoceti) are the only mammals that have evolved this system for use underwater (Lindberg and Pyenson, 2007), where they use sound to both navigate and locate prey (Au, 1993). To navigate underwater, odontocetes generate and transmit high-frequency sound from the forehead using a complex system of muscles, air sacs, and fat bodies, including the large, conical melon (Cranford et al., 1996; McKenna et al., 2011). Sound emitted from the forehead is then transmitted into the underwater environment, and its returning echoes are received via mandibular fat bodies, which articulate directly with acoustically isolated outer ear bones (i.e., the tympanic bullae) of the skull (Nummela et al., 2004; Cranford and Krysl, 2008). This process has been elucidated through a combination of experimental work directly with live individuals in laboratory settings (e.g., Lawerence and Schevill, 1956; Norris, 1969) and anatomical investigations on postmortem specimens (e.g., Cranford et al., 2008). Generally, most in vivo experiments have involved delphinoids (e.g., *Tursiops*, *Delphinapterus*, or *Phocoena*), although investigations with live "river dolphins" (e.g., *Inia*, *Platanista*) have also been reported in the literature (Herald et al., 1969; Pilleri, 1974).

The so-called "river dolphins" are secondarily freshwater odontocete lineages that are represented by the living genera *Inia*, *Platanista*, and the recently extinct *Lipotes* (Simpson, 1945; Rice, 1998; Nikaido et al., 2001; Hamilton et al., 2001; Pyenson, 2009). Typically, *Pontoporia* is included in the latter list, although it is predominantly coastal to estuarine in habitat; *Sotalia fluviatilis*, a delphinid that inhabits freshwater river mouths of Amazonia, is rarely included because of its broad similarity to its coastal marine sister taxon *Sotalia guianensis* (Cunha et al., 2005; Caballero et al., 2007). The first systematic considerations of "river dolphins" (Simpson, 1945; Kasuya, 1973) implied a single evolutionary origin for their freshwater distributions from globally distributed marine ancestors. More recent molecular (Nikaido et al., 2001; Hamilton et al., 2001; May-Collado and Agnarsson, 2006; Steeman et al., 2009) and morphological (Geisler et al., 2011) work confirm the paraphyly of this group. This revised phylogenetic arrangement, along with the biogeography of these lineages, supports at least three independent invasions of freshwater habitats (besides the Delphinidae, S. fluviatilis, incursion into fluvial waters): 1) *Platanista* spp.; and 2) *Lipotes*, which are both endemic to different freshwater systems of Asia; and 3) *Inia* in the Amazon and Orinoco basins of South America (Best and da Silva, 1989; 1993; Fig. 1).

Intriguingly, "river dolphins" display a suite of convergent morphological specializations that have been widely observed in the descriptive and systematic literature, creating confusion about the relationships of these taxa with other odontocetes. This suite of features includes many traits that diverge from the majority of marine odontocetes, such as: flexible necks with unfused cervical vertebrae; wide, paddle-like flippers; reduced or absent dorsal fins; reduced orbits and eyes; and elongate rostra with lingual accessory cusps on the posterior dentition (Rice, 1998; Arnason and Gullberg, 1996; Messenger and McGuire, 1998; Heyning, 1997; Simpson, 1945; Muizon, 1994; 1988a; Cassens et al., 2000; Hamilton et al., 2001). Many of these traits have also been identified in odontocetes besides "river dolphins," or their near, extinct relatives (e.g., Ischyrorhynchus). For example, elongate rostra and complex posterior dentition has been identified in eurhinodelphinids and squalodontids (Fordyce, 1994). Nonetheless, the strong molecular phylogenetic framework underpinning the paraphyly of "river dolphins" clarifies the interpretation of these commonalities as homoplasious, and thus likelyreflect adaptations to these traits related to freshwater habitats.

It is less clear, however, if the morphology underpinning sound generation and reception shows similar convergence. *Platanista*, for example, is unique among “river dolphins” in possessing pneumatic maxillary crests that expand anterodorsally along its face, effectively cradling any forehead soft tissue structures in bone (Mead and Fordyce, 2009:51). The function and acoustic properties of these crests have been proposed to act as an acoustic mirror, producing a more focused beam, likely directed downward, which in part helps to explain Platanista's side-swimming behavior (Herald et al., 1969; Purves and

Pilleri, 1983). Similarly, in terms of sound reception, the tympanic bullae and periotics of "river dolphins" have also been noted for their disparity relative to marine odontocetes (e.g., Kasuya, 1973), but detailed comparisons in a quantitative framework remain undone.

Here, we investigate one specific morphological component of sound reception by focusing on the periotic, an element that is often recovered from extant field collections during carcass preparation because it is dense, robust and relatively well protected from initial scavenging, despite being easily lost from decaying carcasses (Fordyce and Muizon, 2001; Schäfer, 1972). These taphonomic properties also permit the periotic to be equally well represented in the fossil record of odontocetes (Uhen and Pyenson, 2007), and we thus incorporate data from both extant and fossil odontocetes in this dataset (Fig. 1, Table S1). Previous work (Ketten and Wartzok, 1990; Ketten, 1992) has suggested specific, linear periotic dimensions associated with acoustic signals; we selected many of these measurements, and included additional new ones. Our goal, in assembling this dataset, was to test if external and internal periotic morphology differed between freshwater and marine odontocetes. By including fossils, we also sought to test the possible environmental assignments, based a priori from sedimentological data, for these extinct taxa. In this study, we introduced such information to provide important temporal and paleoenvironmental contexts that can better constrain evolutionary hypotheses about the origin of these traits.

VI.3. Materials and Methods

Our dataset included linear measurements (Table 1, Fig. 2) from the periotics of extant and extinct odontocetes that correlate with known acoustic frequencies (see Table 2, Fig. 1). We collected a total of 18 measurements from 114 specimens that covered the following taxonomic breadth: Delphinidae (n = 28); Delphinoidea indeterminate (n = 1); Iniidae (n = 16); Inioidea indeterminate (n = 7); Kentriodontidae (n = 24); Monodontidae (n = 1); Odobenocetopsidae (n = 2); Phocoenidae (n = 20); Physeteridae (n = 1); Platanistidae (n = 3); Platanistoidea (n = 2); and Pontoporiidae (n = 9) (see Table S1 for detailed taxonomy of less inclusive taxa). These measurements were analyzed in two different ways: first as raw data; and then divided by the total width of the median portion of the periotic (Fig. 1, Table 1; measurement 10), to control for size disparity. To test for environmental correlations, we pre-classified the data matrix with groupings based on the observed habitat environment, as follows: riverine; fully marine; and estuarine (including coastal, shallow and epicontinental sea with freshwater input; see Table S1). In the case of the fossil specimens, environmental and geologic age categories were defined compiling locality, sedimentologic and paleoecologic data available in the literature (e.g., Achurra, 2004; Cione et al., 2005a,b; Ward and Andrews, 2008; Whitmore and Kaltenbach, 2008; Achurra et al., 2009; Visaggi and Godfrey, 2010; see also Table S1). For the extant specimens, the distribution data of the species were compiled from literature (Reeves et al., 2002; Shirihai and Jarrett, 2009; see Table S1). Although data on the environmental context for fossil taxa may reflect a variety of taphonomic biases (Uhen and Pyenson, 2007), we assumed that the depositional environment for these specimens effectively was similar to their original habitat. We equally tested any age-related signals by pre-classifying the dataset by geologic age, in the following groupings: early Miocene; middle Miocene; late Miocene; Pliocene; and Pleistocene-Holocene. For acoustic properties, which were compiled from the literature in Table 2, we elected to use the emitted frequency data, because it is likely correlated to the perceived hearing frequencies, though not in a 1:1 correspondence (Au et al., 2000). Also, perceived hearing frequency is a value that is much more broadly sampled in the literature. Lastly, only acoustic sensitivity data were available for *Inia*, but it is similar to the peak frequency emitted (Au et al., 2000; see Table 2).

To compare geologic and environmental signals of the dataset with phylogenetic history, we also grouped our data taxonomically by family and genus levels following Steeman et al. (2009) and Geisler et al. (2011; see Table S1). Although supra-familial relationships among extant cetaceans, especially among odontocetes, have not yet reached a consensus, we decided to use Steeman et al. (2009) and Geisler et al. (2011) as a proxy for phylogeny. We allotted our taxa among the following stem and crown groups (stem-Inioidea, Iniidae, Pontoporiidae, Delphinidae, Kentriodontidae, Phocoenidae, Platanistidae, stem-Platanistoidea, *Odobenocetops+Delphinapterus*) and superfamily level

(Platanistoidea, Inioidea, Delphinoidea).

We then conducted multivariate analysis of variance and canonical variate analysis (MANOVA and CVA, respectively) using PAST 2.11 (Hammer et al., 2001). When no difference was confirmed between selected groups, we merged them and repeated the analysis with a new arrangement. For example, there was no significant difference between early and late Pliocene age groups, so we repeated the analysis by merging both groups in one Pliocene group. We used the CVA biplot option in PAST to interpret the canonical axes as they scale CVA loadings by the pooled within-group covariance matrix.

The main measurements in the multivariate analysis biplots were then analyzed in a paired comparison analysis, with a Kruskal-Wallis ranked test for significance, which assessed the differences among the selected measurements. Useful comparisons between pairs of measurements were also performed. These selected measurements corresponded to the most influential ones, which had the largest values in the CVA loadings as well as in biplot relative importance by explaining the variance in canonical axes. This methodological step allowed us to simplify the quantification of multivariate variance and explain morphological differences between groups in a simpler way.

VI.3.1. Institutional Abbreviations

IDSM: Instituto de Desenvolvimento Sustentavel Mamiraua, Tefe, Brazil;

MACN: Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MLP: Museo de La Plata, La Plata, Argentina; MNHN: Museum national d'Histoire naturelle, Paris, France; MPC: Museo Paleontológico de Caldera, Atacama Region, Chile; SGO-PV: Area Paleontología, Museo Nacional de Historia Natural, Santiago, Chile; UFSC: Laboratorio de Mamíferos Aquáticos, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, Brazil; USNM: Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia, U.S.A.

VI. 3. 2. Computed Volumetric Tomography

We evaluated the internal cochlear morphology of the periotics (Supplementary Table 1) in our dataset using computed tomography (CT), a technology that permits high-resolution and precise imaging of small and obscured anatomical structures without modifying or destroying original voucher specimens. Specifically, in this study, we used volumetric CT with a cone beam array (I-Cat, from Imaging Science International), which provided resolution of the internal periotic morphology without gaps and with 0.2 mm precision. CT scanning with the cone beam method allowed us to scan an entire set of periotics oriented in the same plane (fixed to a wood plate with wax), thereby avoiding the effects of reflection (i.e., mirroring), and damage to the specimens.

Lastly, this method produced a relative density spectrum for the specimens.

The resultant DICOM images were analyzed and rendered in OsiriX (Rosset et al., 2004); we used the open polygon tool to collect all of the measurements. The measurements are described in Table 1 (see also Fig. 2).

VI. 4. Results

VI. 4. 1. Morphology

This section summarizes the 5 most salient morphological groups observed in our results. These periotic groupings are described along three main anatomical portions (*sensu* Mead and Fordyce, 2009): the periotic processes (anterior and posterior); the pars cochlearis; and the inner morphology of the cochlea, which were clearly recognized, along with the cochlear duct, from cone-beam tomography imaging. The cochlear duct itself lies inside the pars cochlearis and it is positioned with its base at the ventral surface of the periotic and the apex at the dorsal surface of the periotic, connecting to the acoustic meatus (see Fig. 2 for periotic orientations). When possible, we discussed the inner cochlear duct morphology and orientation in connection to the external pars cochlearis morphology (sensu Mead and Fordyce, 2009:111-133, and references therein).

In general, we were able to determine that external pars cochlearis morphology were consistently discriminated riverine from marine taxa. For example, the riverine odontocetes studied herein (e.g., *Inia*, *Platanista*, and an iniid from the Ituzaingó Formation of Argentina [MACN 9231]) presented a consistently rounded, slender and high pars cochlearis morphology (Fig. 3). By comparison, marine and estuarine taxa (e.g., *Sotalia guianensis* and *Pontoporia,* Fig. 3) exhibited a dorsal-ventrally globose and thick pars cochlearis.

These external, morphological distinctions paralleled cone-beam tomography results (see Table S1), which showed that the larger cochlear duct sizes directly corresponded to larger external pars cochlearis sizes (see Fig. 3).

The first morphological category, is characterized by the periotics of *Platanista*, which exhibited an overall distinct morphology and they were larger, in absolute size, than every other odontocete periotic in this dataset. Notably, the pars cochlearis in *Platanista* was oval in shape, with a rounded medial surface and rectilineal anterior and posterior surfaces, which can be observed clearly in ventral and dorsal views (Fig. 3). The internal acoustic meatus was circular in shape, as seen medially, which is a condition only observed in other platanistoid periotics (e.g., the extinct *Notocetus*). The anterior process in *Platanista* was elongate and robust, while the posterior process was reduced and narrow. The anterior process showed a noticeable anteromedial deviation. The lateral surface (in ventral view) was expanded, as in *Inia geoffrensis* and the Ituzaingó Formation iniid (MACN 9231; Fig. 3).

Second, *Inia* showed an equally distinct morphology as well, with an extreme reduction and anteroposteriorly orientation of the anterior and posterior processes. The pars cochlearis was rounded (in ventral view) and slender (in medial view), with a marked, mediolaterally oriented sulcus. The internal acoustic meatus was circular as in *Platanista*, but it was not visible in the medial view. Compared with fossil Iniidae from our dataset, *Inia* only differed by an absence of the pars cochlearis sulcus and the oval shape of the internal acoustic meatus. MACN 9231 showed a widely exposed facial canal.

The third morphological category, in contrast to *Platanista* and *Inia*, was an overall slender morphology, characterized by *Phocoena*. The anterior process here was narrow and both processes were largely separated from the pars cochlearis, whose lateral surface was almost absent, in contrast to *Platanista* and iniids.

The fourth category, characterized by *Brachydelphis mazeasi*, a fossil inioid, had a relatively small periotic, with a diminished anterior process comparable to *Pontoporia* and *Pliopontos*. *Brachydelphis* differed from these latter taxa by having a broad and rounded posterior process and a pars cochlearis triangular in shape with a clear, medially pointed apex. The anterior process was pointed in its anterior extremity and bent medially, with it being closer to the pars cochlearis. The lateral surface of the anterior process was also somewhat expanded, in contrast to phocoenid and pontoporiid morphology.

The fifth and last morphological category is represented by *Delphinodon dividum*, which is broadly similar to extant delphinids in periotic morphology, in having an elongate and rectangular anterior process, which was deflected in an anteromedial direction. Its pars cochlearis was oval in shape, similar to *Platanista* (see above, Fig. 3). The internal acoustic meatus was oval in shape, with the endocranial opening of the facial canal exposed dorsally. Its lateral surface was straight and slightly expanded, with the tympanic hiatus anterior-posteriorly elongated when compared to *Brachydelphis*, for example.

VI. 4. 2. Cochlear duct versus *pars cochlearis* shape

The volumetric tomography performed for nine specimens of different groups (see Table 2 and Table S1) provided access to the cochlear and general inner ear bony morphology in a non-destructive manner. The cochlear shape varied from a globose pars cochlearis and expanded cochlear duct to a more compressed cochlea with a similarly flattened pars cochlearis (Fig. 3, 4). We noted that a bulbous profile of the pars cochlearis generally corresponded to a more dorsoventrally expanded cochlear duct, as observed in *Sotalia guianensis*. Equally, we noted that a slender pars cochlearis profile corresponded to a dorsoventrally compressed cochlear duct in *Inia*. The relationship between both features was more diffuse in *Phocoena*. These patterns are largely quantified in the results from our analyses, which showed that the main variables in the environmental morphometric analysis were pars cochlearis proportions, as detailed below (see 3.3, Figs. 5-7). Measurements from the internal portion of the cochlea, including the cochlear duct (i.e., the maximum diameter of the cochlear duct in the base and the maximum distance between the apical and basal portion of the cochlear duct; see Wartzok and Ketten, 1999), were strongly correlated with measurements taken at the external portion, the pars cochlearis. Specifically, the inner measurements corresponded to 59-74% of the external bony measurements, including different species from different clades and geologic ages (see Fig. 3).

The pars cochlearis diameter or width was not recovered as an accurate representative of the maximum diameter of the cochlea. Nevertheless, the differences between thickness and the width of the cochlear duct, as observed in the external pars cochlearis morphometrics, hinted at a positive correlation, where *Inia*, the only riverine species examined with tomography, showed one of the smallest cochlear duct heights in the dataset (Fig. 8). On the other hand, the fully marine species were distributed at the opposite extreme of the scatterplot in Fig. 8, showing the largest cochlear duct heights. Estuarine or coastal species were located between these extremes, yet they appeared to group closer to marine taxa.

VI. 4. 3. Taxonomic versus environmental and time variables

The main features of the periotic morphology that varied across taxa, time and environment were the relative proportions among the pars cochlearis, and the anterior and posterior processes. Previous authors have noted that the relative orientation of the latter features, along with their associated foramina, were valuable for discriminating among odontocete taxa at the generic level (Kasuya, 1973; Barnes, 1985; Muizon, 1988). Here, we have determined that some of these characteristics also clustered into discrete groups based on geologic age and known environmental preferences. For example, both overall periotic size and the relative size of the anterior and posterior processes (in an anteroposterior direction) were strongly correlated with geologic age (Fig. 5). Equally, pars cochlearis shape was strongly correlated with environment: cochlea from extant "river dolphins" were taller, more rounded, and more slender than those from oceanic delphinoids (Fig. 7).

Significant results were not recovered for genus-level taxonomic groups in our CVA results. Nevertheless, groupings at family-suprafamilial levels (CVA ; Fig. 6) recovered some of the groups as significant, although the first canonical axis only explained 64% of the variation, and both of the axes explained together less then 80% of the total variation. Notably, Delphinidae were significantly different from all groups, with Iniidae, Pontoporiidae and Phocoenidae following

Delphinidae in descending order of significant differences in the pairwise comparisons. Regardless, the most important measurements in both canonical axes were the diameter of the malleus fossa (measurement 7) and the length of the anterior process (measurements 5 and 6), although the latter was less important than the former.

VI. 4. 4. Morphometry and environment

In the test for correspondence of these morphometric features with their environmental origin, the CVA results showed significant differences between each pairwise comparison with each environmental group (i.e., morphometry versus fully marine, coastal/estuarine, and riverine; Table S1). The overall variance was better explained by the first canonical axis (87.5%), where the most important measurements were: length of periotic (measurement 1); width and height of the pars cochlearis (measurements 2, 8, and 11); length of acoustic internal meatus (measurement 4); and width of the periotic (measurement 10). Thus, the majority of these measurements were related to the pars cochlearis shape. Variance for the second canonical axis was represented by the internal acoustic meatus (measurement 3) and the width of the pars cochlearis (measurement 8), but only 12.5% of the variance in the data was explained by this axis. Moreover, there was little differentiation among the groupings in this axis as well. For the size-independent dataset, CVA results were similar to the raw data, with first canonical axis explaining 87.1% of the data and dominated by the following measurements: periotic length (measurement 1); malleus fossa size (measurement 7); pars cochlearis height (measurement 11); and anterior process length (measurement 5).

Interestingly, the most relevant measurement in this size-corrected analysis was the maximum thickness of the pars cochlearis (measurement 15), which explained approximately 20% of the first canonical axis alone. For the second canonical axis, only 12.9% of the variance was explained, with little differences among the possible groupings. For this latter axis, the important measurements were width of the fossa for the stapedial muscle (measurement 13), the maximum and minimum thicknesses of the pars cochlearis (measurements 15, 16), the epitympanic hiatus width (measurement 17), and the internal acoustic meatus depth (measurement 18), which all accounted for approximately 25% of the variance.

We also compared inner ear morphology, from tomography data, against environmental classifications because previous authors have suggested that inner ear measurements were functionally relevant to hearing (Ketten, 1992, Wartzok and Ketten, 1999; Wever et al., 1971, Miller et al. 2006). The morphometric analyses of these measurements (Table 1) recovered the pars cochlearis external width, height, and thickness as significant variables, and because these linear dimensions essentially correlated with inner cochlear shape and length, as expected, and, most importantly, these analyses group specific taxa into cochlear types proposed previously (Wever et al., 1971; Ketten, 1992; Ketten and Wartzok, 1990).

In this sense, the paired comparisons (measurement *versus* measurement) revealed that the best fit ($p < 0.01$) in differences between the groups were thickness versus height and width of pars cochlearis (Fig. 7). These results are in agreement with the aforementioned functional scheme, where the more elongate and thinner pars cochlearis morphology reflected the cochlear duct morphologic types I and II (see Section 4.3 for further discussion).

Our results also demonstrated that the shape of internal acoustic meatus was significantly correlated with environmental type: namely, its width (measurement 3) explained the variance of the coastal and estuarine group and its length (measurement 4) correlated with the riverine group. The significance of the internal acoustic meatus, however, was secondary to the aforementioned, primary measurements.

VI. 4. 4. 1. Environmental classification of fossil taxa.

We generated *a priori* environmental categorizations for fossil specimens by searching the source literature for associated sedimentologic and paleoecologic data (as detailed in Section 2, Table S1). Although these data inform only about the environment of final deposition (thanatocoenosis), we view these data as reasonable approximations of the original source habitat (biocenosis) for these extinct taxa based on the general fidelity of extant death assemblages to their source communities (e.g., live-dead studies detailed by Pyenson, 2010; 2011). Nevertheless, the *post hoc* predictions of the CVA results can also work as tests for the likely original habitats of extinct odontocetes. The analyses conducted herein permit the categorization of fossil taxa to specific environmental types. For example, *Delphinodon dividum*, a kentriodontid from the Miocene of the western Atlantic Ocean, was similar to *Delphinapterus* in having CVA classify it as a riverine taxon, dictated mostly by its slender pars cochlearis profile. Another fossil taxon,

Odobenocetops, an enigmatic walrus-convergent odontocete known from the Pliocene of Peru (Muizon, 1993) was also an outlier, with results spread across the total distribution of the coastal/epicontinental/estuarine specimens. Such a difference could easily be interpreted as a consequence of its relatively large size, but the size-independent matrix showed that it nonetheless was located at the extremes of the scatterplot distribution.

Other specimens misclassified (i.e., *a priori* classification differing from statistical predictions) were: *Lophocetus pappus* and *Lophocetus calvertensis* from the Calvert Fm.; *Brachydelphis mazeasi* from Pisco Fm. (given: coastal; predicted:

fully marine); *Phocoena phocoena* (given: marine; predicted: riverine); and *Kentriodon* sp. from the Calvert Fm. (given: fully marine; predicted: coastal/estuarine).

Finally, *Platanista* showed conflicting results between its given (riverine) category and its predicted (fully marine) one. The jackknife results from the predicted categories added 10 more misclassified taxa: *Inia geoffrensis*; *Neophocoena phocaenoides*; three specimens referred to Pontoporiidae indet. (two as fully marine and one as riverine); and two additional *L. pappus* specimens.

VI. 4. 5. Morphometry and geologic time

We also tested the classification of geological ages groups, by age (6 groups, from the early Miocene to Holocene) and by major splits in taxonomic diversity and morphological disparity. In odontocetes, it has been suggested that stem groups dominated early Miocene assemblages, whereas the middle Miocene marks the onset of crown group dominance that persisted until the Holocene(Fordyce, 1980; Steeman et al., 2009; Cozzuol, 1996; Cione et al., 2005, a, b). In this hypothesis there would be two morphologically distinct groups, which are the stem-groups present still at the early Miocene, from the crown groups that became dominant from the middle Miocene to Holocene (Table S1). Fordyce and Muizon (2001), for example, argued that taxonomic diversity in Platanistoidea and Delphinida followed patterns of competitive exclusion during the late Paleogene and early to mid Neogene, although this idea has not been thoroughly tested.

The age classification differences in the present analysis were significantly different only for the extant species ($p < 0.01$) in the pairwise comparisons of the MANOVA and CVA (see Table S1 and Fig.1 for geologic age groups depiction). This result could arise from dividing the sample size into 7 groups, which generates 6 canonical axes to explain the amount of variation, being the first 2 axes less than 80% of this variation. Nevertheless, different measurements were relevant following this new arrangement of the groups, sorted by geological age. In the first canonical axis, the main measurements were: total length of periotic (measurement 1); length of the anterior process (measurements 5 and 6); the length of internal acoustic meatus (measurement 4); followed by the width of internal acoustic meatus (measurement 3) and in a lesser degree, the width of pars cochlearis (measurement 2) and total periotic width (measurement 10).

We also compared size-independent data by grouping them into three geologic age groups (early Miocene; middle Miocene to late Pliocene; and Holocene). These groups were separated based on the observed distribution of the specimens in the aforementioned scatterplots and classification matrix, which all recovered significantly different groups ($p < 0.01$) with different relevant measurements. The second axis showed the most of the separation between early Miocene and the others groups, but this axis explained approximately 25% of the variation, which makes these results less robust. The measurements that were relevant in this axis were, listed in descending order, total length of periotic (measurement 1) and length of the anterior process (measurements 5 and 6). Meanwhile, the first canonical axis, which explained most of the variation (~75%) within the younger groups, the most important measurements were the length of internal acoustic meatus (non-functional measurement 4), total periotic width (measurement 10) and pars cochlearis height (functionally relevant measurement 11).

The latter structure morphologies would be different since the middle Miocene, meanwhile, other measurements point it out for environment grouping analysis (i.e. functional measurements) were not relevant in the geologic time perspective.

VI. 5. Discussion

VI. 5. 1. Ear morphology correspondence to echolocation type and environmental preference

The correspondence between odontocete cochlear morphology (both inner and external) and echolocation type was been proposed in the literature 40 years ago, with some reinterpretation in subsequent, but singular studies (Miller et al., 2006; Wever et al., 1971; Ketten, 1992; Wartzok and Ketten, 1999). Our study is the first to integrate a morphometric dataset (including extant and extinct taxa) within a robust statistical context. We found that the inner cochlear and the external pars cochlearis morphology were tightly correlated and we propose that these features should be used as ecomorphologic indicators of environmental preference, for both extant and extinct taxa. We nonetheless caution that the accuracy of these correlations depend on appropriate and independent contexts (i.e., sedimentological data). The robust results showing the discrimination of riverine versus marine and coastal-estuarine classifications for fossil and extant odontocetes strongly suggest the potential for periotic features are valuable indicators of environmental preference, primarily based on the correspondence of these structures to the frequency range of hearing and the particular acoustic properties of water in these environments.

Interestingly, the non-functional measurements, here considered as control measurements (e.g., anterior process size [5, 6]), were not important in the environmental analysis with the only exception of the total length of the anterior process, although they were influential for discriminating geologic and taxonomic effects. Muizon (1988a) originally observed that the absolute and relative size of the processes correlated with both taxonomic and geologic age groups, but measurements related to other functional structures, such as the size of the malleus fossa and internal acoustic meatus proportions, were secondarily important in most of our analyses.

VI. 5. 2. Periotic morphology classification/misclassification of environment

In some instances, CVA results grouped the periotic shapes of some taxa in conflicted with their actual environmental type. For example, our results classified *Delphinapterus leucas* as riverine, despite its actual coastal to estuarine habitat. This result is interesting not only because *Delphinapterus* inhabits an intermediate environment (e.g., some populations in the St. Lawrence Seaway, which is mixed coastal and estuarine), but it also possesses a unique echolocation type. Behavioral studies of show *Delphinapterus* emitting click trains (rather than isolated clicks; Madsen et al. 2004) at very high frequencies, but with a bimodal structure (70 and 112 kHz), a feature that is congruent with their cochlear duct morphology (Type I, 2.25 turns; Table 2). Some have attributed this unusual sound emission pattern to their ability to survive in pack ice-dominated environments (Madsen et al., 2004).

Delphinodon dividum was similar to *Delphinapterus* in the multivaritate analysis. We suggest that such findings should be considered in any further paleobiological interpretations for this taxon. In *Odobenocetops* the overall very distinct morphology as shown by the CVA results may indicate some unknown functional significance, which remains unrevealed.

For *Phocoena*, it was (pre)classified as marine (given its present distribution) although Ketten (1992) and Wartzok and Ketten (1999) reported narrow banded beam characteristics (frequency >100 kHz; Akamatsu et al., 1994) more typical of extant riverine species. Morphological observations did not reveal this pattern at the outset, although morphometric and statistical analyses were able to recover a morphological affinity of *Phocoena* with riverine species. In this case, the riverine classification of *Phocoena* can be attributed to the correspondence of the external periotic morphology with the type I cochlear morphology and hence, its narrow-banded echolocation (see section 4.3). Nevertheless, the environmental mis-classification does not have a simple explanation, as it should be related to the more coastal preference for most *Phocoena* species. Alternatively, it may be argued that these differences show a disconnection between echolocation clicks acoustic properties and the hearing anatomy, but the overall accordance with the rest of the dataset suggests otherwise.

Regarding *Platanista*, the conflicting results (misclassification as fully marine) may stem from its plesiomorphic features, which reflect a closer marine ancestry with fossil platanistoids, which are entirely known from marine deposits (see Fordyce, 1994; but see Geisler et al., 2011, for a different interpretation).

Interestingly, in the list of specimens that were misclassified in the predictions, *Brachydelphis* from middle to late Miocene, was not distinguishable from the early Miocene groups. This result is in agreement with other observations, mentioned elsewhere, that this genus has a basal position in Delphinida (Gutstein et al., 2009; Cozzuol, 2010; Geisler et al., 2011) rather than a derived position within Pontoporiidae, as originally proposed by Muizon (1988b). We also observed the same mis-classification in *Belonodelphis* (holotype specimen) and *Australithax* (paratype specimen).

VI. 5. 3. Functional implications of inner ear morphology

The volumetric tomography data (nine specimens of different groups) were slightly different from the overall patterns observed by Ketten (1992) and Wartzok and Ketten (1999). These authors stated that higher frequency hearing (type I) would be associated to more compressed cochleae, which have fewer turns and a greater expansion of the outer osseous spiral lamina in the membrane length (Fig. 4, Table 2). This functional implication is possible in light of basilar membrane morphometrics (e.g., the width to thickness ratio) and the outer spiral lamina extension as acceptable proxies of stiffness of this membrane (von Bekesy, 1960, Ketten, 1984, Wever, 1971) at a given scale permitting a relative definition of echolocation types (for a review see Miller et al. 2006). These features allow the morphologic discrimination of the two main types of echolocation observed in living species. In riverine and coastal species, there is a low frequency cut off in the echolocation beam, which produces a narrow-banded click structure, while fully marine species present both, high and low peak frequency, producing a bimodal sound structure (e.g., *T. truncatus* and *S. attenuata*; Table 2, Miller et al. 2006). This is slightly different from the scheme proposed by Wartzok and Ketten (1999) of cochlear types: type I cochlea and echolocation high peak frequency (100kHz) would be associated with a more broad, turned and contracted cochlea, that have the base to apex axis oriented rather ventromedially than dorsal-ventrally; and type II cochleae would have the base to apex axis oriented dorsal-ventrally with a more expanded cochleae, associated with echolocation broader ranges including a lower peak frequency (~40 to 70 kHz).

In this study we were able to determine that external morphological measurements can be associated with riverine and marine habitats. This relationship was particularly well supported by the broad dataset, composed of taxa from different environments, geographic regions and taxonomic groups, specifically sampled to test if external and internal periotic morphology differed between freshwater and marine odontocetes. By including fossils, we also sought to test the possible environmental assignments, based a priori on sedimentologic data, for these extinct taxa. We introduced such information with the purpose of providing the proper temporal and paleoenvironmental contexts.

Our study fits squarely in previous sets of observations that notes the external and osteological convergences among the so-called "river dolphins". In parallel, there has also been indication that functional aspects of "river dolphin" echolocation has converged on similar solutions for producing and receiving sound in an environment unlike the putative oceanic conditions of their ancestors. The freshwater systems inhabited by extant "river dolphins" differ in acoustic and optic properties from marine ones, including: water temperature, which alone can affect the propagation of echolocation signals (Wartzok and Ketten, 1999); turbidity; and complex, physical obstacles that are seasonally present in the flooded forest environments of Amazonia, for example (Martin and da Silva, 2004; Martin et al., 2004). It is plausible that such environmental differences in the acoustic properties of riverine (i.e., high temperature, low visibility, small areas full of obstacles) versus marine (i.e., lower temperature, high visibility, wide-open areas) habitats have led to the different ecomorphologies of marine and riverine dolphin hearing systems. Alternatively, different prey types could also be a factor in sound production differences, but there is no evidence for this supposition currently (see Madsen et al., 2004).

VI. 5. 4. Acoustic parameters and morphology

When the acoustic parameters used for echolocation in living odontocetes are compared with our results in morphology, taxonomy, environment and age (Table 2), it is notable that the acoustic proprieties sort mainly by emitted frequencies in two ways: first, with a low-peak of frequency, giving a bimodal structure to the echolocation beam observed in marine species (not measured here) as *T. truncatus* and *S. attenuata* and other delphinidans (see also Morisaka and Connor, 2007; Wartzok and Ketten, 1999); and, second, with riverine species emitting only a high peak frequency (Miller et al., 2006).

To explain these two different patterns, Morisaka and Connor (2007) have suggested the narrow-band echolocation clicks (emission) pattern and its low frequency cut off was linked to the loss of whistle (emission) in *Pontoporia*, *Cephalorhynchus* and the Phocoenidae family. Nevertheless, here we only could confirm that there is a relationship between environment and the shape of the cochlear duct and pars cochlearis (i.e., part of the hearing system). In this sense, it is also plausible to suggest that the morphological differences (type I and type II, hearing) are functionally related to the low frequency cut off, where the frequency range is reduced to one (instead of two) narrow-band higher frequency beam (emission) in accordance with the possible loss of the cochlear portion responsible for hearing at lower frequencies. In any case, the emitted frequencies may be not very different than the actual acoustic sensitivity (hearing). For example, in *Inia* the auditory sensitivity is at a lower frequency than the one emitted, but only by a small amount (-10 kHz; see table 2).

VI. 5. 5 Evolutionary scenarios for the marine-freshwater transition in odontocetes

Our results provide one set of tools that may assist other lines of evidence in resolving outstanding questions about the pattern and timing of odontocete invasions in freshwater ecosystems during the Neogene. Generally, environmental transformations that occurred during the Neogene have been proposed as drivers of large-scale cetacean evolutionary change (Fordyce, 1980; Nikaido et al., 2001; Steeman et al., 2009). Specifically, Steeman et al. (2009) tested competing hypotheses to explain extant cetacean diversification: whether abiotic drivers, such as, physical restructuring of the oceans, played a major role in the radiation of extant cetaceans (Fordyce, 1980; 2003); or if extant cetacean diversity was driven by rapid changes into an open adaptive zone, such as the initial radiation in stem Cetacea (Nikaido et al., 2001). Steeman et al. (2009) obtained strong correlations between molecular clock estimations, which restricted extant lineage diversification to two periods of major oceanic restructuring (35–31 and 13-4 Ma), the latter inferred through time-series curves of global ocean productivity proxies, temperature (Zachos et al., 2001) and sea-level fluctuations (Miller et al. 2005). It is important to note that Steeman et al. (2009), however, did not directly incorporate fossil diversity data to test their competing scenarios, nor rigorously constrain their molecular clock calibrations with fossil data following now-established best practices (Parham et al. 2012)

In this light, the multiple origins of "river dolphins" provide a compelling series of case studies where known marine to freshwater transitions ought to be linked to patent physical, environmental changes during their evolutionary histories.

South America provides important datasets towards addressing this issue. The orogeny of the Andes, the re-direction of major river systems, and closing and opening of major ocean seaways during the Neogene all provide ample instances of geologic-scale changes that would have factored into the diversification of lineages at the interface of marine and freshwater environments. Extant lineages in this continent (*Inia*, *Pontoporia*) provide a valuable source of extant molecular datasets to understand recent divergences among populations (Hamilton et al., 2001; Banguera-Hinestroza et al., 2002), but deeper divergences from ancestral marine odontocetes remains outside of the scope of these data. However, this continent preserves an abundant and rich record of fossil odontocetes from different sedimentary basins (Cozzuol, 1988; 1996; Cione et al., 2005a; 2009; Gutstein et al., 2009).

In South America, the timing of the marine to freshwater transition in odontocetes likely occurred between 13 and 4 million years ago (middle Miocene through early Pliocene). Marine transgressions across the Brazil Craton during the middle Miocene (Latrubesse et al., 2007; Hoorn et al., 2010) would have created an entirely new set of habitats in a region that currently consists of terrestrial Neotropical forest ecosystems, extending from the northern portion of South America to as far south as Argentina, forming a body of water termed the Paranean Sea (Donato, 2006; Latrubesse et al., 2007; 2010; Cione et al., 2010; Horn et al., 2010). The timing of this inland continental flooding of South America coincides with the most diverse period of the Inioidea (Cozzuol, 2010), a group that encompasses the extant Amazon River dolphin (*Inia*) and many fossil genera spread from the North Atlantic to the South Pacific (late Miocene to early Pliocene), including the freshwater systems of northeastern Argentina (late Miocene) as well as the estuarine extant species, *Pontoporia* (Allen, 1941; Muizon, 1983; 1988 a,b; Pyenson and Hoch, 2007; Godfrey and Barnes, 2008; Gutstein et al., 2009; Cozzuol, 1988; 1996, 2010; Gibson and Geisler, 2009). Subsequent to the middle Miocene eustatic sea-level maxima (Miller et al., 2005; Hamilton et al., 2001), inland flooding subsided, likely isolating some lineages, although it is unclear if such a mechanism explains the specific freshwater origin for *Inia*, which remains the singular representative of this once diverse clade in the Amazon-Orinoco River systems. Nevertheless, several reviews of South American Neogene geology (Hoorn, 2009; Hoorn et al., 2010) have pointed to the importance of geological-scale mechanisms for generating Amazonian biodiversity, such as the uplift and orogeny of the northern Andes.

Interestingly, another species endemic to the Amazon River system, the tucuxi (*Sotalia fluviatilis*) has been interpreted as a recent re-entrant to freshwater systems because its nearest relatives (*S. guianensis* and other delphinids) are fully marine taxa (Caballero et al., 2007). Also, compared to *Inia*, it inhabits a region more downstream and hears at an intermediate frequency range 80-95 kHz (although it is not clear whether it has also a bimodal or narrow-band echolocation beam; Kamminga et al., 1993). Molecular divergence time estimates between *S. fluviatilis* and its sister taxon, *S. guianensis*, proposed a Pleistocene split (~1.2-1.0 Ma), hint that eustatic sea-level changes during this interval might also play a role in driving the evolution of this delphinid freshwater invasion.

VI. 6. Conclusions

Our results demonstrate that the pars cochlearis morphology was related to the inner cochlear types and that this correspondence also existed with external periotic morphology. Additionally, both pars cochlearis and acoustic meatus shape reflected the different acoustic properties of the environments that their respective taxa inhabit, which allowed us to differentiate between riverine versus marine (i.e., fully marine or coastal or estuarine) environments. Although previous work had shown that pars cochlearis dimensions partitioned odontocetes into cochlear morphotypes (*sensu* Ketten, 1992), our study used morphometry and robust statistical analyses to discriminate between morphologies and their representative environmental categories. These results also outline one possible source of evidence (i.e., periotic morphology) for deciphering environmental preferences of extinct odontocetes. In terms of the geologic time perspective, we found morphological separations among odontocete periotics from the early Miocene, middle Miocene and late Miocene to Holocene, a finding supported previously only by qualitative studies in the literature (Muizon, 1987; 1988a; Cozzuol, 1996). This timing is in accordance to regional (Hamilton, 2001) and recently more global (Steeman et al., 2009) analyses that both emphasize the primacy of physical (i.e., geologic and oceanographic, respectively) drivers in the evolutionary history of cetaceans, especially over congruent timeframe with the ecomorphological proxies outlined in this study.

VI. 7. Acknowledgements

We thank two anonymous reviewers for insightful and thorough comments that greatly improved the quality of this manuscript. This paper represents part of a dissertation completed at Facultad de Ciencias, Universidad de Chile. This work would not be possible without assistance from collections managers and curators of many collections in different countries: from Chile, David Rubilar-Rogers from MNHN in Santiago; from Brazil, Miriam Marmontel at Instituto Mamiraua in Tefe, Paulo C. Simoes-Lopes at UFSC in Florianopolis, and Danilo Saraiva at Museo de Ciencias Naturais (Pontificia Universidade Católica) in Belo Horizonte; from Argentina, Alejandro Kramarz at MACN in Buenos Aires and Marcelo Reguero at MLP in La Plata; from France, Christine Argot from MNHN in Paris; from the United Kingdom, Richard Sabin at the Natural History Museum, London; from the U.S.A., David Bohaska (Paleobiology) and Charles Potter (Vertebrate Zoology) at the Smithsonian Institution's NMNH, in Washington D.C., and Stephen Godfrey at the Calvert Marine Museum, in Maryland. We wish to thank Rodrigo Passoni (Cefalo-X, Florianópolis, Brazil) for the permission and care to perform the cone-beam tomography at his clinic. We also thank David Rubilar-Rogers who read and improved prior versions of this manuscript and Paulo Simoes-Lopes; Jorge Velez-Juarbe for helpful discussions about periotic morphology. C.S.G was funded by CONICYT, Becas Chile, Departamento de Postgrado y Postítulo of the Vicerrectoría de Asuntos Académicos of Universidad de Chile and the

Smithsonian Institution's Remington Kellogg Fund. This manuscript was also written with support from the Smithsonian Institution's Remington Kellogg Fund and a National Geographic Society Committee on Research Exploration grant (8903-11) to N.D.P. R.E.Y.-Y. was funded by a master's degree CONICYT-Chile scholarship from the Programa de Formación de Capital Humano Avanzado. This paper is Caldera Paleontology Project contribution No. 2.

VI. 8. References

Au, W. W. L., 1993. The sonar of dolphins. Springer-Verlag, New York.

Au, W.W.L., Kastelein, R.A., Rippe, T. & Schooneman, N.M. 1999. Transmission beam pattern and echolocation signals of a harbor porpoise (Phocoena phocoena). Journal of the Acoustic Socierty of America 106, 3699–3705.

Au, W.W.L., Popper, A.N., Fay, R.R., 2000. Hearing by Whales and Dolphins, Springer Handbook of Auditory Research. Springer-Verlag.

Au, W. W. L., R. A. Kastelein, K. J. Benoit-Bird, T. W. Cranford, and M. F. McKenna. 2006. Acoustic radiation from the head of echolocating harbor porpoises (Phocoena phocoena). Journal of Experimental Biology 209, 2726-2733.

Achurra, L., 2004. Cambios del nivel del mar y evolución tectónica de la cuenca de Neogena de Caldera, III Region M.S. thesis, Departamento de Geología, Universidad de Chile, Santiago, Chile. 138 pp.

Achurra, L. E., Lacassie, J. P., Le Roux, J. P., Marquardt, C., Belmar, M., Ruiz-del-Solar, J., and Ishman, S. E., 2009. Manganese nodules in the Miocene Bahía Inglesa Formation, north-central Chile: Petrography, geochemistry, genesis and palaeoceanographic significance. Sedimentary Geology 217, 128-139.

Akamatsu, Y., Hatakeyama, T., Kojima, T., and Soeda, H., 1994. Echolocation rates of two harbor porpoises (Phocoena phocoena). Marine Mammal Science 10, 401-411.

Allen, G.M., 1941. A fossil river dolphin from Florida. Bulletin of the Museum of Comparative Zoology 89,1-8.

Arnason, U., Gullberg, A., 1996. Cytochrome b Nucleotide Sequences Lineages of Extant Cetaceans. Molecular Biology 13, 407-417.

Banguera-Hinestroza, E., Cardenas, H., Ruiz-García, M., Marmontel, M., Gaitán, E., Vásquez, R., and García-Vallejo, F., 2002. Molecular identification of evolutionarily significant units in the Amazon River dolphin Inia sp. (Cetacea: Iniidae). Journal of Heredity 93, 312-322.

Barnes, L. G., 1985. Fossil pontoporiid dolphins (Mammalia, Cetacea) from the Pacific coast of North America. Contributions in Science 363, 1-34.

Best, R. C., da Silva, V. M. F., 1989. Amazon river dolphin, Boto. Inia geoffrensis (de Blainville, 1817), in: Ridgway, S. H., and Harrison, R. J., (Eds). Handbook of marine mammals. Volume 4. River dolphins and the larger toothed whales. Academic Press, London, pp. 1–23.

Best, R. C., and da Silva, V. M. F., 1993. Inia geoffrensis. Mammalian Species

426, 1–8.

Caballero, S., Trujillo, F., Vianna, J. A., Barrios-Garrido, H., Montiel, M. G., Beltrán-Pedreros, S., Marmontel, M., Santos, M. C., Rossi-Santos, M., Santos, F. R., and Baker, C. S., 2007. Taxonomic status of the genus Sotalia: species level ranking for "tucuxi" (Sotalia fluviatilis) and "costero" (Sotalia guianensis) Dolphins. Marine Mammal Science 23, 358-386.

Cassens, I., Vicario, S., Waddell, V. G., Balchowsky, H., Van Belle, D., Ding, W., Fan, C., Mohan, R. S., Simões-Lopes, P. C., Bastida, R., Meyer, A., Stanhope, M. J., and Milinkovitch, M. C., 2000. Independent adaptation to riverine habitats allowed survival of ancient cetacean lineages. Proceedings of the National Academy of Sciences USA 97, 11343-11347.

Cione, A. L., Dahdul, W. M., Lundberg, J. G., Machado-Allison, A., 2009. Megapiranha paranensis, a new genus and species of Serrasalmidae (Characiformes, Teleostei) from the upper Miocene of Argentina. Journal of Vertebrate Paleontology 29, 350-358.

Cione, A. L, Azpelicueta, M. M., Casciotta, J. R., and Dozo, M. T., 2005a. Tropical freshwater teleosts form Miocene beds of eastern Patagonia, southern Argentina. Geobios 38, 29-42.

Cione, A. L., Casciotta, J. R., Azpelicueta, M., Barla, M. J., and Cozzuol, M. A., 2005b. Peces marinos y continentales del Mioceno del área mesopotámica argentina. Edad y relaciones biogeográficas. Historia 14, 49 – 64.

Cione, A. L., Hospitaleche, C. A., Perez, L. M., Laza, J. H., and Cesar, I., 2010.

Trace fossils on penguin bones from the Miocene of Chubut, southern Argentina. Alcheringa 34, 433-454.

Cozzuol, M. A., 1988. Una nueva especie de Saurodelphis Burmeister 1891 (Cetacea: Iniidae) del "Mesopotamiense" (Mioceno tardío-Plioceno temprano) de la Provincia de Entre Ríos, Argentina. Ameghiniana 25, 39-45.

Cozzuol, M. A., 1996. The record of aquatic mammals in southern South America. Munchner Geowissenschaftliche Abhandlungen 30, 321-342.

Cozzuol, M. A., 2010. Fossil record and the evolutionary history of Inioidea, in: Ruiz-Garcia, M., and Shostell, J. M. (Eds.), Biology, evolution and conservation of river dolphins within South America and Asia. Nova Science Publishers, pp. 193-217.

Cranford, T. W., Amundin, M., and Norris, K.S., 1996. Functional morphology and homology in the odontocete nasal complex: implications for sound generation. Journal of Morphology 228, 223–285.

Cranford, T. W., and Krysl, P., 2008. Acoustic pathways revealed: simulated sound transmission and reception in Cuvier's beaked whale (Ziphius cavirostris). Bioinspiration and Biomimetics 3, 1-10.

Cranford, T.W., McKenna, M.F., Soldevilla, M.S., Wiggins, S.M., Goldbogen, J. a, Shadwick, R.E., Krysl, P., St Leger, J. a, Hildebrand, J. a, 2008. Anatomic geometry of sound transmission and reception in Cuvier's beaked whale (Ziphius cavirostris). Anatomical Record 291, 353–78.

Cunha, H. A., da Silva, V. M. F., Lailson-Brito, J., Jr., Santos, M. C. O., Flores, P.

A. C., Martin, A. R., Azevedo, A. F., Fragoso, A. B. L., Zanelatto, R. C., and Solé-Cava, A. M., 2005. Riverine and marine ecotypes of Sotalia dolphins are different species. Marine Biology 148, 449–457.

Donato, M., 2006. Historical biogeography of the family Tristiridae (Orthoptera: Acridomorpha) applying dispersal–vicariance analysis. Journal of Arid Environments 66, 421-434.

Evans, W. E. 1973. A discussion of echolocation by cetaceans based on experiments with marine delphinids and one species of freshwater river dolphin. The Journal of the Acoustical Society of America 54, 191-199.

Fordyce, R. E., 1980. Whale evolution and Oligocene southern ocean environments. Palaeogeography, Palaeoclimatology, Palaeoecology 31, 319–336.

Fordyce, R. E., 1994. Waipatia maerewhenua, new genus and new species (Waipatiidae, new family), an archaic Late Oligocene dolphin (Cetacea: Odontoceti: Platanistoidea) from New Zealand. Proceedings of the San Diego Museum of Natural History 29, 147-176.

Fordyce, E., and Muizon, C. de, 2001. Evolutionary history of cetaceans: a review. In: Mazin, J.-M., de Buffrenil, V. (Eds.), Secondary adaptations of tetrapods to life in water. Verlag Dr. Friedrich Pfeil, Munchen, München, pp. 169-234.

Fordyce, R.E., 2003. Cetacea evolution and Eocene-Oligocene oceans revisited, in: Prothero D. R., Ivany L. C., Nesbitt, E. A. (Eds.), From greenhouse to icehouse. The marine Eocene-Oligocene transition. Columbia University Press, New York, pp. 154-170.

Geisler, J. H., McGowen, M. R., Yang, G., and Gatesy, J., 2011. A supermatrix analysis of genomic, morphological, and paleontological data from crown Cetacea. BMC Evolutionary Biology 11, 112.

Gibson, M.L., and Geisler, J. H., 2009. A new Pliocene dolphin (Cetacea: Pontoporiidae), from the Lee Creek Mine, North Carolina. Journal of Vertebrate Paleontology 29, 966-971.

Godfrey, S. J., and Barnes, L. G., 2008. A new genus and species of Late Miocene pontoporiid dolphin (Cetacea: Odontoceti) from the St. Mary's Formation in Maryland. Journal of Vertebrate Paleontology 28, 520-528.

Gutstein, C. S., Cozzuol, M. A., Vargas, A. O., Suárez, M., and Schultz, C. L., 2009. Patterns of skull variation of Brachydelphis (Cetacea, Odontoceti, Pontoporiidae) from South-Eastern Pacific Neogene. Journal of Mammalogy 90, 504-519.

Hamilton, H., Caballero, S., Collins, G., and Brownell, R. L., Jr., 2001. Evolution of river dolphins. Proceedings of Biological Sciences of the Royal Society 268, 549-556.

Hammer, Ø., Harper, D. A. T., and Ryan, P. D., 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontologia Electronica 4, 1-9.

Heyning, J. E., 1997. Sperm whale phylogeny revisited: analysis of the morphological evidence. Marine Mammal Science 13, 596–613.

Herald, E. S., Brownell, R. L., Frye, F. L., Morris, E. J., Evans, W. E., and Scott, A. B., 1969. Blind river dolphin: first side-swimming cetacean. Science 166, 1408-1410.

Hoorn, C., 2009. Amazonia, landscape and species evolution: a look into the past. Wiley-Blackwell, London.

Hoorn, C., Wesselingh, F. P., ter Steege, H., Bermudez, M. A., Mora, A., Sevink, J., Sanmartin, I., Sanchez-Meseguer, A., Anderson, C. L., Figueiredo, J. P., Jaramillo, C., Riff, D., Negri, F. R., Hooghiemstra, H., Lundberg, J., Stadler, T., Sarkinen, T., and Antonelli, A., 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. Science 330, 927-931.

Kamminga, C. 1988. Echolocation signal types of odontocetes, in: Nachtigall, E. and Moore, P. W. B., (Eds.) Animal Sonar. Processes and Performance, P. Plenum, New York, pp. 9–22.

Kamminga, C. and Wiersma, H., 1981. Investigations on cetacean sonar II. Acoustical similarities and differences in odontocete sonar signals. Aquatic Mammals. 8, 41–62.

Kamminga, C., Hove, M. V., Engelsma, F. J., and Terry, R. P., 1993. Investigations on cetacean sonar X: A comparative analysis of underwater echolocation clicks of Inia spp. and Sotalia spp. Aquatic Mammals 19, 31-43.

Kasuya, T., 1973. Systematic consideration of recent toothed whale based on the morphology of tympano-periotic bone. Scientific Reports of the Whales

Research Institute, Tokyo 25, 1-103.

Ketten, D. R., 1984. Correlations of morphology with fre- quency for Odontocete cochlea: Systematics and Topology. PhD thesis, The Johns Hopkins University, Baltimore.

Ketten, D. R., and Wartzok, D., 1990. Three-dimensional reconstructions of the dolphin ear, in: Thomas, J., and Kastelein, R. (Eds.), Sensory abilities of cetaceans. Plenum Press, New York, pp. 81-105.

Ketten, D. R., 1992. The cetacean ear: form, frequency and evolution, in: Thomas, J. (Ed.), Marine mammal sensory systems. Plenum Press, New York, pp. 53-75.

Latrubesse, E., da Silva, S., Cozzuol, M. A., and Absy, M. L., 2007. Late Miocene continental sedimentation in southwestern Amazonia and its regional significance: Biotic and geological evidence. Journal of South American Earth Sciences 23, 61-80.

Latrubesse, E. M., Cozzuol, M., da Silva-Caminha, S. A. F., Rigsby, C. A., Absy, M. L., and Jaramillo, C., 2010. The Late Miocene paleogeography of the Amazon Basin and the evolution of the Amazon River system. Earth-Science Reviews 99, 99-124.

Lawrence, B., and Schevill, W. E., 1956. The functional anatomy of the delphinid nose. Bulletin of the Museum of Comparative Zoology 114, 103-151.

Li, S., Wang, K., Wang, D. and Akamatsu, T., 2005. Echolocation signals of the free-ranging Yangtze finless porpoise (Neophocaena phocaenoides asiaeorientialis). The Journal of the Acoustical Society of America 117, 3288.

Lindberg, D. R., and Pyenson, N. D., 2007. Things that go bump in the night: evolutionary interactions between cephalopods and cetaceans in the tertiary. Lethaia, 40, 335–343.

Luo, Z., and K. Marsh. 1. Petrosal (periotic) and inner ear of a Pliocene kogiine whale (Kogiinae, Odontoceti): implications on relationships and hearing evolution of toothed whales. Journal of Vertebrate Paleontology 16, 328-348.

Madsen, P. T., M. Wahlberg, and B. Møhl. 2002. Male sperm whale (Physeter macrocephalus) acoustics in a high-latitude habitat: implications and communication for echolocation. Behavioral Ecology and Sociobiology 53, 31-41.

Madsen, P. T., Kerr, I., and Payne, R., 2004. Echolocation clicks of two free-ranging delphinids with different food preferences: false killer whales Pseudorca crassidens and Risso's dolphin Grampus griseus. Journal of Experimental Biology 207, 1811-1823.

Martin, A. R., and da Silva, V. M. F., 2004. River dolphins and flooded forest: Seasonal habitat use and sexual segregation of botos Inia geoffrensis in an extreme cetacean environment. Journal of Zoology, 263, 295–305.

Martin, A. R., Silva, V. M. F., and Salmon, D. L., 2004. Riverine habitat preferences of botos (Inia geoffrensis) and tucuxis (Sotalia fluviatilis) in the Central Amazon. Marine Mammal Science 20, 189-200.

May-Collado, L. J., and Agnarsson, I., 2006. Cytochrome b and Bayesian inference of whale phylogeny. Molecular Phylogenetics and Evolution 38, 344-354.

May-Collado, L.J., Wartzok, D., 2010. Sounds produced by the tucuxi (Sotalia fluviatilis) from the Napo and Aguarico rivers of Ecuador. Latin American Journal of Aquatic Mammals 8, 131–136.

McKenna, M. F., T. W. Cranford, A. Berta, and N. D. Pyenson. 2011. Morphological diversity of the odontocete melon: implications for acoustic function. Marine Mammal Science. doi: 10.1111/j.1748-7692.2011.00526.x

Mead, J. G., and Fordyce, R.E., 2009. The therian skull - a lexicon with emphasis on the odontocetes. Smithsonian Contributions to Zoology 627, 1-248.

Messenger, S.L., McGuire, J.A., 1998. Morphology, molecules, and the phylogenetics of cetaceans. Systematic Biology 47, 90-124.

Miller, K.G., Kominz, M. a, Browning, J.V., Wright, J.D., Mountain, G.S., Katz, M.E., Sugarman, P.J., Cramer, B.S., Christie-Blick, N., Pekar, S.F., 2005. The Phanerozoic record of global sea-level change. Science 310, 1293-1298.

Miller, B. S., A. L. Zosuls, D. R. Ketten, and D. C. Mountain. 2006. Middle ear stiffness of the bottlenose dolphin Tursiops truncatus. IEEE Journal of Oceanic Engineering 31, 87-94.

Morisaka, T., and R. C. Connor. 2007. Predation by killer whales (Orcinus orca) and the evolution of whistle loss and narrow-band high frequency clicks in odontocetes. Journal of Evolutionary Biology 20, 1439-1458.

Muizon, C. de, 1983. Pliopontos littoralis un nouveau Platanistidae Cetacea du Pliocéne de la côte péruvienne. Comptes Rendus de l'Académie de Sciences de Paris, Série II 296, 1203-1206.

Muizon, C. de, 1987. The affinities of Notocetus vanbenedeni. American Museum Novitates, 1-27.

Muizon, C. de, 1988a. Les relations phylgénétiques des delphinida (Cetacea, Mammalia). Annales de Paleontologie 74, 159-227.

Muizon, C. de, 1988b. Les vertébrés fossiles de la formation Pisco (Pérou): Les odontocètes (Cetacea, Mammalia) du Miocène. Travaux de l'Institut français d'Etudes andines 42, 1-244.

Muizon, C. de, 1993. Walrus-like feeding adaptation in a new cetacean from the Pliocene of Peru. Nature 365, 745-748.

Muizon, C. de, 1994. Are the squalodonts related to the platanistoids? Proceedings of the San Diego Society of Natural History 29,135-146.

Nikaido, M., Matsuno, F., Hamilton, H., Brownell Jr, R., Cao, Y., Ding, W., Zuoyan, Z., Shedlock, A., Fordyce, R., Hasegawa, M., and Okada, N., 2001. Retroposon analysis of major cetacean lineages: The monophyly of toothed whales and the paraphyly of river dolphins. Proceedings of the National Academy of Sciences USA 98, 7384-7389.

Norris, K.S., 1969. The echolocation of marine mammals, in Andersen, H.T. (Ed.) The biology of marine mammals. Academic Press, New York pp. 391-423.

Nummela, S., Thewissen, J. G. M., Bajpai, S., Hussain, S. T., and Kumar, K.,

2004. Eocene evolution of whale hearing. Nature 430, 776-778.

Parham, J.F., P.C.J. Donoghue, C.J. Bell, T.D. Calway, J.J. Head, P.A. Holroyd, J.G. Inoue, R.B. Irmis, W.G. Joyce, D.T. Ksepka, J.S.L. Patané, N.D. Smith, J.E. Tarver, M. Van Tuinen, Z. Yang, K.D. Angielczyk, J. Greenwood, C.A. Hipsley, L. Jacobs, P.J. Makovicky, J. Müller, K.T. Smith, J.M. Theodor, R.C.M. Warnock, and M.J. Benton. 2012. Best practices for justifying fossil calibrations. Systematic Biology 61, 346-359.

Pilleri, G., 1974. Side-swimming, vision, and sense of touch in Platanista indi (Cetacea, Platanistidae). Experientia 30, 100-104.

Purves, P.E., and Pilleri, G.E., 1983. Echolocation in Whales and Dolphins. Academic Press, London.

Pyenson, N.D., and Hoch, E., 2007. Tortonian pontoporiid odontocetes from the eastern north sea. Journal of Vertebrate Paleontology 27, 757-762.

Pyenson, N.D., 2009. Requiem for Lipotes: An evolutionary perspective on marine mammal extinction. Marine Mammal Science 25, 714–724.

Pyenson, N.D., 2010. Carcasses on the coastline: measuring the ecological fidelity of the cetacean stranding record in the eastern North Pacific Ocean. Paleobiology 36, 453-480.

Pyenson, N. D. 2011. The high fidelity of the cetacean stranding record: insights into measuring diversity by integrating taphonomy and macroecology. Proceedings of the Royal Society B: Biological Sciences 278, 3608–3616.

Reeves, R. R., Stewart, B. S., Clapham, P. J., and Powell, J.A., 2002. National

Audubon Society guide to marine mammals of the world. Alfred A. Knopf, New York.

Rosset, A., Spadola, L., and Ratib, O., 2004. OsiriX: an open-source software for navigating in multidimensional DICOM images. Journal of Digital Imaging, 205-216.

Rice, D. W., 1998. Marine mammals of the world: systematics and distribution. Society of Marine Mammalogy Special Publication Number 4, 1-231.

Sauerland, M., Dehnhardt, G., 1998. Underwater audiogram of a tucuxi (Sotalia fluviatilis guianensis). The Journal of the Acoustical Society of America 103, 1199–204.

Schäfer, W., 1972. Ecology and paleoecology of marine environments. University of Chicago Press, Chicago.

Schotten, M., Au, W. W. L., Lammers, M. O., and Aubauer, R., 2004. Echolocation recordings and localization of wild spinner dolphins Stenella longirostris and pantropical spotted dolphins S. attenuata using a four hydrophone array, in: Thomas, J. A., Moss, C. F. and Vater, M. M., (Eds.) Echolocation in Bats and Dolphins. University of Chicago Press, Chicago, pp. 393–400.

Simpson, G. G., 1945. The principles of classification and a classification of mammals. Bulletin of the American Museum of Natural History 85, 1-350.

Shirihai, H., and Jarret, B., 2009. Whales, dolphins and seals. A guide to the marine mammals of the world. A & C Black Publishers Limited, London.

Steeman, M. E., Hebsgaard, M. B., Fordyce, R. E., Ho, S. Y. W., Rabosky, D. L., Nielsen, R., Rahbek, C., Glenner, H., Sørensen, M.V., and Willerslev, E., 2009. Radiation of extant cetaceans driven by restructuring of the oceans. Systematic Biology 58, 573-85.

Uhen, M.D., and Pyenson, N.D., 2007. Diversity estimates, biases, and historiographic effects: resolving cetacean diversity in the Tertiary. Palaeontologia Electronica 10, 1–22.

Visaggi, C. C., and Godfrey, S.J., 2010. Variation in composition and abundance of Miocene shark teeth from Calvert Cliffs, Maryland. Journal of Vertebrate Paleontology 30, 26-35.

von Bekesy G., 1960. Experiments in Hearing. EG Wever (trans). New York: McGraw-Hill.

von Fersen, L., Kamminga, L.C. & Seidl, A., 2000. Estudios preliminares sobre el comportamiento de un ejemplar de franciscana (Pontoporia blainvillei) en Mundo Marino, Argentina, in: UNEP/ CMS (Eds.) Report of the Third Workshop for Coordinated Research and Conservation of the Franciscana Dolphin (Pontoporia blainvillei) in the Southwestern Atlantic, pp. 30–33.

Wartzok, D., and Ketten, D.R., 1999. Marine mammal sensory systems, in: Reynolds, J. and Rommel, S. (Eds.), Biology of marine mammals. Smithsonian Institution Press, pp. 117-175.

Ward, L. W., and Andrews, G.W., 2008. Stratigraphy of the Calvert, Choptank, and St. Mary's Formations (Miocene) in the Chesapeake Bay area, Maryland

and Virginia. Virginia Museum of Natural History Memoir 9, 1-169.

Wiersma, H., 1982. Investigations on cetacean sonar IV: A comparison of wave shapes of odontocete sonar signals. Aquatic Mammals. 9, 57–67.

Wever, E.G., McCormick, J.G., Palin, J., and Ridgway, S.H., 1971. Cochlea of the dolphin, Tursiops truncatus: the basilar membrane. Proceedings of the National Academy of Sciences USA 68, 2708-2711.

Whitmore, F., and Kaltenbach, J., 2008. Neogene Cetacea of the Lee Creek Phosphate Mine, North Carolina. Virginia Museum of Natural History, Special Publication 14, 181-269.

Zachos, J.C., Pagani, M., Sloan, L., Thomas, E., and Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292, 686-693.

Table 1 - Description of measurement made in the periotics. See also Figure 2. The measurements taken through cone-beam tomography images are indicated with *.

Measurement Number	Description
1	Total length of periotic
2	Width of *pars cochlearis* from anteriormost point to cochlear window
3	Width of internal *acoustic meatus*
4	Length of internal *acoustic meatus*
5	Length of anterior process: from anterior incisure to the anteriormost point of the anterior process
6	Length of anterior process: from parabular process to the anteriormost point of the anterior process
7	Maximum diameter (antero posterior) of the *malleus* fossa
8	Total width of the *pars cochlearis*9Distance from fossa incudis to the apex of the *pars cochlearis* (medially)
10	Total width of the periotic in the median region from the epitympanic hiatus to the apex of the *pars cochlearis* (medially)
11	Height of pars cochlearis from vestibular window to the apex of the *pars cochlearis* (medially)
12	Cochlear window diameter (medio laterally)
13	Width of the fossa for stapedial muscle
14	Depth of the fossa for stapedial muscle
15	Maximum thickness of *pars cochlearis*
16	Minimum thickness of *pars cochlearis* on its apex
17	Width of epitympanic hiatus
18	Depth of acoustic internal meatus
19	Height of pars cochlearis in transversal view*
20	Maximun diameter of the cochlea, in transversal view*
21	Maximum thickness of the *pars cochlearis*, in transversal view*
22	Maximum dorsoventral expansion of the cochlear canal from the apex to the base, in transversal view*

Table 2 - Comparisons of periotic morphology, habitat preference and frequency preferences. CT) Computed tomography; MRI) Magnetic ressonance. The frequencies included are the best frequency and frequency range, respectively.

Taxa	Description	pars cochlearis dorsoventral/ mediolateral profile	N turns/ cochlear duct type	emitted frequency (kHz)	acoustic properties of the echolocation beam	data source
Delphinidae						
Stenella attenuata	marine	?	2.5* Type II	40-140 40-60 and 120-140	bimodal	Wartzok and Ketten 1999, Schotten *et al.* 2004
Tursiops truncatus	marine	globose/rounded	2.25* Type II	34.5-131.9 67 and 114	bimodal	Nakamura (1999), Wartzok and Ketten 1999
Sotalia fluviatilis	riverine	globose/rounded	2**	88.35 (SD = 3.01)	?	CTscan, May-Collado and Wartzok, 2010
Sotalia guianensis	estuarine	globose/rounded	1,75**	80-95; 64-105	?	cone beam CT, Kamminga 1988, Kamminga et al. (1993), Sauerland and Dehnhard, 1998
Delphinidae indet.	marine	globose/rounded	1,5** Type I	?	?	cone beam CT
Phocoenidae						
Phocoena spinipinnis	estuarine	slender/pointed	1,5** Type I	?	?	cone beam CT
Phocoena phocoena	estuarine	slender/pointed	1.5* Type I	118-128; 139	narrow-band	Ketten (1992), Au *et al.* (1999, 2006)
Neophocoena phocaenoids	coastal/riverine	slightly flattened	?	125; 87-145	one-peak	Li et al. 2005, Nakamura et al. 1999
Monodontidae						
Delphinapterus leucas	coastal/ estuarine	slightly flattened	2,25**	71 and 112; 46.6-125.7	bimodal	cone beam CT
Pontoporiidae						

Pontoporia blainvillei	estuarine	globose/rounded	1,75** Type I	130 (SD=10)	narrow-band	cone beam CT, von Fersen et al., 2000
Iniidae						
Inia geoffrensis	riverine	slightly flattened	1.5* Type II 2**	**emitted** 16-170 (best freq. 60-80); 85-100 **auditory sensivity** 75-90	**narrow-band** (narrow sonar beam 20-30 degrees)	cone beam CT, Evans 1973, Kamminga and Weirsma 1981, Weirsma 1982
Platanistoidea						
Squalodontoid	marine	slightly flattened	1,75** Type I	?	?	Luo and Marsh (1996)
cf. *Notocetus vanbenedeni*	marine	slightly flatened	1,75** Type I	?	?	cone beam CT (referred specimen)
Platanistidae						
Platanista gangetica	riverine	slightly flatened	?	15-60?/20-100	?	Herald *et al.* (1969)
Physeteriidae						
Physeteriidae indet.	marine	globose/rounded	1,75**	?	?	cone beam CT
Physeter catodon	marine	globose/rounded	1.75*	15, 5-24	one peak	Madsen et al. 2002

*taken from Wartzok and Ketten (1999)
**present work

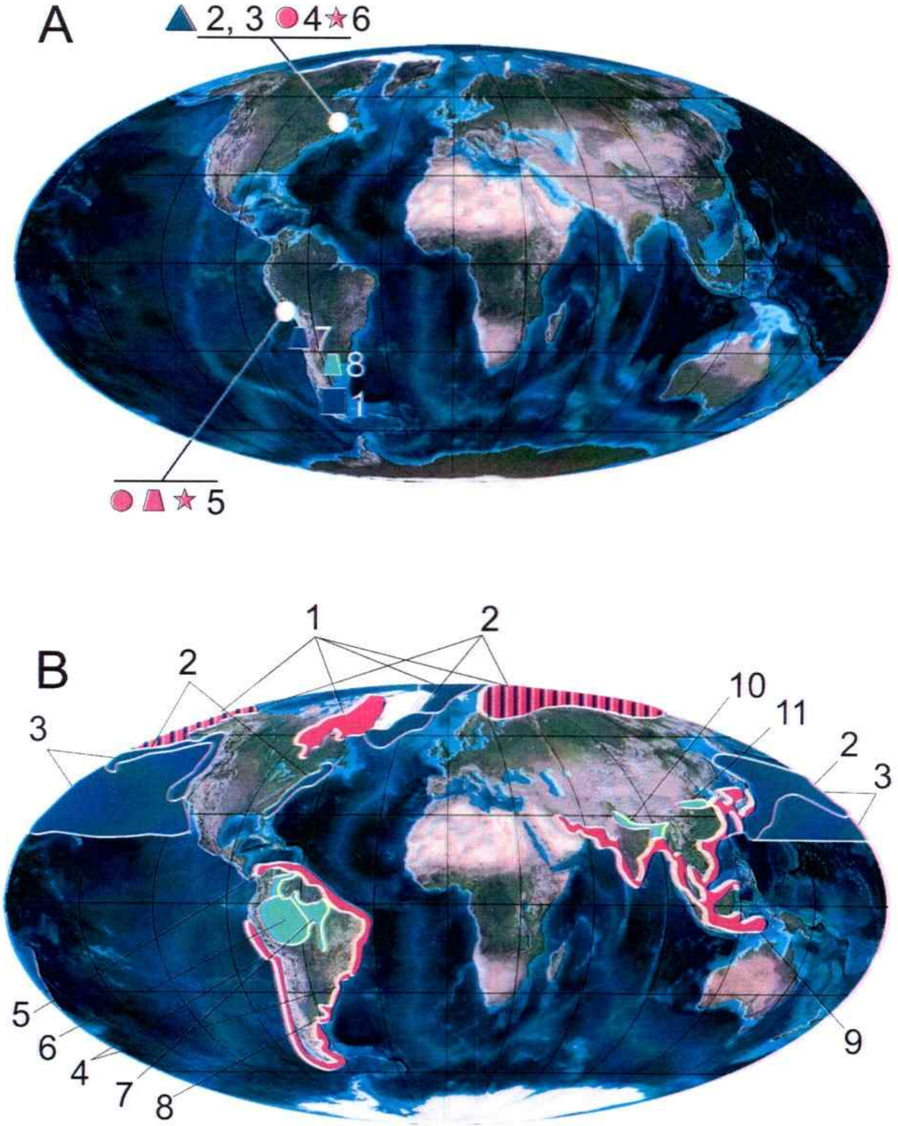


Figure 1 – Paleogeographic reconstruction from the Neogene (A) and the present day (B). The geologic record is plotted in the Neogene map (A) following: square, early Miocene; triangle, early-middle Miocene; circle, middle miocene; lozenge, late Miocene; star, early Pliocene. The geologic formations are indicated as follows: 1) Gaiman Fm.; 2) Choptank Fm.; 3) Calvert Fm.; 4) Pungo River Fm.; 5) Pisco Fm.; 6) Yorktown Fm.; 7) Bahia Inglesa Fm.; 8) Ituzaingó Fm. Symbol color indicates: marine (blue); estuarine,

epicontinental and shallow sea (red); and freshwater (green). Present day color distributions (B) follow the same code, with species: 1) Delphinapterus; 2) Phocoena phocoena; 3) Phocoenoides; 4) Phocoena spinipinnis;, 5) Sotalia guianensis, 6) Tucuxi, Sotalia fluviatilis, 7) Amazon river dolphin, Inia geoffrensis, 8) La plata dolphin, Pontoporia blainvillei; 9) Finless porpoise, Neophocaena phocaenoids, 10) Ganges river dolphin, Platanista gangetica; 11) Baiji, Lipotes vexliffer (this species was not measured); Inia (7) and S. fluviatilis (6) are partially superimposed in the amazon region. Paleogeographic maps were modified from R. Blakey, Northern Arizona University, available at http://jan.ucc.nau.edu/~rcb7/mollglobe.html.

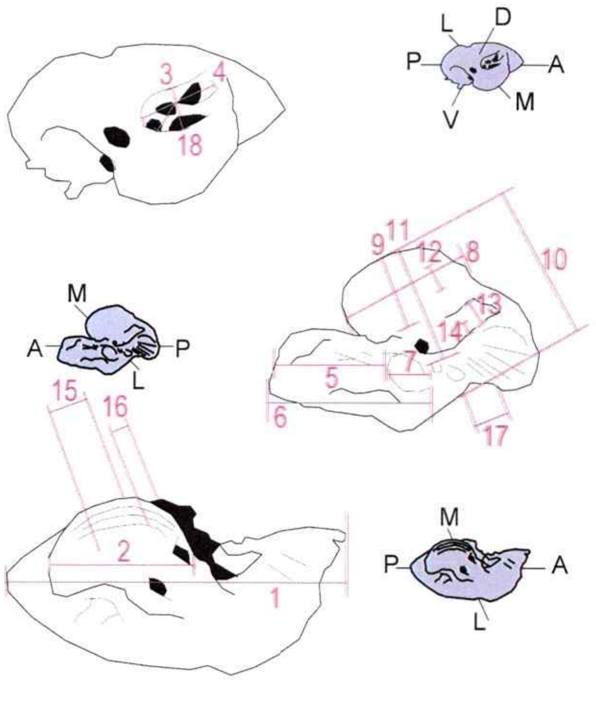


Figure 2 - Schematic drawings of a generalized odontocete periotic in A) dorsal, B) ventral and C) medial-dorsal view, showing measurements used herein. The anatomical positioning of the views are indicated in the shadowed schemes: A) anterior, P) posterior, L) lateral, M) medial, D) dorsal and V) ventral. For a detailed description of the measurements, see table 1.

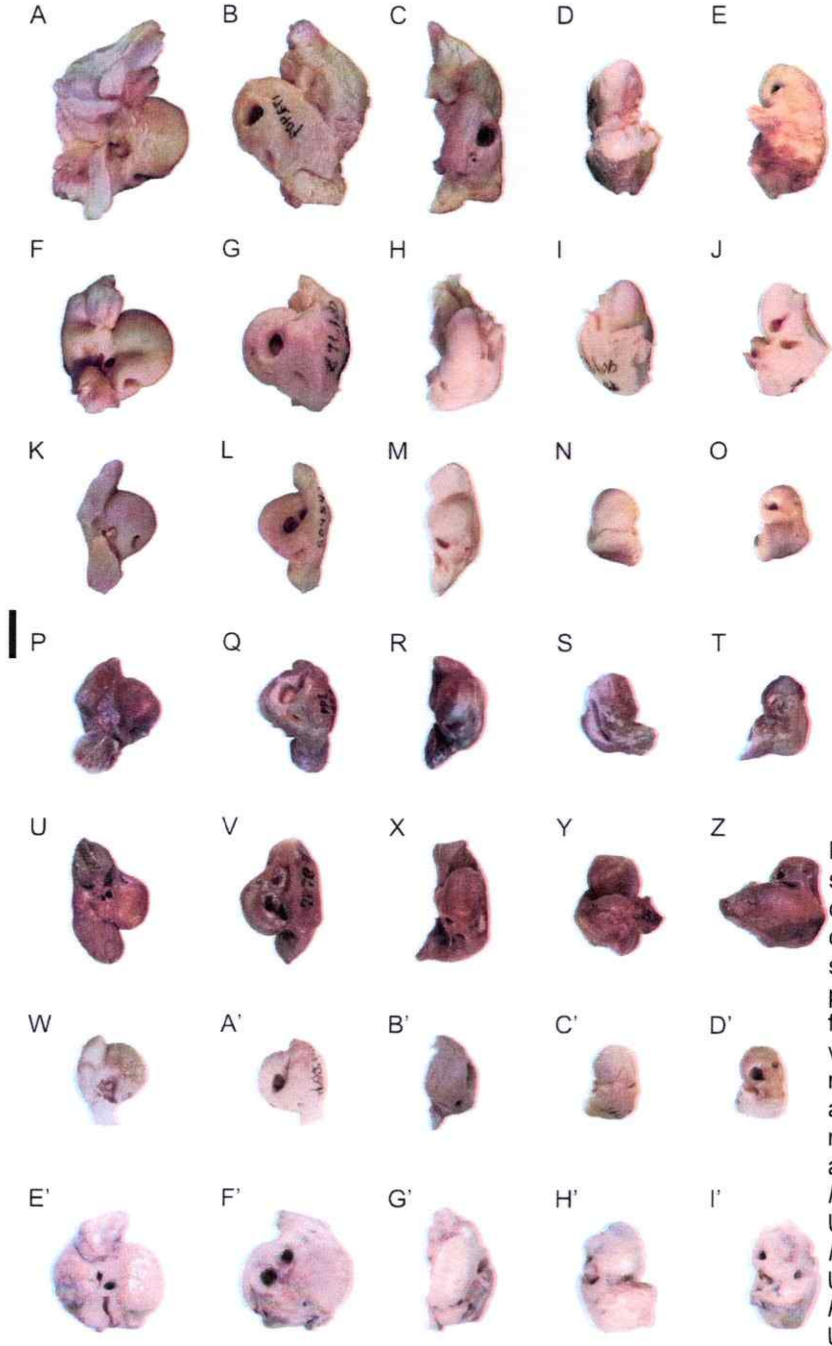


Figure 3 - Periotics of selected taxa in the dataset (for a complete list of taxa see table S1) The periotics are shown, from left to right, in ventral, dorsal, medial, posterior and anterior views. Each row shows a species, as follows: A-E) *Platanista gangetica* USNM 176409; F-J) *Inia geoffrensis* USNM 396166; K-O) *Phocoena phocoena* USNM 504543; P-T) *Brachydelphis mazeasi* (MHNH PPI 121; U-Z) *Delphinodon dividum* (USNM 7278); W-D') *Pontoporia blainvillei* (USNM 482715). E'-I') Iniidae from Ituzaingó Formation, Entre Rios, Argentina (MACN 9231) Scale bar = 1 cm.

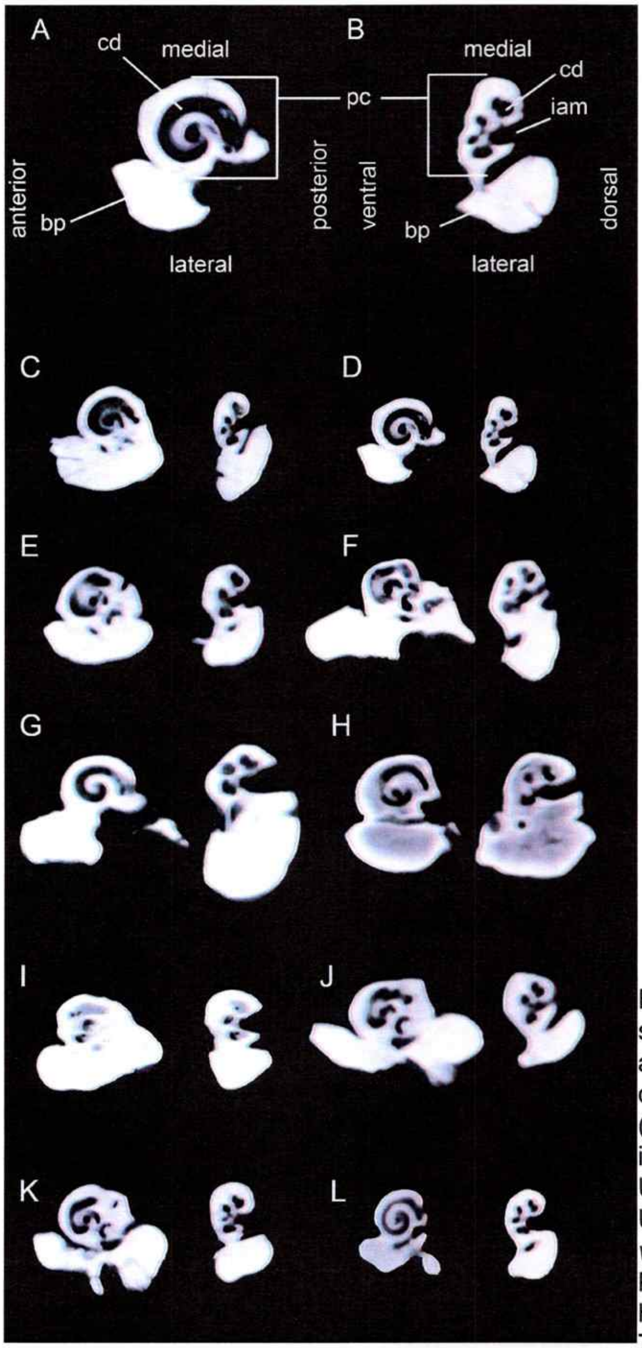


Figure 4 - Cone beam tomography slices of ten periotic specimens A-B) at coronal (A) and transversal (B) cuts of *Inia geoffrensis* MCN-M32 (also in C) with the structures indicated. D) *Phocoena spinipinnis* UFSC 1025, E) *Sotalia guianensis* UFSC 1293, F) cf. *Notocetus vanbenedeni* MLP 76-IX-25, G) Platanistoidea indet. MPEF-PV 517, H) Delphinidae indet. MLP 76-IX-2-7, I) *Delphinapterus leucas* MLP 1484, J) Physeteriidae indet., K) *Pontoporia blainvillei* UFSC 1093, L) *Sotalia fluviatilis* USNM 504316. Anatomical abbreviations: cd) cochlear duct, iam) internal acoustic meatus, pc) pars cochlearis, bp) periotic body. All cuts are standardized to show the same pars cochlearis size.

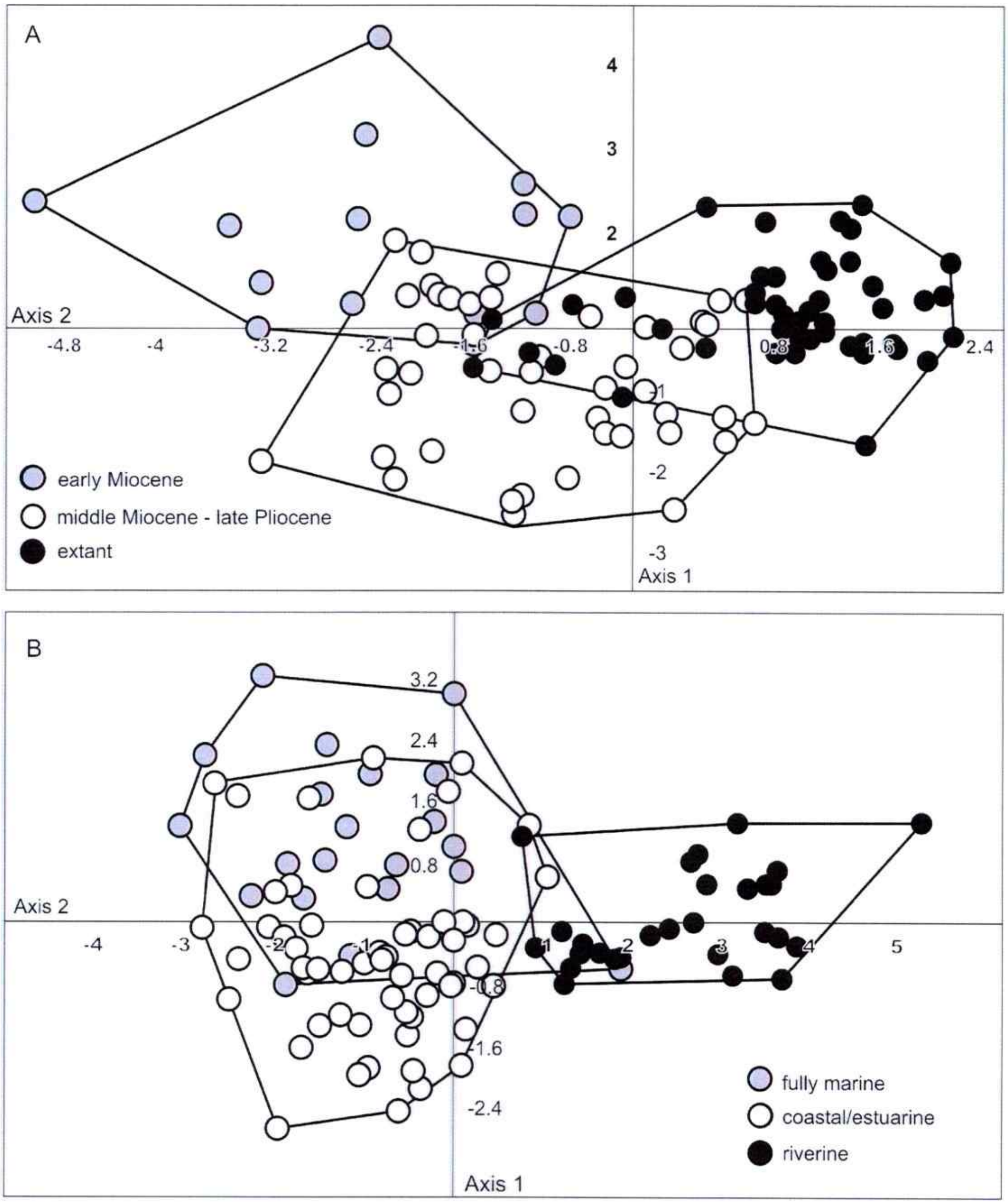


Figure 5 - Scatterplot of the CVA analysis of the geologic age groups that were significantly ($p < 0.01$) different (A); and of the three environmental groups (B), where only the marine-riverine and riverine-estuarine pairs were significantly different ($p < 0.01$; see also Table S1).

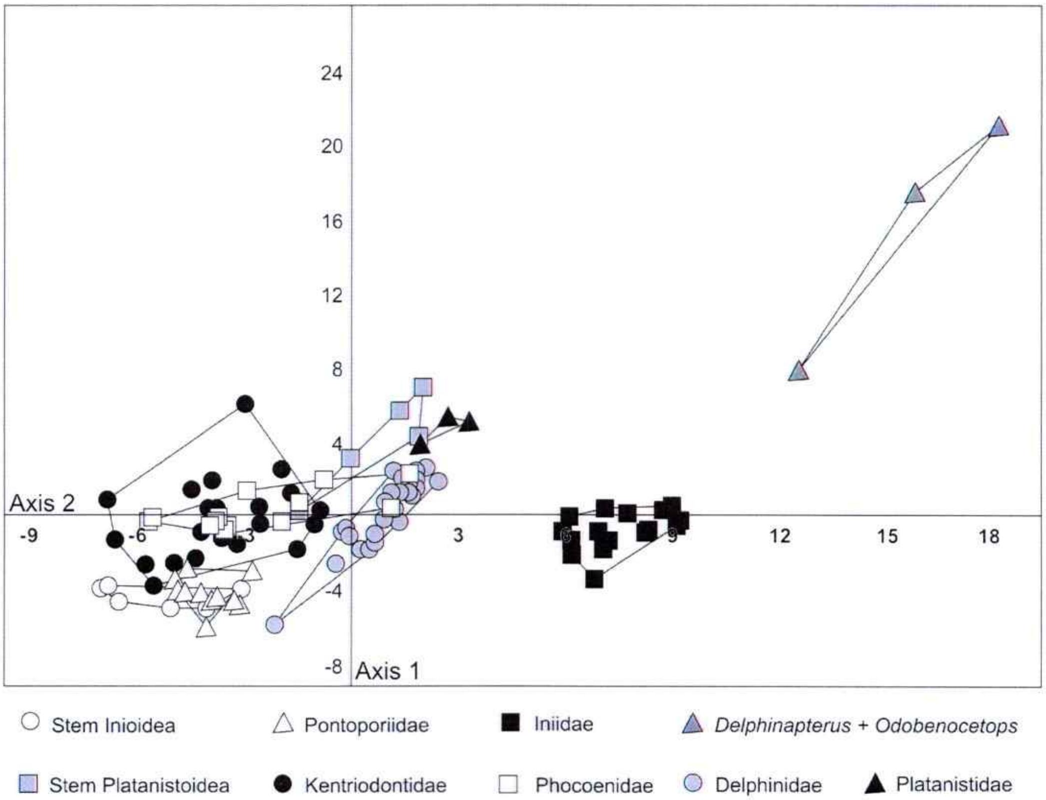


Figure 6 - Scatterplot of the CVA analysis of the taxonomic groups, divided in stem and crown taxa of the different super-family of Odontoceti (see also table S1).

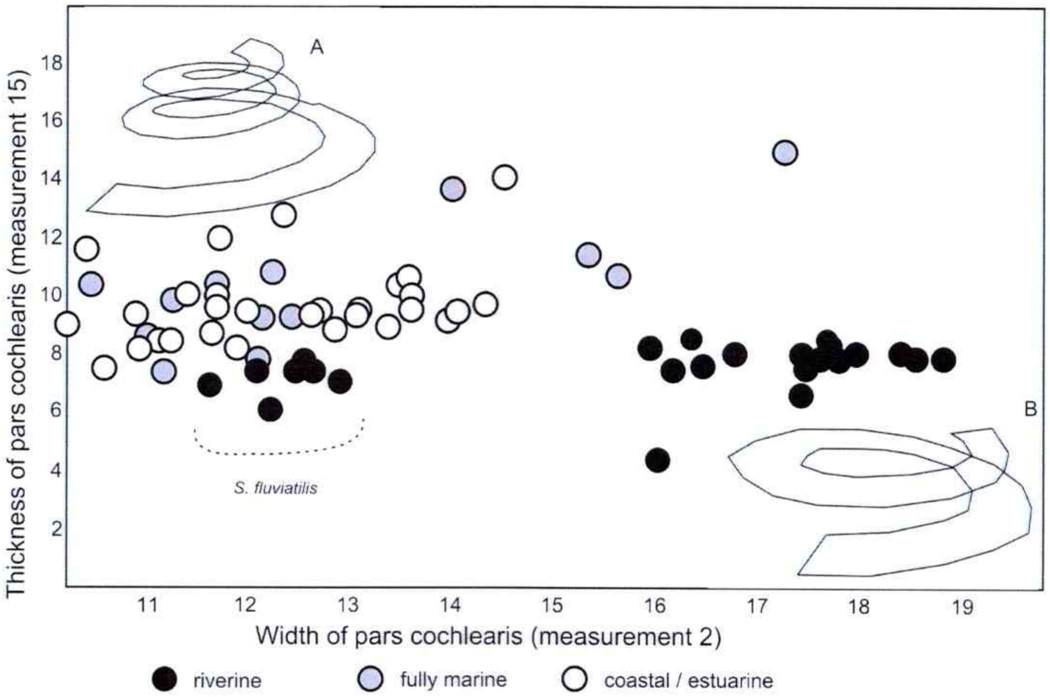


Figure 7 -Scatterplot of thickness versus width of pars cochlearis. and schematic drawing of a cochlear duct in *Sotalia guianensis* (A) and *Inia* (B).

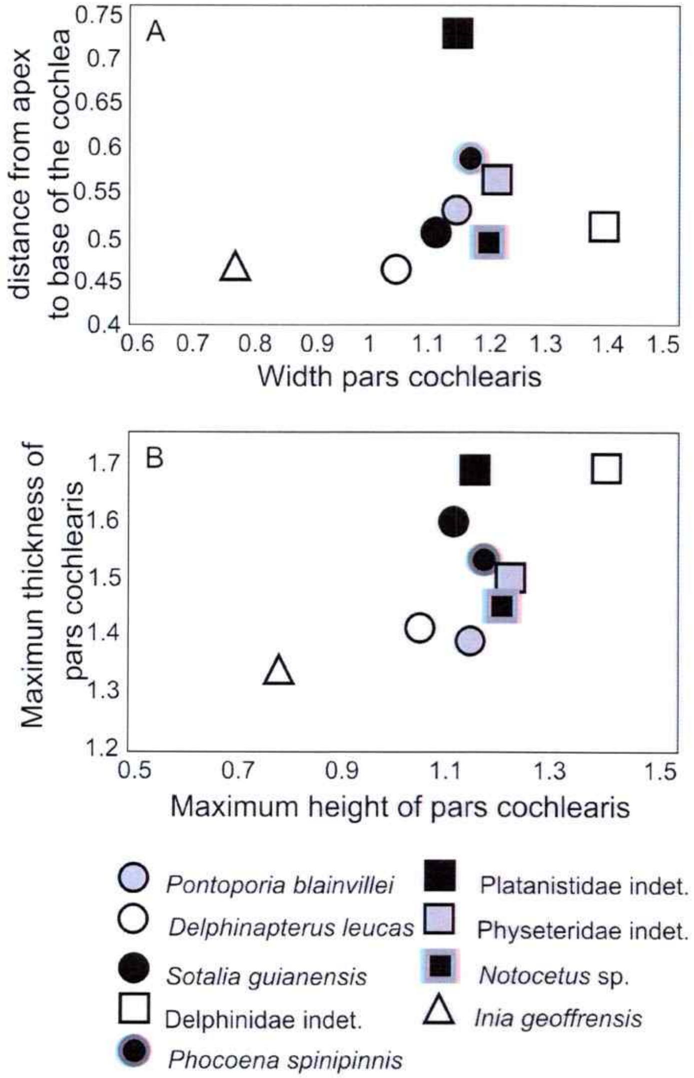


Figure 8 - Comparisons between A) pars cochlearis (external; x) and cochlear duct proportions (internal; y); and B) cochlear duct maximum height (x) versus maximum thickness (y). For descriptions of the measurements, see Table 1.

Supplementary table 1

Specimens used in all morphometric and statistic analysis. The groups used at the CVA analysis (environmental, geologic ages and taxonomic) are indicated with its the original data and reference. The specimens that were submitted to cone-beam tomography are indicated with*.

Taxa	Specimen Number	Taxonomic Group (more inclusive)	Taxonomic Group (less inclusive)	Environment/ Paleoenvironment	Environmental group used here	Geological Age	Geological Age groups (significantly different groups)	Geological Formation / locality data		References
Sotalia guianensis	UFSC 1083	Delphinoidea	Delphinidae	Coastal and estuarine	Coastal/Estuarine	Holocene	Holocene	Florianopolis, SC – South Brazil	Cenozoic	Reeves et al. 2002, Shirihai and Jarrett, 2006
	UFSC 1104									
	UFSC 1130									
	UFSC 1174									
	UFSC 1175									
	UFSC 1178									
	UFSC 1180									
	UFSC 1219									
	UFSC 1226									
	UFSC 1223									
	UFSC 1239									
	UFSC 1291									
	UFSC 1293*									
	UFSC 1296									
Sotalia fluviatilis	IDSM Sf 9503		Delphinidae	Riverine	Riverine	Holocene	Holocene	Tefe, Amazonas, North Brasil	Cenozoic	Reeves et al. 2002, Shirihai and Jarrett, 2006
	IDSM Sf 9509									
	IDSM Sf 9702									
	IDSM 2001-01									
	IDSM Sf 2005-04									
	IDSM Sf 2005-03									
	IDSM Sf 2005-05									
	IDSM Sf 2005-06									
	IDSM Sf 2006-04									
	IDSM Sf 2006-05									
	IDSM Sf 2007-03									
Delphinidae indet.	SGO-PV 1132		Delphinidae	Marine	Fully Marine	Late Miocene	middle Miocene to late Pliocene	Bahia Inglesa Fm.	Neogene (Cenozoic)	Achurra, 2004, Achurra et al. 2009
	SGO-PV 21401									

	MLP 76-IX-2-7							Entre rios		Cozzuol, 1996, Cozzol 1987
	MACN 9236			Riverine	Riverine			Ituzaingo Fm.		Achurra, 2004, Achurra et al. 2009
	USNM 449643 G			Estuarine	Coastal/Estuarine	early middle - middle Miocene		Pungo river Fm.		Ward 2008
Phocoena dalli	USNM 219334		Phocoenidae	Marine	Fully Marine	Holocene	Holocene		Cenozoic	Reeves et al. 2002, Shirihai and Jarrett, 2006
Phocoena spinipinnis	USNM 550281		Phocoenidae	Coastal	Coastal/Estuarine	Holocene	Holocene		Cenozoic	Reeves et al. 2002, Shirihai and Jarrett, 2006
	UFSC 1025*							Florianopolis, SC -- South Brazil		
Neophocoena phocoenoides	USNM 49544		Phocoenidae	Coastal and estuarine	Coastal/Estuarine	Holocene	Holocene		Cenozoic	Reeves et al. 2002, Shirihai and Jarrett, 2006
	USNM 240862									
Phocoena phocoena	USNM 550152		Phocoenidae	Marine	Fully Marine	Holocene	Holocene		Cenozoic	Reeves et al. 2002, Shirihai and Jarrett, 2006
	USNM 504606									
	USNM 504757									
Phocoenidae indet.	USNM 360076		Phocoenidae	Estuarine	Coastal/Estuarine	early middle - mi	middle Miocene to late Pliocene	Pungo river Fm.	Neogene (Cenozoic)	Ward 2008, Whitmore and Kaltenbach, 2008
	USNM 360061			Marine	Fully Marine	early Pliocene		Yorktown Fm,		
Australithax intermedia	MNHN PPI 112		Phocoenidae	Epicontinental sea	Coastal/Estuarine	late Miocene	middle Miocene to late Pliocene	Pisco Fm	Neogene (Cenozoic)	Muizon 1988
	MNHN PPI 111									
Phocoenidae	MPC 3001		Phocoenidae	Marine	Fully Marine	late Miocene	middle Miocene to late Pliocene	Bahía Inglesa Fm	Neogene (Cenozoic)	Achurra, 2004, Achurra et al. 2009
	SGO-PV 21402									
Lomacetus ginsburg	MNHN PPI 238		Phocoenidae	Shalow sea, coastal	Coastal/Estuarine	late Miocene	middle Miocene to late Pliocene	Pisco Fm	Neogene (Cenozoic)	Muizon 1988
	MNHN PPI 98									
	MNHN PPI 100									
	MNHN PPI 96									
	MNHN PPI 101									
Neophocoena phocaenoids	USNM 240002		Phocoenidae	Coastal and riverine	Coastal/Estuarine	Holocene	Holocene		Cenozoic	Reeves et al. 2002, Shirihai and Jarrett, 2006
	USNM 24001									
Kentriodontidae indet.	USNM 449643 G	Stem-Delphinoidea	Kentriodontidae	Estuarine	Coastal/Estuarine	middle Miocene	middle Miocene to late Pliocene	Pungo river Fm.	Neogene (Cenozoic)	Ward 2008, Whitmore and Kaltenbach, 2008
	USNM 182984									
Kentriodon sp.	USNM 187313		Kentriodontidae	Marine	Fully Marine	middle Miocene	middle Miocene to late Pliocene	Calvert Fm	Neogene (Cenozoic)	Ward 2008
	USNM 453041									
Lophocetus pappus	USNM 15985		Kentriodontidae	Marine	Fully Marine	middle Miocene	middle Miocene to late Pliocene	Calvert Fm.	Neogene (Cenozoic)	Ward 2008
	USNM 449649			Estuarine	Coastal/Estuarine	middle Miocene	middle Miocene to late Pliocene	Pungo river Fm.	Neogene (Cenozoic)	Ward 2008, Whitmore and Kaltenbach, 2008

	USNM 425525									
cf. Liolithax sp.	USNM 449638 A		Kentriodontidae	Estuarine	Coastal/Estuarine	middle Miocene	middle Miocene to late Pliocene	Pungo river Fm.	Neogene (Cenozoic)	Ward 2008, Whitmore and Kaltenbach, 2008
	USNM 449639 B									
cf. Liolithax pappus	USNM 425526		Kentriodontidae	Estuarine	Coastal/Estuarine	middle Miocene	middle Miocene to late Pliocene	Pungo river Fm.	Neogene (Cenozoic)	Ward 2008, Whitmore and Kaltenbach, 2008
Lophocetus calvertensis	USNM 16314		Kentriodontidae	Marine	Fully Marine	middle Miocene	middle Miocene to late Pliocene	Choptank Fm.	Neogene (Cenozoic)	Ward 2008
Delphinodon dividum	USNM 7278		Kentriodontidae	Marine	Fully Marine	middle Miocene	middle Miocene to late Pliocene	Choptank Fm.	Neogene (Cenozoic)	Ward 2008
Macrokentriodon morani	USNM 534031		Kentriodontidae	Marine	Fully Marine	middle Miocene	middle Miocene to late Pliocene	Calvert Fm.	Neogene (Cenozoic)	Ward 2008
Kentriodon pernix	USNM 8060		Kentriodontidae	Marine	Fully Marine	middle Miocene	middle Miocene to late Pliocene	Choptank Fm.	Neogene (Cenozoic)	Ward 2008
	USNM 8061							Calvert Fm.		
Atocetus iquensis	MNHN PPI 114		Kentriodontidae	Epicontinental sea	Coastal/Estuarine	middle Miocene	middle Miocene to late Pliocene	Pisco Fm	Neogene (Cenozoic)	Muizon 1988
	MNHN PPI 113									
	MNHN PPI 115									
	MNHN PPI 120									
Belonodelphis sp.	MNHN PPI 231		Kentriodontidae	Epicontinental sea	Coastal/Estuarine	middle Miocene	middle Miocene to late Pliocene	Pisco Fm	Neogene (Cenozoic)	Muizon 1988
Kentriodontidae sp.	SGO-PV 1121		Kentriodontidae	Epicontinental sea	Coastal/Estuarine	late Miocene	middle Miocene to late Pliocene	Bahía Inglesa Fm	Neogene (Cenozoic)	Achurra, 2004, Achurra et al. 2009
	SGO-PV 1134									
Delphinapterus leucas	MLP 1484*	Monodontidae + Odobenocetopsidae	Monodontidae	Shalow sea, coastal, e	Coastal/Estuarine	Holocene	Holocene		Cenozoic	Reeves et al. 2002, Shirihai and Jarrett, 2006
Odobenocetops leptodon	MNHN SAO 202		Odobenocetopsida	Shalow sea, coastal	Coastal/Estuarine	early Pliocene	middle Miocene to late Pliocene	Pisco Fm	Neogene (Cenozoic)	Muizon 1993, Muizon and Domning 2002
Odobenocetops peruvianus	MNHN SAS 1614		Odobenocetopsida	Shalow sea, coastal	Coastal/Estuarine	early Pliocene	middle Miocene to late Pliocene	Pisco Fm	Neogene (Cenozoic)	Muizon 1993, Muizon and Domning 2002
Pontoporia sp,	USNM 457174	Inioidea	Pontoporiidae	Marine	Fully Marine	early Pliocene	middle Miocene to late Pliocene	Yorktown Fm,	Neogene (Cenozoic)	Ward 2008, Whitmore and Kaltenbach, 2008
	USNM 449663			Estuarine	Coastal/Estuarine	early middle - middle Miocene		Pungo River Fm.		
cf. Pontoporia	USNM 449671		Pontoporiidae	Estuarine	Coastal/Estuarine	early middle - middle Miocene	middle Miocene to late Pliocene	Pungo river Fm.	Neogene (Cenozoic)	Ward 2008, Whitmore and Kaltenbach, 2008
	USNM 360073			Marine	Fully Marine	early Pliocene		Yorktown Fm,		
Pontoporiidae indet,	MNHN PPI 232		Pontoporiidae	Epicontinental sea	Coastal/Estuarine	late Miocene	middle Miocene to late Pliocene	Pisco Fm	Neogene (Cenozoic)	Muizon 1988
	MACN 9239			Riverine	Riverine	late Miocene	middle Miocene to late Pliocene	Ituzaingo Fm.	Neogene (Cenozoic)	Cozzuol, 1996, Cozzol 1987
	MACN 9233									
Pliopontos litoralis	MNHN SAS 953		Pontoporiidae	Epicontinental sea	Coastal/Estuarine	early Pliocene	middle Miocene to late Pliocene	Pisco Fm	Neogene (Cenozoic)	Muizon 1983

Pontoporiidae	SGO-PV 21404		Pontoporiidae	Marine	Fully Marine	late Miocene	middle Miocene to late Pliocene	Bahía Inglesa Fm	Neogene (Cenozoic)	Achurra, 2004, Achurra et al. 2009
Pontoporia blainvillei	UFSC 1083*		Pontoporiidae	Estuarine	Coastal/Estuarine	Holocene	Holocene	Florianopolis, SC -- South Brazil		Reeves et al. 2002, Shirihai and Jarrett, 2006, Cremer and Simoes-Lopes 2005
Inia geoffrensis	MCN-M 32*		Iniidae	Riverine	Riverine	Holocene	Holocene	Araguaia, Goias, Central Brazil	Cenozoic	Reeves et al. 2002, Shirihai and Jarrett, 2006
	RDSM Ig 9404									
	RDSM Ig 9403									
	RDSM Ig 9516									
	RDSM Ig 9505									
	IDSM Ig 2001-01									
	IDSM Ig 2002-01									
	IDSM Ig 2005-03									
	RDSM Ig 9601									
	RDSM Ig 9515									
	IDSM Ig 2005-01									
	IDSM Ig 2008-02									
	IDSM Ig 2006-01									
	IDSM Ig 2007-06									
	IDSM Ig 2005-06									
Iniidae	MACN 9231		Iniidae	Riverine	Riverine	late Miocene	middle Miocene to late Pliocene	Ituzaingó Fm.	Neogene (Cenozoic)	Cozzuol, 1996, Cozzol 1987
Inioidea cf. Brachydelphi	USNM 360068	Stem-Inioidea	Inioidea	Marine	Fully Marine	early Pliocene	middle Miocene to late Pliocene	Yorktown Fm.	Neogene (Cenozoic)	Ward 2008
Brachydelphis mazeasi	MNHN PPI 121		Inioidea	Epicontinental sea	Coastal/Estuarine	middle Miocene	middle Miocene to late Pliocene	Pisco Fm	Neogene (Cenozoic)	Muizon 1988
	MNHN PPI 125									
	MNHN PPI 126									
Brachydelphis sp.	MNHN PPI 235		Inioidea	Epicontinental sea	Coastal/Estuarine	middle Miocene	middle Miocene to late Pliocene	Pisco Fm	Neogene (Cenozoic)	Muizon 1988
	MNHN PPI 233									
	MNHN PPI 236									
Physeteriidae indet.	MLP 62*	Physeteriidae	Physeteridae	Marine	Fully Marine	early Miocene	early Miocene	Gaiman Fm.	Neogene (Cenozoic)	Cozzuol 1996, Cione et al 2005a,b
Platanista gangetica	USNM 23456	Platanistoidea	Platanistidae	Riverine	Riverine	Holocene	Holocene	-	Cenozoic	Reeves et al. 2002, Shirihai and Jarrett, 2006
	USNM 172409							-	Cenozoic	Reeves et al. 2002, Shirihai and Jarrett, 2006
Platanistidae indet.	MLP_76-IX-2-6*		Platanistidae	Marine	Fully Marine	early Miocene	early Miocene	Gaiman Fm.	neogene (Cenozoic)	Cozzuol 1996, Cione et al 2005a,b
cf. Notocetus vanbenede	MLP 76-IX-2-5*		Platanistidae	Marine	Fully Marine	early Miocene	early Miocene	Gaiman Fm.		Cozzuol 1996, Cione et al 2005a,b
Notocetus vanbenedeni	MPEF-PV 506		Platanistoidea	Marine	Fully Marine	early Miocene	early Miocene	Gaiman Fm.	Neogene (Cenozoic)	Cozzuol 1996, Cione et al 2005a,b
Platanistoidea indet	MPEF-PV 517*		Platanistoidea	Marine	Fully Marine	early Miocene	early Miocene	Gaiman Fm.	Neogene (Cenozoic)	Cozzuol 1996, Cione et al 2005a,b

CAPITULO 3

FACIAL SOFT TISSUE AND BONY MORPHOLOGY, IMPLICATIONS TO THE EVOLUTION OF ECHOLOCATION ON MARINE AND FRESHWATER DELPHINIDA (CETACEA, ODONTOCETI)

Carolina S. Gutstein, Mario A. Cozzuol, Nicholas D. Pyenson, Constanza P. Figueroa-Bravo, Miriam Marmontel, Mauricio Canals

FACIAL SOFT TISSUE AND BONY MORPHOLOGY, IMPLICATIONS TO THE EVOLUTION OF ECHOLOCATION ON MARINE AND FRESHWATER DELPHINIDA (CETACEA, ODONTOCETI)

C.S. Gutstein[a,b], M.A. Cozzuol[c], N.D. Pyenson[b], C.P. Figueroa-Bravo [a,e,] R.E. Miriam Marmontel[f], M. Canals[a,f]

[a] Laboratorio de Ecofisiología, Facultad de Ciencias, Universidad de Chile, Las Palmeras 3425, Ñuñoa, Santiago, Chile. sgcarolina@gmail.com

[b] Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, Washington DC, 20013-7012, USA. pyensonn@si.edu

[c] Departamento de Zoologia, Instituto Ciências Biológicas, Universidade Federal de Minas Gerais, Av. Antônio Carlos, 6627, Pampulha, 31270-910, Belo Horizonte, MG, Brasil. cozzuol@icb.ufmg.br

[e] fbconstanza@gmail.com

[f] mcanals@uchile.cl

*To whom correspondence should be addressed: sgcarolina@gmail.com

VII. 1. Introduction

Echolocation is a sophisticated biosonar system that has evolved at least three times in distantly related mammals (tenrec shrews, toothed whales, and microchiropteran and egyptian fruit bats). Toothed whales (Odontoceti) are the only mammals that have evolved this system underwater, where they use sound to both navigate and prey-catch (Au 1993). Odontocetes generate and transmit high-frequency sound from the forehead using a complex system of muscles, air sacs, fat bodies, including the melon (Cranford et al., 1996). Sound emitted from the forehead is then transmitted into the underwater environment, and its returning echoes are received via mandibular fat bodies, which articulate directly with acoustically isolated outer ear bones (i.e., the tympanic bullae) of the skull (Nummela et al. 2004; Cranford and Krysl, 2008). Several publications demonstrate the connection between the unique set of facial structures to the echolocation ability of the odontocetes (Clarke et al. 2003, Cranford et al., 1996, 2008, Harper et al., 2008, McKenna et al. 2011).

The phylogenetic relationships of the dolphins that are restricted to fluvial systems around the world support at least two independent secondary invasions of freshwater habitats. The biogeography of these lineages, which are restricted to freshwater systems with independent tectonic and geomorphologic histories, supports at least three independent invasions: both *Platanista* spp. and *Lipotes* are endemic to different freshwater systems of Asia (India and China, respectively, despite the fact that *Lipotes* is much closer related to the Inioidea than to Platanistoidea); *Inia* in Amazon and Orinoco basin in South America (Best and da Silva, 1989, 1993; Best, 1993). Although *Pontoporia* has been characterized as a "river dolphin," it is predominantly distributed in coastal and estuarine waters off the Atlantic side of southeastern Brazil, Uruguay and Argentina (Cremer and Simoes Lopes 2005, Siciliano, 1994; Crespo et al. 1998).

The "river dolphins", however, display a suite of convergent morphological specializations that have been widely observed in the descriptive and systematic literature and include many traits that diverge from the majority of marine odontocetes, such as: flexible necks with unfused cervical vertebrae; wide, paddle-like flippers; reduced or absent dorsal fins; reduced orbits and eyes; and elongate rostrum with lingual accessory cusps on the posterior dentition (Rice, 1998; Arnason and Gullberg, 1995; Messenger and McGuire, 1998; Heyning, 1997; Simpson, 1945; Muizon, 1994; 1988a; Cassens *et al.*, 2000; Hamilton *et al.*, 2001).

Osteologic morphological changes through the independent river dolphins lineages are also found in the pattern of telescoping of the skull, the acquisition of an elaborate air filled maxillary crest in *Platanista* and the super high frequency (>100 kHz) they use to echolocate (also observed in *Phocoena* and *Pontoporia*). Actually, the latter can be functionally related to the low frequency cut-off (Miller *et al.* 2006) which is in a higher frequency in the narrow-band structure of the echolocation beam species, in contrast to the bimodal pattern observed in most marine dolphins (mostly Delphinoidea; Ketten, 1992, Wartzok and Ketten, 1999).

This is not surprising considering the level of modification that show the odontocetes, as observed for example in the delphinidae subcircular canals in the marine common dolphins (Spoor *et al.,* 2002). For instance, many of these traits have also been identified in odontocetes besides "river dolphins," or their near, extinct relatives (e.g., *Ischyrorhynchus*). For example, elongate rostrum and complex posterior dentition has been identified in eurhinodelphinids, dalpiazinids, and squalodontids (Fordyce, 1994). Nonetheless, the strong molecular phylogenetic framework underpinning the paraphyly of "river dolphins" clarifies the interpretation of these commonalities as homoplasious, and thus likely related to the invasion of freshwater habitats (Geisler *et al.* 2011).

In parallel with these external and osteological convergences, there is also indication that functional aspects of "river dolphin" echolocation has converged on similar solutions for producing and receiving sound in an environment unlike the putative oceanic conditions of their ancestors. All of the freshwater systems inhabited by extant "river dolphins" differ in acoustic and optic properties from marine ones, such as: water temperature, which alone can affect echolocation signals (Wartzok and Ketten, 1999); turbidity; and complex, physical obstacles that are seasonally present in the flooded forest environments of Amazonia (Martin and da Silva, 2004; Martin et al., 2004). It is plausible that such environmental differences in the acoustic properties of riverine (i.e., high temperature, low visibility, small areas full of obstacles) versus marine (i.e., lower temperature, high visibility, wide-open areas) habitats has driven differences in sound production.

Recent work has been able to identify the correlation between environmental shift and periotic morphology, using palaeonvironmental and habitat preference data (Gutstein *et al.* accepted). Here we test for a similar pattern on skull morphology, specially facial, sinuses and air sacs morphology. We design here a new set of measurements specifically to test this hypothesis.

Here, we investigate specific morphological components of sound emission, production and reception by focusing on the basicranial and facial region of the skull, particularly difficult to access due to poor record of complete skull. The sampling effort was exhaustive and focalized in south american and north american extant and extinct species of Delphinida, with some specimens of other related groups as the river dolphins, baiji (Lipotidae) and the ganges river dolphin (Platanistidae). Our goal, in assembling this dataset, was to test if facial and basicranial morphology differed between freshwater and marine odontocetes.

Proxies for soft tissue structures known to be related to the echolocation were created to access this issue from the morphometric point of view as well as descriptive of the tissue morphology of still undescribed taxa.

By including fossils, we also sought to test the possible environmental assignments, based *a priori* in sedimentologic data, for these extinct taxa as well. In this study, we introduce such information with the purpose of providing the proper temporal and paleoenvironmental contexts for the features.

VII. 2. Materials and Methods

Our dataset included linear measurements from the skulls of extant and extinct odontocetes that correlate with known facial structures related to the echolocation ability (Cranford et al., 1996, McKenna et al. 2011). We collected a total of 50 measurements from 131 specimens (Table S1 and S2) that covered the following taxonomic breadth: Platanistoidea (Platanistidae, n = 5); Lipotoidea (Lipotidae, n=2); Inioidea (Iniidae, n =23, Inioidea *incertae sedis,* n = 1, stem-Inioidea, n=11; Pontoporiidae, n =20); Delphinoidea (Kentriodontidae, n = 14; Odobenocetopsidae, n =1; Phocoenidae, n = 13; Delphinidae, n = 41; see Table S1 for a detailed taxonomy of less inclusive taxa).

These measurements were analyzed in two different ways: first as raw data; and then divided by the total width on the antorbital notch width (Fig. 2, Table S2; measurement 7) and alternatively the transformation available in the software Paleontological Statistics (PAST v. 2.11, Hammer et al. 2001) to control for size disparity.

The data matrix was pre-classified with groupings based on the observed habitat environment, as follows: riverine (46); fully marine (26); and coastal/estuarine (58), the latter including coastal, shallow and epicontinental sea with freshwater input (see supplementary information 1, Table S1, Fig. 1). In the case of the fossil specimens, environmental and geologic age categories were defined compiling locality, sedimentologic and paleoecologic data available in the literature (e.g., Achurra, 2004; Cione et al., 2005a,b; Ward, 2008; Whitmore and Kaltenbach, 2008; Achurra et al., 2009; Visaggi and Godfrey, 2010, see also Table S1, Fig. 2). For the extant specimens the distribution data of the species were compiled from literature (based on Shirihai and Jarrett, 2009, otherwise indicated; Fig. 2; see Supplementary information 1, Table S1).

Although data on the environmental context for fossil taxa may reflect a variety of taphonomic biases (Uhen and Pyenson, 2007), we assumed that the depositional environment for these specimens effectively was similar to their original habitat. We equally tested any age-related signals by pre-classifying the dataset by geologic age, in the following groupings: early Miocene (8); middle Miocene (7); late Miocene (24); early Pliocene (4); and Pleistocene-Holocene (86; see supplementary information 1, Table S1, Fig. 1).

To contrast geologic and environmental signals of the dataset with phylogenetic history we also grouped taxonomically by family and by genus following Steeman et al. (2009) and Geisler et al. (2011; see Table S1).

We then conducted principal components (PCA), variance (MANOVA), discriminant (CVA) and cluster analysis, using PAST 2.11 (Hammer et al., 2001). In the case of the CVA, when no difference was confirmed between selected groups, we merged them and repeated the analysis with a new arrangement.

For example, there was no significant difference between early and late Pliocene age groups, so we repeated the analysis by merging both groups in one Pliocene group. We used the CVA biplot calculation (in PAST) to interpret the canonical axes as it scale the CVA loadings by the pooled within-group covariance matrix. We observe the predicted versus resultant classification given (confusion matrix) by the determinant test (CVA), describing the taxa that were successfully classified in the groups, this confusion matrix was also submitted to resampling test (jackknife).

The main measurements in the multivariate analysis biplots were then analyzed in a paired comparison analysis, with a Kruskal-Wallis ranked test for significance, which assessed the differences among the selected measurements. Useful comparisons between pairs of measurements were also performed. These measurements corresponded to the most influential ones, which had the largest values in the CVA loadings as well as in its biplot, reflecting the relative importance by explaining the variance in canonical axes. This methodological step allowed us to simplify the quantification of multivariate variance and explain morphological differences between groups more directly.

VII. 2. 1. Institutional Abbreviations

IDSM: Instituto de Desenvolvimento Sustentavel Mamiraua, Tefe, Brasil; MACN: Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MLP: Museo de La Plata, La Plata, Argentina; MNHN: Museum national d'Histoire naturelle, Paris, France; MPC: Museo Paleontológico de Caldera at Caldera, Atacama Region, Chile; SGO-PV: Area Paleontología at the Museo Nacional de Historia Natural in Santiago, Chile; UFSC: Laboratorio de Mamíferos Aquáticos, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, Brazil; UNIR-PLVM: Universidade Federal de Rondônia, Paleontologia Vertebrados, Mamíferos; USNM: Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.

VII. 2. 2. Computed Tomography

We evaluated facial soft tissue morphology and its correlation with recognizable bony markers in our dataset using computed tomography (CT), a technology that permits high-resolution, precise imaging of small and obscured anatomical structures without modifying or destroying original voucher specimens. This method produced a relative density spectrum for the specimens which is useful to recognize the target structures as they present different density thresholds, as the melon and air sacs and sinuses, for example. The resultant DICOM images were analyzed and rendered in OsiriX (Rosset et al., 2004); we used the open polygon tool to collect all of the measurements. The measurements are described in Table S2.

The CT-scans obtained from six specimens, representing three families of Delphinida: Iniidae (*Inia geoffrensis*, n=1), Pontoporiidae (*Pontoporia blainvillei*, n=2), Delphinidae (*Cephalorhynchus eutropia*, *S. fluviatilis* and *S. guianensis*, n=2). MRI were also performed in *Cephalorhynchus*, *Pontoporia*, *Sotalia guianensis* and were examined together facilitating the recognition of muscles and other connective tissue structures with a closer range of densities.

VII. 2. 3. Morphology

The dissected specimens were *Inia geoffrensis* (IDSM Ig 2010-x), *Phocoena phocoena* (USNM DO5281, n=1), *Pontoporia blainvillei* (UFSC 1094, n=1) and *Cephalorhynchus eutropia* (CEU09LLi54, n=1). The dissections were designed to observe the insertions on the skull of the facial structures known to be related with the echolocation (i.e. nasal tract aïr sacs, melon, theca; Cranford et al., 1996) and the innervation and muscles related, following Harper *et al.* (2008).

VII. 3. Results

The exploratory PCA and cluster analysis performed recovered some agrupation in environmental groups and mainly in geological age groups. When pre-classified the groups that are in the base are coastal/estuarine and fully marine, the riverine are dispersed in three distal groups on the dendrogram. When analyzed with the transposed matrix, making the variables the measurements itself (R techniche, Manly 2004), the different regions of the proxy measurements were recovered, the melon dimensions proxies (measurements 1, 3, 6, 17) group together, as well as the air sacs (measurement 9, 10 and 12), bursae (measurement 18, 19) and air sinuses (measurements 27-32) dimensions proxies.

VII. 3. 1. Soft-tissue anatomy

VII. 3. 1. 1. Delphinoidea: Delphinidae

Cephalorynchus eutropia, *S. guianensis* and *S. fluviatilis* are characterized by a small and short rostrum. His skull is spherical in shape and has a sharp vertex at the back. This bone morphology presented regarding the soft parts of the facial region, such as the vestibular sacs, and nasofrontal premaxillar.

Furthermore, it was observed by the density threshold analysis, the anterior or rostral structures, such as melon, and adnexal structures, such as the theca (Cranford et al., 1996, Schenckan 1976), the latter is composed of connective tissue. Also, it was possible to observe the course of the maxillary branch of the trigeminal nerve, from the initial portion of the antorbital reentrancy into the round foramen in the ventral portion, and ending at the dorsal infraorbital foramen. This specimen (adult) present a rounded and shortened melon, as in *S. guianensis* and *S. fluviatilis*. It is important to consider that the specimen of *S.guianensis* is a fetus and, therefore, ontogenetic changes could be accounted for the morphologic differences. Nevertheless, the standardized measurements were able to recover similar proportions to the S. guianensis specimens, showing no allometric tendency in the melon growth of the genus, and appearing very similar in the overall anatomy found in *C. eutropia.*

The *S. fluvialtilis* specimen corresponds to an adult, so that it was known a rounded melon and shortened, as in *S. guianensis.* It is important to consider that the copy of *S. guianensis* is a fetus and for them there are ontogenetic changes that were considered by a correction in comparison with an adult specimen of *S. fluviatillis*, looking at an anatomy very similar to *C. eutropia.*

VII. 3. 1. 2. Delphinoidea: Phocoenidae

This kind of coastal dolphin is characterized by a small and short rostrum. The skull is spherical in overall shape and has a sharp elevated vertex at the posterior portion. Immediately more anterior structures, such as, vestibular, nasofrontal and premaxillary sacs, and the melon were observed in parasagittal slices. The vestibular sac is the bigger, approximately three folds the other sacs and it has a thick and wrinkled texture, being skin colored in the interior. The nasofrontal sac extends almost vertically oriented, being accommodated in the excavation present along the narial margin of the maxilla posteriorly to the end of the premaxilla. Just anterior above the premaxilla convex plate lies the last pair of scas (premaxillary sacs) the less voluminous of the three pairs. The theca is not easily discernible in gross morphology. This specimen showed a rounded and shortened melon, as in *S. guianensis* and *C. eutropia*, lying above the lateral rostral and nasal plug muscles which present dorsolaterally oriented fibers, which have a thickened region in the medial region near the base of the rostrum.

VII. 3. 1. 3. Inioidea: Pontoporiidae

This species is characterized by a more elongated skull anteroposteriorly and wider latero-medially. In the back of the skull, there is a vertex flat and slightly elevated. This bone morphology, features related to soft structures of the facial region, such as the vestibular sacs, and premaxillary nasofrontal addition to the older more rostral structures, such as melon, and adnexal structures, such as the theca (Cranford *et al.*, 1996, Schenckan, 1976). This makes it possible to observe an extension of the melon flow is asymmetric to the right side only, as mentioned in McKenna *et al.* (2011) between the melon and nasofrontal air sacs, mainly, and also with premaxillary sacs (Huggenberger *et al.*, 2010). There is a high complexity in the nasofrontal sacs, being subdivided and pronounced in the upper portion directly over the posterior portion of the premaxilla, these are located in anterior-posterior orientation. Also, located directly by the vestibular sacs posterior-dorsal direction. The latter are united antero-medially and separated from a paired way as in the Delphinoidea (*sensu* Schenckan, 1976). It was not observed the great asymmetric expansion observed in the right vestibular sac, noted in Schenckan (1976), both of which vestibular sacs extending posteriorly to the bony nostril, the left posterior extends slightly more than the right. Found more dorsally to occupy the back of the skull and are not filling in a concave space as there is no frontal prominence of the vertex as in

Inia geoffrensis. The air sacs can also be observed premaxillar although they have a much lower level, on the other air sacs. All air sacs are smooth texture, without ridges or creases as shown in Delphinoidea. The air sacs are symmetrical in both sides. In this region, just anterior and dorsal to the air sac is a region intermediate density, which is interpreted as the theca of connective tissue. In the most anterior portion of the face, the melon is the main observed structure, so mostly circular and is positioned in the anteroposterior last third of the facial region. *Inia geoffrensis*, unlike the anterior termination *Pontoporia blainvillei* melon is abrupt, not gradual, and has a density of around -100 H.U. (Houndsfield units). The melon lies above facial muscles that are interpreted as the tendinous insertions of the melon (*sensu* Harper *et al.*, 2008). It was observed in dissections performed on two specimens (one adult and one fetus) that the antero-medial groove present in the premaxilla corresponds to the insertion of the nasal plug muscle and juxtaposed to it, is lateral to the rostral oblique muscle which is the base and the inclusion of melon in the skull.

VII. 3. 1. 4. Inioidea: Iniidae

Inia geoffrensis is characterized by the presence in the more posterior region of the skull, a vertex very pronounced and concentrated only in the median region, formed by the frontal which is very conspicuous, with the so-called "knob-like process". This rare bone morphology, features related to soft structures of the facial region, such as the vestibular sacs, and nasofrontal premaxillar also more earlier structures (rostral), such as melon and related structures, such as the theca (Cranford et al., 1996, Schenckan 1976). The latter allow us to observe the remarkable development of the vestibular sacs, which are united and not separated anteromedially or paired as observed in the Delphinoidea (*sensu* Schenckan, 1976). The vestibular sacs filled almost the entire concave space generated by the prominence of the frontal on the vertex. It was also observed the highly complex in the nasofrontal sac anterior portion subdivided directly on the posterior portion of the concavity premaxilla and the nasal side, the latter are positioned vertically (dorso-ventral oriented). The premaxillary sacs can also be observed but have a smaller volume relative to the other air sacs. All sacs are of smooth texture, different to the wrinkled texture observed in Delphinoidea. The air sacs are symmetrical right and left. In this region, just anterior and dorsal air sac, there is a region of intermediate density, which is interpreted as the connective tissue theca. The most anterior portion of the face, the melon is the main observed structure, a large cylinder fatty (occupies about ⅔ of the facial region, with a density close to the -100 H.U.), more elongated (in the anteroposterior axis) that widened (sagittal), from the portion of the bony nostril dorsal to the anterior end of the face (forehead). There is also a connection of fatty tissue between the melon and posterior nasofrontal sac. The melon is over a series of facial muscles that are interpreted as the tendinous insertions of the melon (Harper et al. 2008). Through the dissections it was observed (in both specimens) that the anteromedial groove present in the premaxilla corresponds to the insertion of the nasal plug muscle juxtaposed to it lies the lateral rostral oblique muscle that forms the basis and the inclusion of the melon in the skull.

VII. 3. 2. Development of proxies for facial morphology on skull patterns

The facial region of odontocetes, defined by Mead and Fordyce (2009), comprehends the rostral elements (maxilla and premaxilla) that are located more dorsal than the overall mammalian pattern, until the vertex in it posterior end. In the anteriormost portion of the face two muscles were observed. The first is the nasal plug muscle which runs from the median premaxilla to the nasal passage and from the tip of the melon until its caudal portion lying over the bony naris when relaxed (Harper *et al.* 2008). The second is the rostral oblique muscle which conforms the tendinous attachment of the melon and the premaxilla, these pair of muscles run parallel to the former and widens posteriorly, see Fig. 4), from the tip of the melon to the level of the premaxillary foramina posteriorly. Laterally the *nasal plug* muscle is restricted to the anteromedial sulcus of the premaxilla at least in its connection with the premaxilla bone. Meanwhile, the *rostral oblique* muscle reaches part of the maxilla until the level of the dorsal infraorbital foramina occupying the concave space formed in the maxilla near the lateral border of the maxilla. Posteriorly lies the origin of the *pars antero internus* muscle in the region of the posterior dorsal infraorbitary foramina (Harper *et al.* 2008).

In all dissections performed, it was clearly observed in all the species the contact of the base of the melon (nasal plug and rostral muscles) on median portion of the premaxilla, specifically the line following the anteromedial sulcus (*sensu* Mead and Fordyce 2009). It was also observed that in this precise position the muscular fibers are oriented median-laterally to both sides as described by Harper et al. (2008).

The melon shape proxies were centered in length and width as a measure of the overall shape, from cylindrical to spherical, observed in the CT and MRI images. The melon length proxy was defined from the anteromedial sulcus to the posterolateral sulcus of premaxilla. Alternatively, it was also taken from the anteromedial sulcus to the posterior end of premaxilla. The width of the melon proxy was not so directly defined, because the scars have no constant positioning in a clear bony landmark (suture, sulcus or crest), therefore it was defined here as the braincase width (at the postorbital process of frontal and at the nuchal crest level) as a maximum size.

The main qualitative differences between the species was the overall shape of the melon (cylindrical to spherical) and the air sacs shape, dimensions and mainly were their contact on the skull vertex (Fig. 4). In this sense the melon of *Inia* is more cylindrical than spherical, being much longer than wide (12.01 x 5.7 cm), meanwhile *Pontoporia* presented a shorter melon, with an abrupt and flat anterior end, and hence more spherical (3.9 x 6.113 cm), not very rounded in transverse view, nevertheless (Fig. 5). By the other hand *S. guianensis,* presented a perfectly rounded shape and spherical in proportions. It was observed that the melon anteriormost point was correlated with the anteromedial sulcus of premaxilla where the muscle fibers diverge dorsolaterally. Based on these observations we designed some possible proxies for the melon width (measurements 3, 4 and 7) and length (measurements 6 and 17; Fig. 2).

The vestibular sac was also enlarged in the related extant *Pontoporia* (Fig. 4 and 5) but it has not the half-moon shape of *Inia* and as it do not present an elevated vertex, the vestibular do not surround it as well. Instead the vestibular sac morphology of *Pontoporia* is rather oval in shape, being more anteroposteriorly elongate than the ones in Delphinoidea as *Sotalia guianensis* and *Cephalorhynchus eutropia* and *Phocoena phocoena*. In *Pontoporia* the nasofrontal sac fossa is horizontally positioned, meanwhile in *Phocoena*, *Inia* and *Sotalia* it is inclined dorsally.

The premaxillary and nasofrontal sac was the one holding more contact with the bone, being the second attached to the maxillae, premaxillae and nasals, attaching at the corresponding fossae. Specially, in *Inia* and *Phocoena* where the nasals form a concave space (measurement 8, 10 and 11) which also receives it as well as the bursae (measurement 18-21). *Cephalorhynchus, Pontoporia* and *Sotalia* specimens only showed a smooth surface at the maxillae in the naris edge and the lateral border of the nasals. In *Phocoena* the space between the premaxilla posteriormost portion and nasals anterior corner is elongate, deeply excavated (concave) and supports the nasofrontal air sac and the bursae. The premaxillary sacs occupied most of the concave space on the premaxillae from the nasals to the premaxillary foramina on *Cephalorhynchus* and *Sotalia* and at the posteriormost portion of the convex surface of the premaxilla in the case of *Pontoporia*, *Phocoena* and *Inia*. In the same manner we studied the contacts and expansions of the air sinus in ventral view, mostly using the MRI and CT-scans images. In the same manner, measurements were defined on the maximum distances of all sinus excavations or scars and its total expansion (measurements 27-32). For example, it was observed a correspondence with the melon length and width with its cranial markers (Fig. 3 and 5).

Mckenna et al. 2011 calculated the disparity index as a proxy of the bursae asymmetry. Nevertheless, here we used the nasal measurements as a more approximate proxy, as in the different families it may change in proportions and level of "excavation" of the bone morphology of the nasals (i.e. *Phocoena*, *Inia* and *Pontoporia* in a lesser degree) as observed in the dissection and MRI, CT-scan, as the premaxilla is more related here with the premaxillary sacs shape.

VII. 3. 3. Morphometry and Systematics

The CVA analysis was performed with systematic groups, using at first the family level given a total of eight groups, as follows: Lipotidae, Platanistoidea, stem-Inioidea (*Brachydelphis+Goniodelphis*), Iniidae, Pontoporiidae, Kentriodontidae, Delphinidae, Phocoenidae. There were no significant differences between any of the groups. The analysis was repeated using a more inclusive level "super-Family", as follows: Lipotoidea, Platanistoidea, Inioidea and Delphinoidea (Fig. 6). The groups can be easily recognized at the scatterplot, nevertheless the only significantly different group ($p<0.01$) was Delphinoidea from Platanistoidea and Inioidea and vice-versa. These results suggests that some phylogenetic history may be reflected in that set of measurements, but the important measurements are different than the echolocation functional proxies as observed in Fig. 5). The biplot of the CVA analysis (eigenvalues corrected to the scatterplot statistic space) indicate that the most relevant measurements in this analysis are the width of the skull at the nuchal crest (measurement 6, Fig. 2) and a tentative proxy for the peribullary sinus (thickness of the basiocciptal crest in the pterygoid- basiocciptal suture, measurement 49, Fig. 2, 3). At the super-family level one of the length of melon proxies (measurement 17) was also at the most relevant measurements, nevertheless there was at least another 10 measurements with nearly the same relative importance to explain the variance on the two canonical axis.

The classification that was concordant with the predictions resultant from the paired Hotelling's discriminant ranged from 94% (Inioidea) to 100% (Lipotoidea, Platanistoidea, Delphinoidea) from the pre-classified groups, and was greatly reduced after the jackknife (0% for Lipotoidea, 60% for Platanistoidea, 80% for Delphinoidea and Inioidea).

VII. 3. 4. Morphometry and geologic time

These groups can be easily recognized at the scatterplot, nevertheless the only significantly different group (p<0.01) was Pleistocene-Holocene from middle Miocene-Pliocene and early Miocene and vice-versa.

The CVA analysis was performed reordering the data matrix in 5 geologic age groups, as follows: Pleistocene-Holocene, early Pliocene, late Miocene, middle Miocene, early Miocene (at this stage the Pleistocene was fused to Holocene since there was only one specimen from the earlier epoch; also the late Pliocene is not considered due to lack of specimens in the sample). There were no significant differences between late Miocene, middle Miocene and Pliocene epochs therefore this three were then fused to repeat the analysis, using the following three groups: Pleistocene-Holocene, middle Miocene-early Pliocene, early Miocene. These groups can be easily recognized at the scatterplot (Fig. 7), nevertheless the only significantly different group (p<0.01) was Pleistocene-Holocene from middle Miocene-early Pliocene and early Miocene and vice-versa.

These results show that geologic time is important to take into consideration on explaining the morphologic variation of the odontocetes measured here. The differentiation observed between the oldest specimens (early Miocene) occurs in the second canonical axis and, following the biplot of the CVA, the set of measurements that are proxies to the melon length (measurements 6 and 17) and premaxillary air sacs (measurements 10 and 11).

Meanwhile the first canonical axis, which accounts for most of the difference between the more recent groups: Pleistocene-Holocene and middle Miocene-early Pliocene. In this axis the most important measurements are again the set of melon length proxies and the size of orbit and external bony naris). In this way, contrary to the observed in the systematic analysis (item 3.2), the measurements that are relevant to explain the variation among the geologic age groups are indeed related to the echolocation functional proxies, see also Fig. 5).

The given-predicted groups classification resulting from the paired Hotelling's discriminant test were 96% of the extant specimens were concordantly predicted, 83% of the middle Miocene, 100% for early Miocene, late Miocene and Pliocene groups, 88% of the middle Miocene group. 100% of the extant specimens (85% after jackknife) were concordantly predicted, 94% (74% after jackknife) of the middle Miocene to late Pliocene group and 100% of the middle Miocene group (71% after jackknife).

VII. 3. 5. Morphometry and environment

The CVA analysis was performed reordering the data matrix in three environmental groups, as follows: riverine; fully marine; and coastal/estuarine (as explained in section 2 and supplementary information 1, Table S1, Fig. 1). The first axis (x, Fig. 8) separates the marine (including coastal/estuarine) of the riverine specimens and the main measurements that explain this separation are:

SITUACION ACTUAL DE BIOLOGIA AMBIENTAL:

Actualmente nos encontramos desorganizados como carrera y por ende no tenemos delegados que nos representen en el consejo de delegados de ciencias. Como carrera necesitamos de tu opinion y participacion para revertir esta situacion!

Falta de delegados

CECADES

Malla de carrera

Problemas medio ambientales en Chile

Secma

AEBCH

Perfil de egreso

Asamblea de carrera
Jueves 20/13.30/G108

Pasalo a algun compañero o botalo en los basureros de reciclaje cercanos melon length (6, 17) and width proxies (3) and orbit size (35). Meanwhile the marine and coastal/estuarine are overlaped in the first axis, but are separated by the second axis (y, Fig. 8), mainly by bursae size proxy (18), and melon width proxies (3, 8). As the coastal/estuarine group was not significantly different from marine specimens and only nearly the fully marine were different from riverine, probably due to reduced sample size in the latter comparing to the other groups, we reordered the groups fusing the groups fully marine and coastal/estuarine into one group (marine). This last analysis was performed with the Discriminant/Hotelling test on PAST, was significant with no 'misclassification' between the two groups.

The important measurements (highlighted in the multivariate analysis) were analyzed separately using Kruskal-Wallis test and x/y plots (measurements 2, 3, 5, 6, 7, 9, 10, 16, 17, 18, 22, 25, 27, 29; Fig. 8, Table S3). The measurements which show significant differences in the environmental groups are the melon length proxies (6, 17), orbit size (35), bursae size proxy (18, 19), air supply length and width proxy (22, 25), premaxillary sac width proxy (12), melon width proxy (2) and air sinuses total extension proxy (27-32; Table S4). The melon length proxies recovered an equally strong signal and the environment are remarkable (significant in all comparisons and both environmental group division, Table S4). The disparity index (Cranford *et al.*, 1996, McKenna *et al.*, 2011) was calculated for the nasals length as a proxy for the bursae asymmetry and it was significantly different between the fully marine group and both coastal/estuarine and riverine.

The given-predicted groups classification resultant from the paired Hotelling's discriminant test were: significant to riverine versus coastal/estuarine comparison and not for the remaining pairs.100% of the riverine group specimens were concordantly predicted (91% after jackknife), 96% of the coastal/estuarine group were concordantly predicted (77 % after jackknife), 92% of the fully marine group (56 % after jackknife).

VII. 3. 5. 1. Environmental classification of fossil taxa.

In both analysis considering two and three environmental groups there was little 'mis-classification' between the given and the predicted group classification, markedly it was possible to corroborate the paleoenvironmental data of the fossil specimens with the morphotype attributed to the environmental groups. *Atocetus iquensis* (MNHN PPI 113) and *Neophocoena phocaenoids* (USNM 240003) was 'mis-classified' (given: coastal/estuarine) as marine (predicted). Meanwhile, *Lophocetus repenningi* (USNM 205297) and *Brachydelphis mazeasi* (SGO.PV 749) was 'mis-classified' from marine (given) as coastal/estuarine (predicted). Moreover, the remaining *Neophocoena* specimens were all mis-classified when performing a jackknife to the classifications (confusion matrix), one predicted as riverine (USNM 240002) and the other to fully marine (USNM 240001). The jackknife added additional mis-classifications including one riverine to coastal/estuarine group, *Inia* sp. (UNIR-

PLVM-005, from Pleistocene of Rio Madeira Fm.), and predicted/given differences from coastal/estuarine to fully marine were observed at the following specimens: two specimens (of 25) of *S. guianensis* (UFSC 1083, 1175), a *Atocetus iquensis* specimen (MNHN PPI 115), *Lomacetus gingsburg* (MNHN PPI 104), a *Pliopontos littoralis* specimen (MNHN PPI 931) and *Pontistes rectifrons* (holotype, MACN 3190), *Schyzodelphis crassanglum* (USNM 11977, three (of eight) *Pontoporia blainvillei* specimens (UFSC 1216, 1217, 1290), and *Phocoena phocoena* (USNM 504606) from coastal/estuarine to fully marine.

The predicted/given differences from fully marine to coastal/estuarine: were a Kentriodontidae indet. (USNM 547211) *and L. repenningi* (USNM 23886) and *L. pappus* (USNM 15985), aff. *Lomacetus* (MPC 4), *Brachydelphis mazeasi* (SGO.PV 748), both *Brachydelphis* new form specimens (SGO.PV 972, 1109), a *Pliopontos* sp. (MPC 302) and aff. *Piscolithax* (MPC 229).

The fossil specimens which were undoubtedly classified as indicated by its paleoenvironment were: riverine, *Ischyrorhynchus vanbenedeni* (MACN); costal/estuarine, *Atocetus iquensis* (MNHN PPI 114), *Piscolithax longirostris* (MNHN SAS 933) and *Australithax* (MNHN PPI 65), *Goniodelphis hudsoni* (MCZ 3920) and *Stenasodelphis russelae* (CMM V 2234), *Pliopontos littoralis* (MNHN PPI 953, 193); fully marine, *Kentriodon* sp. (USNM 317782), *K. pernix* (USNM 171077), *Delphinodon dividum* (USNM 7278), five of six *Brachydelphis mazeasi* (SGO.PV 746, 747, 750, 968, MPC 3052), *Pontistes* sp. (SGO.PV 751, 964, 1082, MPC 3052), *Pliopontos* sp. (MPC 3034) and a Pontoporiidae indet. (MPC

3037).

VII. 4. Discussion

The multivariate analysis failed to recovered systematically based groups, but was able to recover significant geologic age and environmental groups. Although it was only significant in broader defined categories which are, more inclusive, additional sample could change the significance, finding more significative values to the marine specimens, which has half the sample sizes of the other groups.

These ecomorphological correlations are in accordance with previous work on periotic and cochlear morphology and its classification into environmental and age groups in the same way the analysis performed here (Gutstein *et al.* accepted).

In these analysis, it was repeatedly recovered the melon length proxies proposed here (i.e.: measurements 6 and 17) as one of the most important measurements to both geologic age and environmental groups. As it has been hypothesized that the melon length would related mainly with the focalization abilities, since the melon works similarly as a focusing lens (like a band filter) for the sound produced (Cranford and Krysl 2008), and since the length of the melon of *Inia geoffrensis* was a magnitude of difference from most of the melons of the other species (except *Cephalorhynchus*) here we propose that maybe one of the functions for a long melon would be a more focused echolocation beam which is in accordance with the unique habitat *Inia* inhabits all amazon and orinoco fluvial systems microhabitats including the varzea (flooded grassland and forest; Pilleri and Gihr, 1977, Best and da Silva, 1993 and references therein). Nevertheless, if this is the case it would have been originated before the river dolphins have invaded the fluvial systems (late Miocene) since it is one of the elements which is highlighted in the middle Miocene. The one exception to this would be *Sotalia fluviatilis* which has a later entrance in the river system, during the Pliocene-Pleistocene (Cunha et al. 2005), and has a sister species *S. guianensis* from which they separate by the melon length proxies (among other measurements). In the qualitative analysis, though, there was no morphological difference detected between the species in the gnus *Sotalia*.

As stated above, the external morphology convergences are common on river dolphins of different phylogenetic and biogeographic histories. It is less clear, however, if the morphology underpinning sound generation and reception shows similar convergence. *Platanista*, for example, is unique among "river dolphins" in possessing pneumatic maxillary crests that expand antero-dorsally along the face, effectively cradling any forehead soft tissue structures in bone (Mead and Fordyce, 2009:51). The function and acoustic properties of these crests has been proposed to act as an acoustic mirror, producing a more focused beam, likely directed downward, which in part helps to explain *Platanista*'s side-swimming behavior (Purves and Pilleri, 1983).

Likewise, Pilleri and Gihr (1979), described the possibly of the expanded crests of the maxilla in *Inia* and *Ischyrorhynchus*, nevertheless these assumptions are not very well supported with the fossil remain itself and it was considered when the platanistoids were considered relatives of the south american river dolphins, this phylogenetic arrangement was recovered in a recent cladistic analysis (Geisler et al. 2012). This analysis was revisited, being the positioning of *Ischyrorhynchus* in platanistoids reinterpreted as an artifact of equivocal coding for several characters for this genus (Gutstein et al. this volume) recovering a monophyletic Inioidea (including *Inia*, *Ischyrorhynchus*, *Meherrinia*) separated of Platanistoidea.

VII. 4. 1. Depicting morphometry into morphofunctional anatomy

The length of the melon was relevant to the classification of environments and geological age. The length of the melon has been suggested as a functional characteristic related to the increased ability to filter the sound and focusing the beam of sound produced.

An enhanced focusing capability is also coherent with the complex habitat of life of the river dolphins (i.e. varzea, Best and da Silva 1993). It has been reported a super-high frequency (>100 kHz) and high maneuverability (the only dolphin to swim backwards and that presents a highly flexible neck used to scan the uneven surface of the flooded forest) in the Amazon dolphin (Pilleri and Gihr, 1977, Klima et al., 1980) and the ganges river dolphin (also known as susu) as the only dolphin to swim and prey upside-down and side-swimming (Pilleri, 1974; Herald et al. 1969).

It has been proposed that the melon length is related to the focusing ability of the dolphin (Cranford 1999). Further speculation on sperm whales echolocation abilities and deep foraging habits in *Kogia*, but not observed in *Ziphius* (rather short melon) have been elaborate on this premise (Mackenna *et al.*, 2011). Harper et al. (2008) would be than possible to change the melon shape, related to enhancing the focusing ability.

However, melon length has also been proposed as cut-off of the lower limit to the frequencies of the sound produced (Mackenna et al. 2011) and that this difference would be allometric (independent of head size). No clear pattern has emerged, however, size of bursae complex and the melon are clearly important components to consider to determine estimated frequencies (Cranford *et al.* 1996).

On the other hand, the air sacs have an overall distribution maintained in the groups of Delphinida, being the Inioidea complex, subdivided, smooth in texture and well adjusted to the underlying skull bone (this last one is also observed in *Phocoena*, Delphinoidea) and the Delphinidae (Delphinoidea) have thick, pigmented and wrinkled vestibular sacs. These findings are in accordance with the observed in previous works (Schenkkan, 1976; Cranford et al., 1996).

It has been proposed that the air sacs surrounding the melon would be related to a more focused beam of echolocation, the air spaces arrangements would function as an acoustic concave mirror (Pilleri and Gihr, 1979), given the air-tissue boundary it generates reflection of the sound wave.

VII. 5. References

Allen, G.M., 1941. A fossil river dolphin from Florida. Bulletin of the Museum of Comparative Zoology 89(1):1-8.

Arnason and Gullberg, 1995. Cytochrome b Nucleotide Sequences Lineages of Extant Cetaceans and the Identification of Five Primary. Molecular Biology 2(1993):407-418.

Best, R. C., da Silva, V. M. F., 1993. Inia geoffrensis. The American Society of Mammalogists. Mammalian Species 426:1–8.

Cassens, I., S. Vicario, V. G. Waddell, H. Balchowsky, D. Van Belle, W. Ding, C. Fan, R. S. Mohan, P. C. Simões-Lopes, R. Bastida, A. Meyer, M. J. Stanhope, and M. C. Milinkovitch. 2000. Independent adaptation to riverine habitats allowed survival of ancient cetacean lineages. Proceedings of the National Academy of Sciences of the United States of America 97:11343-7.

Cozzuol, M. A., 1988. Una nueva especie de Saurodelphis Burmeister 1891 (Cetacea: Iniidae) del “Mesopotamiense” (Mioceno tardío-Plioceno temprano) de la Provincia de Entre Ríos, Argentina. Ameghiniana 25:39-45.

Cozzuol, M. A., 1996. The record of aquatic mammals in southern South America. Munchner Geowissenschaftliche Abhandlungen 30:321-342.

Cozzuol, M.A., 2010. Fossil Record and the Evolutionary History of Inioidea, in: Manuel Ruiz-Garcia, Joseph Mark Shostell (Eds.), Biology, Evolution and Conservation of River Dolphins Within South America and Asia. Nova Science Publishers, pp. 193-217.

Clarke, M.R. 2003. Production and control of sound by the small sperm whales, Kogia breviceps and K. sima and their implications for other Cetacea. Journal of the Marine Biological Association of the United Kingdom 83:241-263.

Cranford, T. W., Amundin, M., Norris, K.S., 1996. Functional morphology and homology in the odontocete nasal complex: implications for sound generation. Journal of Morphology 228:223–285.

Cranford, T. W., Krysl, P., 2008. Acoustic pathways revealed: simulated sound transmission and reception in Cuvier’s beaked whale (Ziphius cavirostris). Bioinspiration & Biomimetics 3:1-10.

Crespo, E.A., Harris, G. and González, R. 1998. Group size and distributional range of the Franciscana, Pontoporia blainvillei. Marine Mammal Science 14:845-849.

Geisler, J. H., McGowen, M. R., Yang, G., Gatesy, J., 2011. A supermatrix analysis of genomic, morphological, and paleontological data from crown Cetacea. BMC Evolutionary Biology 11:1-112.

Gutstein, C. S., M. A. Cozzuol, A. O. Vargas, M. E. Suárez, C. L. Schultz, and D. Rubilar-Rogers. 2009. Patterns of skull variation of Brachydelphis (Cetacea, Odontoceti, Pontoporiidae) from South-Easthern Pacific Neogene. Journal of Mammalogy 90:504-519.

Gutstein, C.S., Figueroa-Bravo, C.P., Pyenson, N.D., Yury-Yañez, R.E., Cozzuol, M.A., Canals, M. (accepted) High frequency echolocation, ear morphology, and the marine-freshwater transition: a comparative study of extant and extinct dolphins (Odontoceti). Palaeogeography, Palaeoclimatology, Palaeoecology.

Gutstein, C.S., Godfrey, S. J., Cozzuol, M.A., Simoes-Lopes, P.C., Canals, M. (this volume). New Toothed Whales (Inioidea, Odontoceti) from the Neogene of the South-East Pacific (Atacama Region, Chile) and North Atlantic (North Carolina, U.S.A.): implications to river dolphins distribution and facial morphology.

Hamilton, H., S. Caballero, a G. Collins, and R. L. Brownell. 2001. Evolution of river dolphins. Proceedings of the Royal Society of London. Series B: Biological Sciences 268:549-56.

Heyning, J. E. 1997. Sperm whale phylogeny revisited: Analysis of the morphological evidence. Marine Mammal Science 13:596–613.

Herald, E. S., R. L. Brownell, F. L. Frye, E. J. Morris, W. E. Evans, and A. B. Scott. 1969. Blind river dolphin: First side-swimming cetacean. Science 166:1408.

Klima M, Oelschläger HA, Wünsch D. 1980. Morphology of the pectoral girdle in the Amazon dolphin *Inia geoffrensis* with special reference to the shoulder joint and the movements of the flippers. Z. Saugertierkunde 45:288-309.
Manly, B.F.J. 2004. Multivariate statistics methods: a primer. 3ª ed. Chapman & Hall/CRC press, Washington, pp. 214.

Messenger, S. L., and J. A. McGuire. 1998. Morphology, molecules, and the phylogenetics of cetaceans. Systematic Biology 47:90.

Morgan, G.S. 1994. Miocene and Pliocene marine mammal faunas from the Bone Valley formation of central Florida. Proc. San Diego Soc. Nat. Hist. 29:239-268.

Muizon, C. D. 1983. Pliopontos littoralis un nouveau Platanistidae Cetacea du Pliocene de la cote peruvienne. C. R. Acad. Sc. Paris 296:1101-1104.

Muizon, C. D. 1984. Les vertebres fossiles de la formation pisco (Perou), Deuxieme partie: Les Odontocetes (Cetacea, Mammalia) du Pliocene inferieur de Sud-Sacaco. Recherche Sur Les Civilisations 50.

Muizon, C. D. 1988. Les vertébrés fossiles de la Formation Pisco (Pérou). Troisième partie: Les odontocètes (Cetacea, Mammalia) miocènes. Travaux De l'Institut Français d'É-tudes Andines 42:1–244.

Muizon, C. D. 1988a. Les relations phylgénétiques des delphinida (Cetacea, Mammalia). Annalesde Paleontologie 74:159-227.

Muizon, C. D. 1994. Are the squalodonts related to the platanistoids?. Proceedings of the San Diego Society of Natural History 29:135-146.

Pilleri, G. E. 1974. Side-swimming, vision and sense of touch in Platanista indi (Cetacea, Platanistidae). Experientia 30:100-104.

Pilleri, G. E., and M. Gihr. 1977. Observations on the Bolivian (*Inia boliviensis* d'Orbigny 1834) and the Amazonean Bufeo (*Inia geoffrensis* de Blainville 1817), with description of a new subspecies (*Inia geoffrensis humboldtiana*). Investigations on Cetacea 10:11-76.

Pilleri, G. and M. Gihr. 1979. Skull, sonar field and swimming behaviour of *Ischyrorhynchus vanbenedeni* (Ameghino 1891) and taxonomical position of the genera *Ischyrorhynchus, Saurodelphis, Anisodelphis* and *Pontoplanodes. Investigations on Cetacea*, 10:17-70.

Rice D. W. 1998. Marine Mammals of the World. Systematics and Distribution. Society for Marine Mammalogy, Lawrence, KS, pp. 231.

Siciliano, S. 1994. Review of small cetaceans and fishery interactions in coastal waters of Brazil. Report of the International Whaling Comission, Cambridge, 158:241-250.

Simpson, G. G. 1945. The principles of classification, and a classification of mammals. Bulletin of the Ameri- can Museum of Natural History 85:1-350.

Spoor, F., S. Bajpai, S. T. Hussain, K. Kumar, and J. G. M. Thewissen. 2002. Vestibular evidence for the evolution of aquatic behaviour in early cetaceans. Nature, 417:163-166.

Table I- Comparisons of skull morphology, habitat preference and frequency preferences. CT) Computed tomography; MRI) Magnetic resonance; GM) Gross morphology dissection

Taxa	**environmentpreference**	**Method**	**melon type**	**click frequency**	**N turns cochlear duct/ cochlear type**	**acoustic properties of the echolocation beam**	**anterior end of melon**	**References**
Platanistidae								
Platanista gangetica	riverine	na	?	15-60?/20-100	?	?	?	Herald *et al.* (1969), Pilleri *et al.* (1971)
Delphinidae								
Pseudorca crassidens	marine	na	?	45.7, 100	?	Bimodal	?	Au *et al.* (1995)
Grampus griseus	marine	na	?	30-50; 80-100	2.5 Type II	Bimodal	?	Philips *et al.* (2003)
Delphinus delphis	marine	McKenna *et al.* (2011)	rounded	81.4, 114.8; 71.8-128.8	Type II	Bimodal	convex	Nakamura (1999)
Stenella attenuata	marine	na	?	40-140 40-60 and 120-140	2.5* Type II	Bimodal	?	Wartzok and Ketten (1999), Schotten *et al.* (2004)
Tursiops truncatus	marine	McKenna *et al.* (2011)	rounded	34.5-131.9 67 and 114	2.25* globose/ rounded Type II	Bimodal	convex	Nakamura (1999), Wartzok and Ketten (1999)
Cephalorhynchus eutropia	coastal/ estuarine	CT, MRI, GM	rounded/ big	126	?	?	convex	Götz et al. (2010)
Sotalia guianensis	coastal/ estuarine	CT, MRI, GM	rounded/ big	80-95; 64-105	globose rounded, type II	?	convex	Kamminga (1988), Kamminga *et al.* (1993), Sauerland and Dehnhard (1998)
Sotalia fluviatilis	riverine	CT	rounded	88.35 (SD=3.01)	globose rounded, type II	?	convex	May-Collado and Wartzok (2010)
Phocoenidae								
Phocoena phocoena	coastal/ estuarine	GM	rounded	118-128; 139 max.	1.5 flat type I	narrow-band	convex	Ketten (1992), Au et al. (1999, 2006)
Phocaenoids dalli		na	?	133	?	one peak	?	Kamminga (1988), Kamminga et al. (1993)
Lipotidae								
Lipotes vexliffer	riverine	na	?	112	?	narrow-band	?	Nakamura (1999)
Pontoporiidae								
Pontoporia blainvillei UFSC	coastal/ estuarine	CT, MRI, GM	short / squared	130 (SD=10)	globose rounded, type II	narrow-band	flat	von Fersen et al. (2000)
Iniidae								
Inia geoffrensis USNM 571263, MCN -M 32	riverine, varzea (flooded forest)	CT, GM	elongate/ cylindrical	emitted 16-170 (best freq. 60-80*); 85-100 auditory sensivity 75-90 kHz	1,5*, 2** flat type I	narrow-band	convex, narrow sonar beam 20-30	Evans (1973), Kamminga and Weirsma (1981), Weirsma (1982)
Ziphiidae								
Ziphius cavirostris	marine	na	box-like	40; 15-80	?	one peak	flat	Zimmer *et al.* (2005)
Mesoplodon	marine	na	?	25-43	?	one peak?	?	Johnson *et al.* (2004), Lynn and Reiss (1992)
Berardius	marine	na	?	236-42	?	Bimodal	?	Dawson *et al.* (1998)

*taken from Wartzok and Ketten (1999); **present work

na: non applicable (no data on cochlear duct morphology)

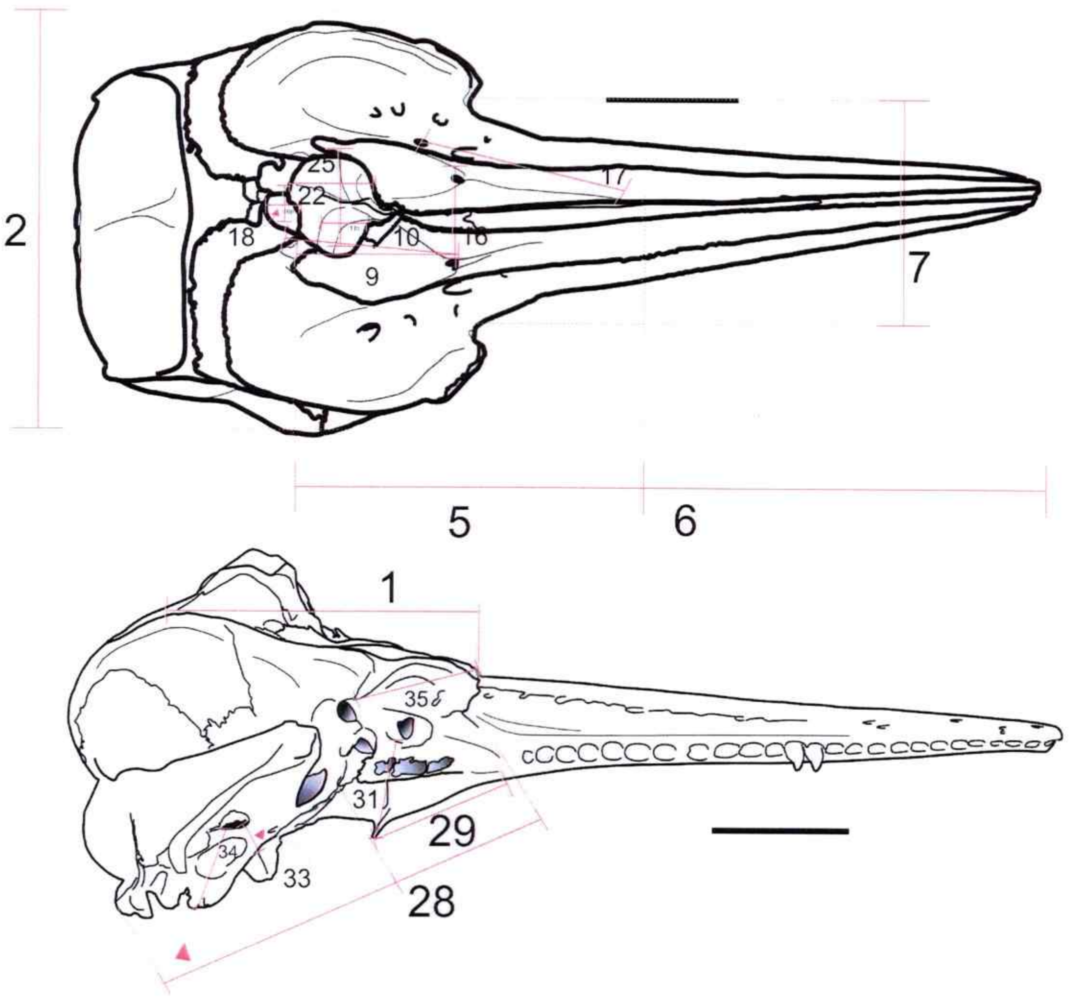


Figure 2 - Schematic drawings of odontocete skull in A) dorsal, B) ventral and C) lateral view, showing the 50 measurements taken. For a detailed description see table 1.

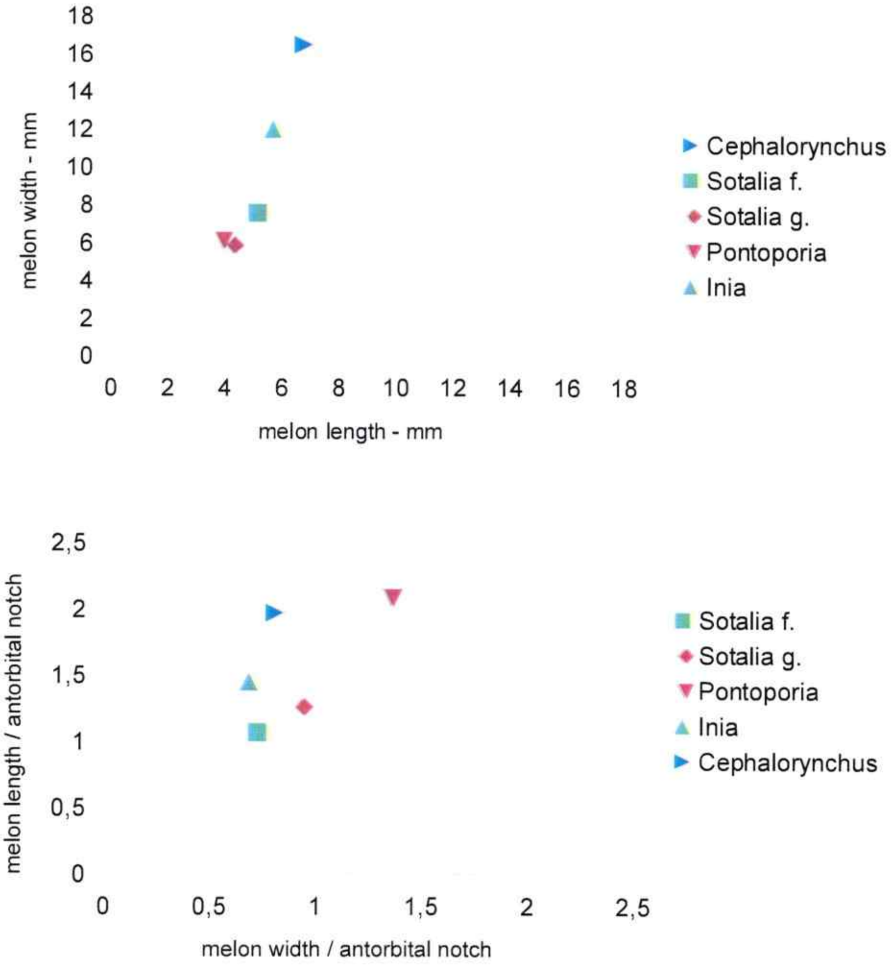


Figure 3 - Scatterplots of the melon length and width in mm. The measurements were taken using computed tomography images of complete heads on OsiriX.

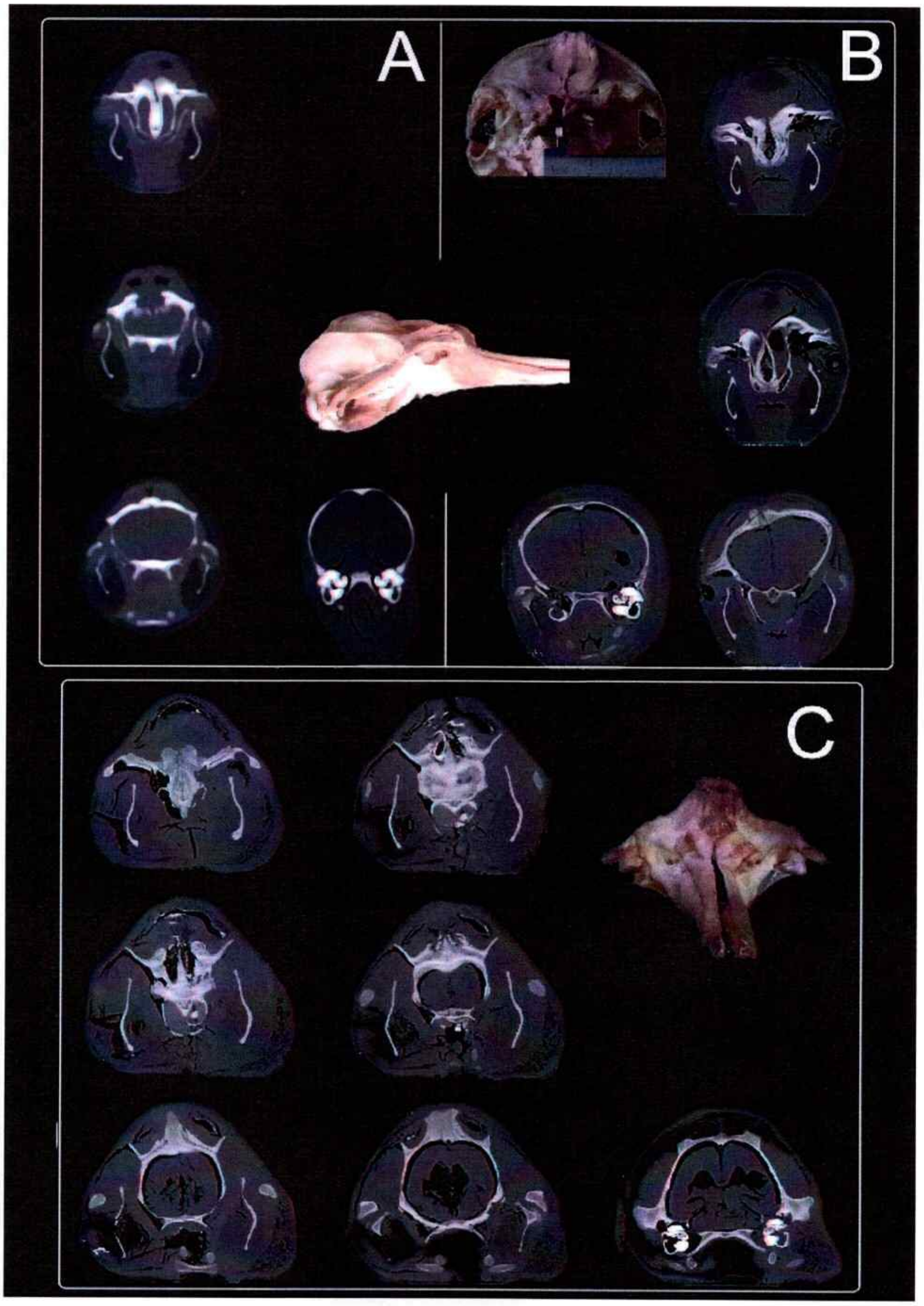


Figure 4 - Computed tomography slices of Delphinida specimens at transversal slices. A) *Pontoporia blainvillei B)* and C) *Inia geoffrensis*

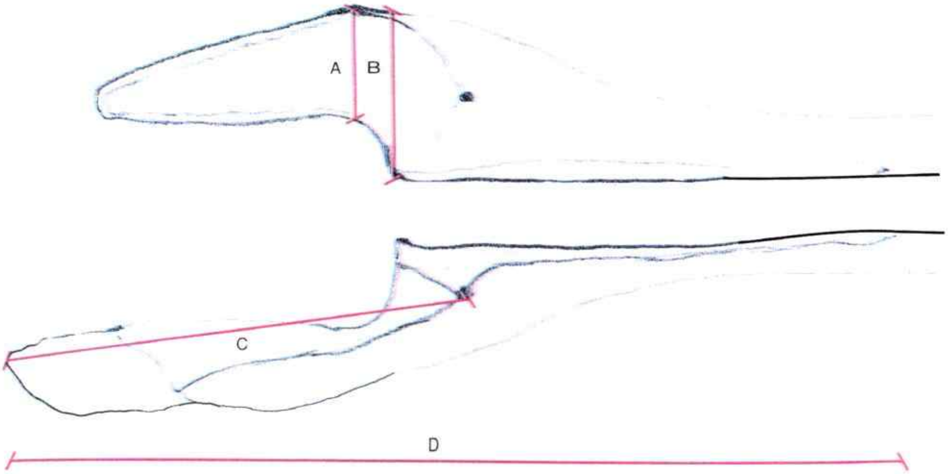


Figure 5 - Schematic linedraw of suggested proxies for facial structures in Delphinida. See Table 2 and Figure 2 for measurements descriptions. (to be done yet, only a draft)

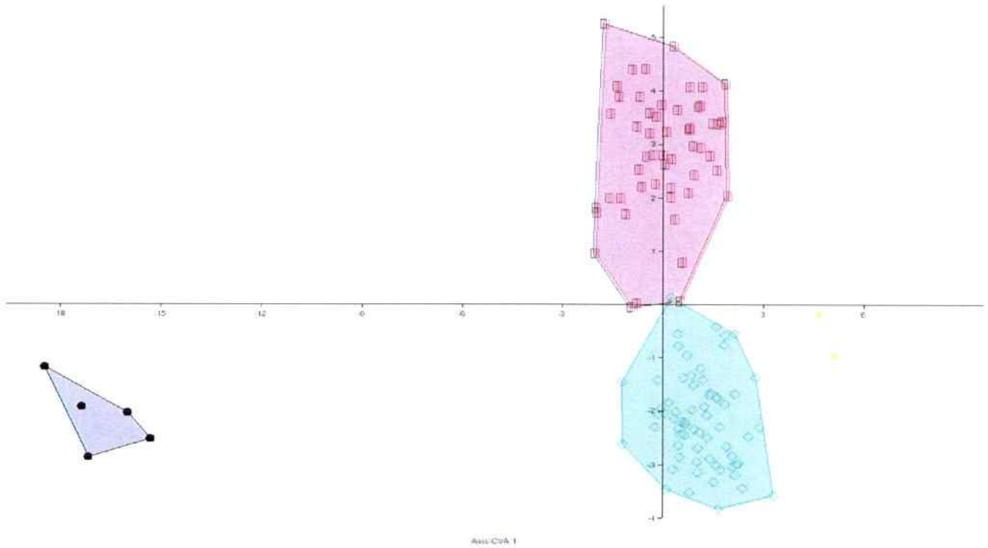


Figure 6 - Scatterplot of the MANOVA/CVA analysis of the systematic groups data matrix re-ordered at superfamily level. Black dots) Platanistoidea; brown bars) Inioidea; green diamonds) Delphinoida; yellow triangles) Lipotoidea.

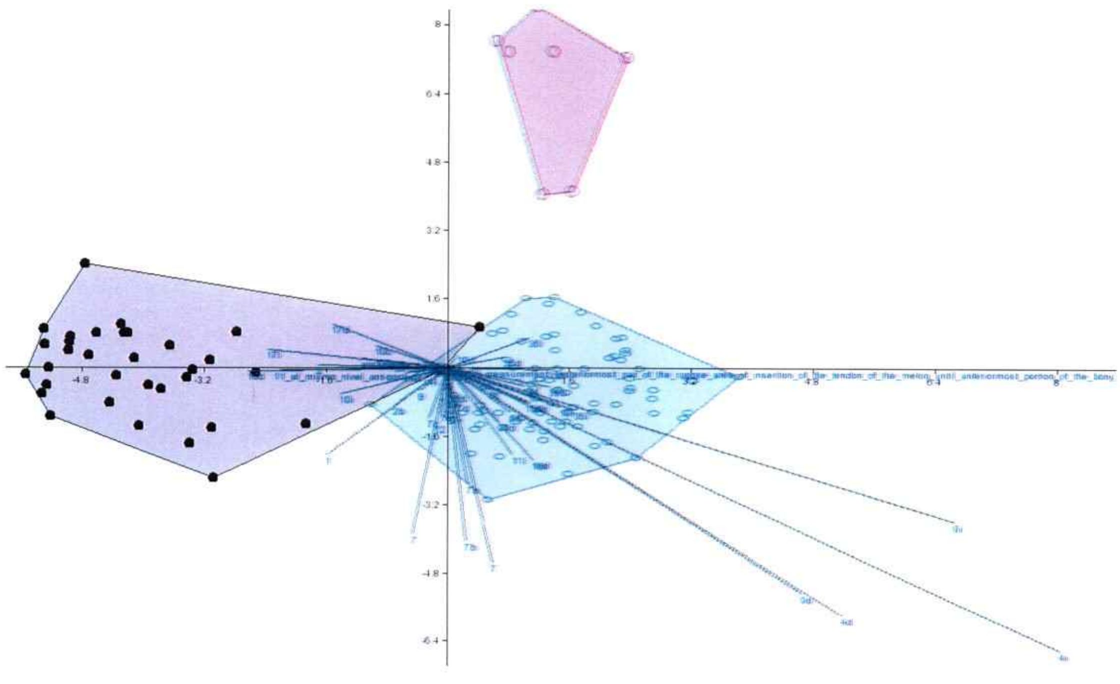


Figure 7 - Scatterplot of the CVA analysis performed in Past (O'Hammer, 1999). The groups are the resultant significantly (p<0.01) different geological ages groups: Black

dots) middle Miocene-Pliocene; turquoise oval circles) Pleistocene+Holocene; magenta open circles) early Miocene.

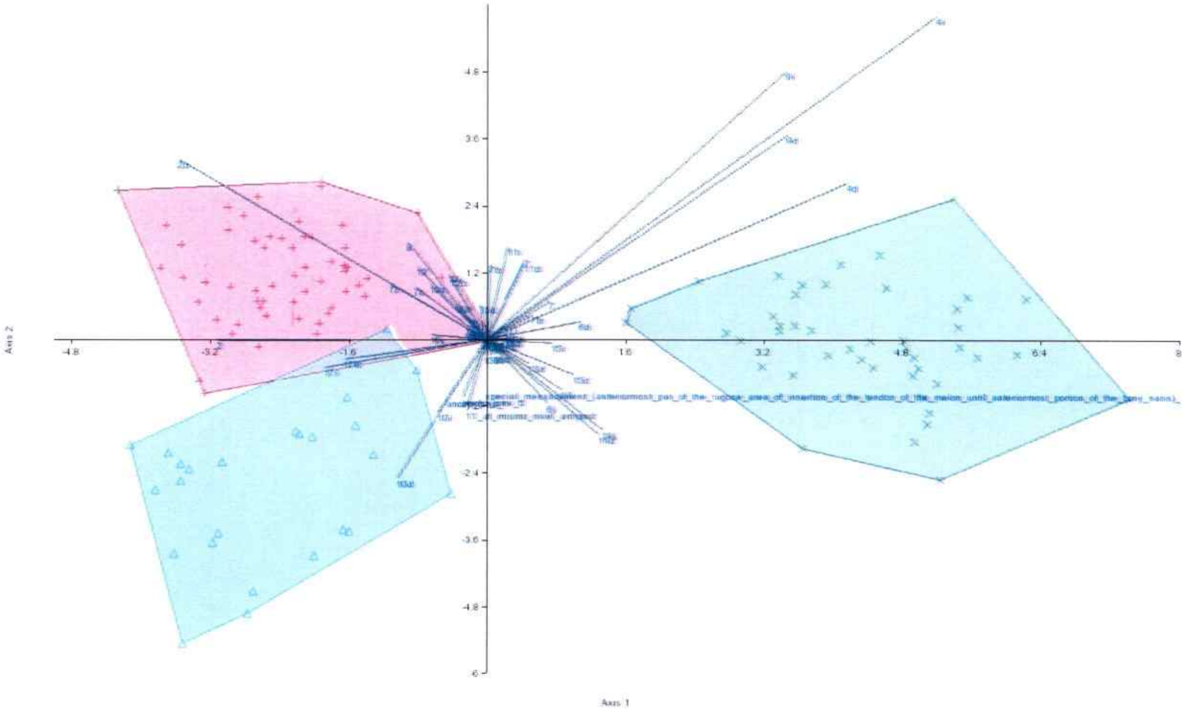


Figure 8 - Scatterplot of the CVA analysis of the three environmental groups, only the marine-riverine and riverine-estuarine pairs were significantly different (p<0.01). In light-blue triangles, specimens from marine habitat; in red crosses, from coastal/estuarine and in green "x" from the riverine habitat specimens.

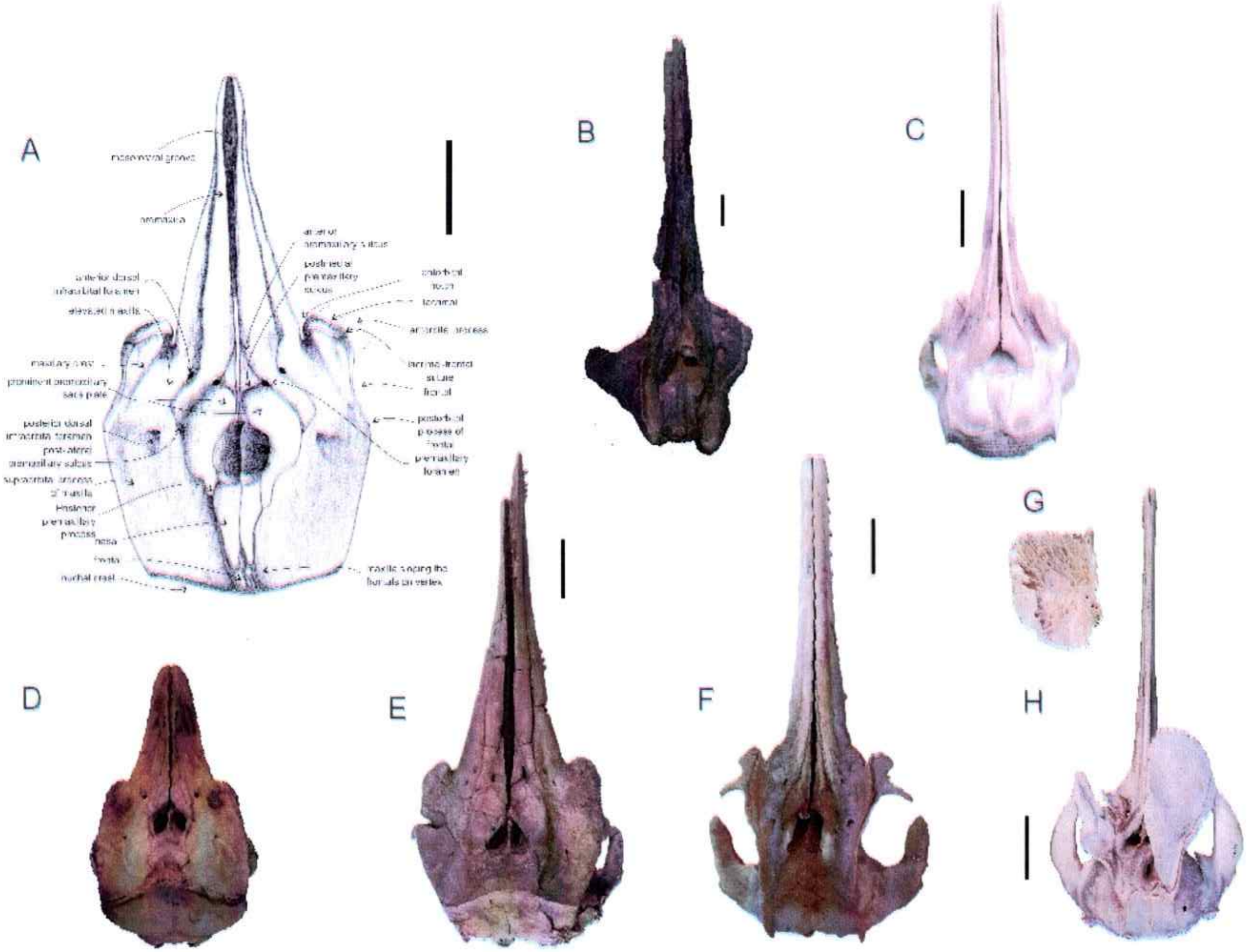


Figure 9 - Skull of selected taxa in the dataset (for a complete list of taxa see table S1). **A)** *Brachydelphis mazeasi* (line draw modeified from Gutstein et al. 2009); B) *Ischyrorhynchus vanbenedeni* (MACN 15135); C) *Pontoporia blainvillei* (UFSC 1290); D) *Phocoena phocoena* USNM 504543; E) *Delphinodon dividum* (USNM 7278); F) *Inia geoffrensis* (IDSM Ig-9301); . G-H) *Platanista gangetica* USNM 176409; G) maxillary crest removed from skull (H) in ventral view. All skulls are scaled to represent the same vertex size (from the anterior end of bony naris to the supracocciptal crest). Escale bars = 5 cm.

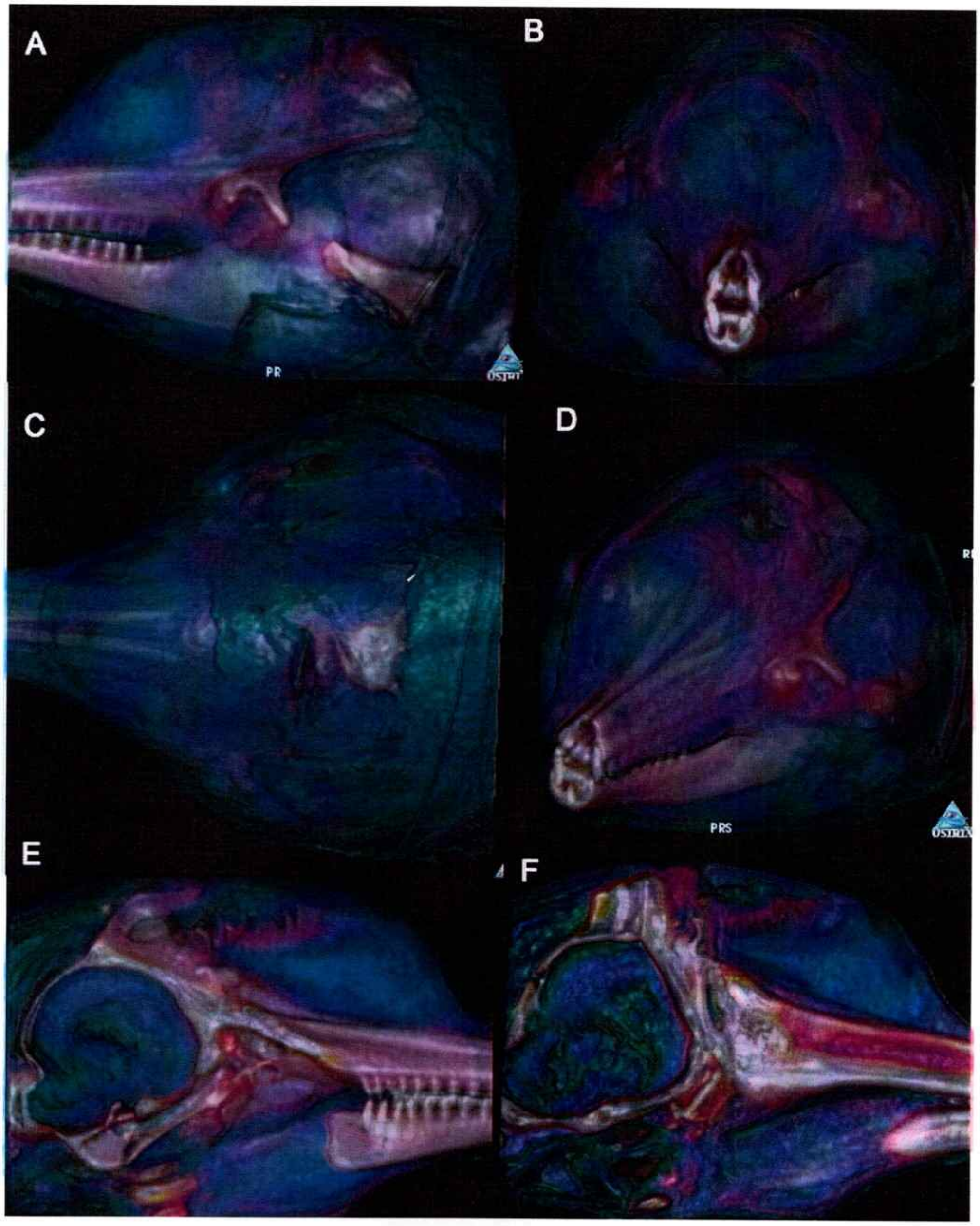


Figure 10 - 3D reconstructions (volume rendering) of the head computed tomography od Inia geoffrensis. The colors represent different gradients of density, being green for air density (-600 HU), blue very low density fat tissue, melon and mandibular fat pads (-100), magenta for regular fat tissue (skin and theca, -50HU) and yellow for bone (500 HU). A) left lateral view, B) frontal view, C) dorsal view, D) fronto lateral view, E) parasagittal cut, F) sagittal view.

SI.1 - Supplementary Information - Capitulo 3

A total of 52 measurements from 131 specimens that covered the following taxonomic breadth: Delphinidae (n = 28), Delphinoidea indeterminate (n = 1), Iniidae (n = 16), Inioidea indeterminate (n = 7), Kentriodontidae (n = 24), Monodontidae (n = 1), Odobenocetopsidae (n = 2), Phocoenidae (n = 20), Physeteridae (n = 1), Platanistidae (n = 3), Platanistoidea (n = 2) and Pontoporiidae (n = 9) (see Table S1 for a detailed taxonomy of less inclusive taxa).

The taxonomic classification was ranked in superfamily, family and genus following Steeman et al. (2006) and Geisler et al. (2011) otherwise indicated (see Table S1), families divided in stem and crown groups (stem-Inioidea, Iniidae, Pontoporiidae, Delphinidae, Kentriodontidae, Phocoenidae, Platanistidae, stem-Platanistoidea, *Odobenocetops+ Delphinapterus*) and superfamily level (Platanistoidea, Inioidea, Delphinoidea), following Steeman et al. (2006) and Geisler et al. (2011) otherwise indicated (see Table S1).

The habitat preferences of the extant dolphin were considered according to the information available in the literature and the locality data available in the collections.

In the same way, the fossil locality data were associated with pertinent bibliography on the sedimentology and hence the interpreted paleoenvironment for each specimen, locality or horizon, depending on the locality data available in the collections visited.

Environmental and geologic age categories were defined compiling locality, sedimentological and palaeoecological data in the case of the fossils (e.g., Achurra, 2004; Cione et al., 2005; Ward, 2008; Whitmore and Kaltenbach, 2008; Achurra et al., 2009; Visaggi and Godfrey, 2010) and distribution data for extant species (Shirihai and Jarrett, 2006). The age, stage or epoch of the specimens were determined in the same manner, pre-classifying the dataset by geologic age, in the following groupings: early Miocene; middle Miocene; late Miocene; Pliocene; and Pleistocene-Holocene.

Afterwards, the data matrix was pre-classified by more general environmental groups, as follows: riverine (only fluvial system); fully marine (shallow fully marine, offshore, neritic, deep marine); and coastal/estuarine (including coastal environment and epicontinental seas with fluvial input, a

nd coastal and riverine habitat preferences; see Table S1). When no difference was confirmed between groups this ones were merged and the analysis was repeated with the new arrangement. For example, there was no significant difference between early and late Pliocene age groups, so the analysis was repeated merging both groups in one Pliocene group.

Although supra-familial relationships among extant cetaceans, especially among odontocetes, have not yet reached a consensus, we decided to use Steeman et al. (2009) and Geisler et al. (2011) as a proxy for phylogeny.

We allocated our taxa among the following stem and crown groups (stem-Inioidea, Iniidae, Pontoporiidae, Delphinidae, Kentriodontidae, Phocoenidae, Platanistidae, stem-Platanistoidea, *Odobenocetops*+Delphinapterus) and superfamily level (Platanistoidea, Inioidea, Delphinoidea). However, between the Inioidea we used the definitions in Cozzuol (2010).

Specimens that do not have measurement 7 (antorbital width, Fig 2) were excluded from the analysis standardized, reducing the diversity of taxa from the analysis in the case of *Hadrodelphis* (CMM V 11) and *Lophocetus calvertensis* (USNM V16314), both grouped in Kentriodontidae (Table S1).

From the original total of 50 new measurements (Table S2), 14 were selected (Table S3), creating a new set of measurements that are useful to compare facial and sinuses (auditive) soft tissue morphology. These were the most important in CVA analysis were then tested against environmental analysis compared by pairs using the Kruskal-Wallis and Mann-Whitney pairwise comparisons (*post hoc*) analysis (Table S4). Also we tested for correlation between some of the measurements as orbit size (35) versus melon length (6,17).

SI.2 Palaeoenvironmental and age data of geological formations

Parana Fm. - The environment here attributed to this formation was shallow marine with fluvial input. The Parana Fm., however, has a rather complex stratigraphy, age and depositional environment being classified differently in several works: shallow marine with deltaic influence (Iriondo, 1973; Del Río, 2000), aereal to sub-aereal with carbonatic reef barrier (Aceñolaza and Aceñolaza, 2000), litoral with fluctuating salinity rather estuarine (Herbst and Zabert, 1987). The age has also been debated by several authors but in general the late Miocene epoch adopted here is mostly accepted from different lines of evidence (vertebrate and invertebrate assemblages, Reinhart, 1876; Rossi de García, 1966; Aceñolaza, 1976; Zabert y Herbst, 1977; Herbst y Zabert, 1987; Cozzuol, 1993). Nevertheless, alternative age assignment has been proposed (mollusc assemblage, middle Miocene, Del Río, 1991). Los estudios paleomagnéticos en las márgenes del río Paraná ubican esta unidad en el Plioceno (Bidegain, 1993).

Bahia Inlgesa Fm. - All the specimens used here, come from a well known bonebed layer of phosphatic hardground and it has been interpreted as deep marine to shoreface environment (Achurra 2004, Achurra et al. 2009, Gutstein et al. 2008, 2009).

Ituzaingó Fm. - This formation is restricted to the filling of channels with fluvial system originated conglomerate, after the paranean sea retraction and it is then limited in time within the late Miocene (Cione et al. 2005).

Pisco Fm. - This formation, comprises long ranged sandstone to mudstone and diatomous with less expressive and rather punctual conglomerate strata from the middle Miocene to the late Pliocene. The specimens used here were recovered from different localities and follow the age ordering described in Muizon (1988, 1983) and DeVries (1998).

Rio Madeira Fm. - This formation has been assigned to the Pleistocene and the paleoenvironment was interpreted as the fluvial system at the amazon basin (Quadros et al. 2006). The only specimen that comes from Rio Madeira Formation come from a level below the radiocarbonic date around 45,000 ybp.

Santa Margarita Fm. - The environmental interpretation for this formation is a shallow fully marine shelf environment occurred during early late Miocene (Tortonian ~10-12 m.y.a., Kirby, 2001).

Calvert Fm.- This formation is widely known by the rich marine vertebrate fauna and it is very well constrained age and environment based on invertebrate and sedimentological data. The cetaceans are also diverse, abundant and widely known and the paleoenvironment has been interpreted as shallow marine to neritic range occurred during the early-middle Miocene (Burdigalian-Langhian; Ward 2008, Visaggi and Godfrey 2010).

St. Mary's Fm.- The paleoenviroment interpreted for this formation is a transition from marine shelf to tidally influenced, and it is restricted in age at the early late Miocene (early Tortonian ~11 m.y.; Kidwell 1997, Visaggi and Godfrey 2010, Ward 2008).

Bone Valley Fm. - The paleoenviroment interpreted for this formation is of an epicontinental sea which occurred during the middle Miocene-early Pliocene (Serravalian-Zanclean: Hemphillian, Morgan, 1994).

Table S2 - Description of the 50 skull measurements taken on the odontocete specimens.

n	Description Measurements
1	Length of braincase from on the level of postero-orbital process of the frontal
2	Length of braincase on the level of postero-orbital process of the frontal
3	Width of braincase on the level of postero-orbital process of the frontal
4	Width of braincase on the level of nuchal crest
5	Total length of premaxilla
6	Distance between the posterior end of the posterior process of the left premaxilla and the anteriormost extension of the anteromedial sulcus of the left premaxilla
7	Distance between the antorbital notches
8	Distance from the right premaxillary foramen to the posteriormost posterolateral process of the right premaxilla
9	Distance from the left premaxillary foramen to the posteriormost posterolateral process of the left premaxilla
10	Length of the right premaxillary sac fossa/plate + nasofrontal sac scars, from the premaxillary foramen to the posteriormost scar of the nasofrontal sac on the maxilla-nasal suture.
11	Length of the right premaxillary sac fossa/plate + nasofrontal sac scars, from the anteriormost point of the premaxillary fossa/plate to the posteriormost scar of the nasofrontal sac on the maxilla-nasal suture.
12	Width of the right premaxillary sac fossa/plate
13	Length of the left premaxillary sac fossa/plate + nasofrontal sac scars, from the premaxillary foramen to the posteriormost scar of the nasofrontal sac on the maxilla-nasal suture.
14	Length of the left premaxillary sac fossa/plate + nasofrontal sac scars, from the anteriormost point of the premaxillary fossa/plate to the posteriormost scar of the nasofrontal sac on the maxilla-nasal suture.
15	Width of the left premaxillary sac fossa/plate
16	Distance between the premaxillary foramina
17	Distance between the posteriormost point of the posterolaterreal sulcus and the anteriorrmost point of the anteromedial sulcus (taken on the left side)

18	Left nasal length, taken anteroposteriorly
19	Right nasal length, taken anteroposteriorly
20	Length of the internasal fossa
21	Width of the internasal fossa
22	Anteroposterior length of the left dorsal opening of the bony naris from the nasal anterior portion to the premaxilla medial portion
23	Anteroposterior length of the right dorsal opening of the bony naris from the nasal anterior portion to the premaxilla medial portion
24	Anteroposterior length of the dorsal opening of the bony naris
25	Maximum width of the dorsal opening of the bony naris on the median portion
26	Width of the dorsal opening of the bony naris on its posterior portion
27	Maximum anteroposterior extension of the right air sinuses, from the anteriormost point of the anterior sinus scar on the maxilla/palatine to the posteriormost portion of the posterior sinus excavation on the paraocciptal
28	Maximum anteroposterior extension of the left air sinuses, from the anteriormost point of the anterior sinus scar on the maxilla/palatine to the posteriormost portion of the posterior sinus excavation on the paraocciptal
29	Length of the left hamular process of the pterygoid
30	Length of the right hamular process of the pterygoid
31	Maximum dorsoventral extension of the right pterygoid sinuses, from the ventralmost point of the pterygoid hamular process to the optic infundibulum dorsally
32	Maximum dorsoventral extension of the left pterygoid sinuses, from the ventralmost point of the pterygoid hamular process to the optic infundibulum dorsally
33	Depth of the left peribullary sinus, from the ventralmost basiocciptal crest to the fenestra oval
34	Depth of the right peribullary sinus, from the ventralmost basiocciptal crest to the fenestra oval
35	Length of the left orbit, distance from the anterorbital to the posterorbital process of the frontal
36	Length of the right orbit, distance from the anterorbital to the posterorbital process of the frontal

37	Length of the left tympano squamosal recess
38	Length of the right tympano squamosal recess
39	Width of the left of the tympano squamosal recess
40	Width of the right of the tympano squamosal recess
41	Maximum depth of the left tympano squamosal recess
42	Maximum depth of the right tympano squamosal recess
43	Depth on the median portion of the left tympano squamosal recess
44	Depth on the median portion of the right tympano squamosal recess
45	Distance from the left posterior sinus until the left pterygoid notch on the basipterygoid hamuli
46	Distance from the right posterior sinus until the right pterygoid notch on the basipterygoid hamuli
47	Thickness of the left basioccipital crest
48	Thickness of the right basioccipital crest
49	Thickness of the basiocciptal at the level of the pterygoid suture
50	Minimum thickness of the basioccptal crest at its edge

Table S3 - Description of the skull measurements taken on the odontocete specimens, 14 measurements of 50 were selected which resulted proxies to infer soft tissue anatomy.

n	Description Measurements	Proxy to:	Related to:
1	Width of braincase on the level of postero-orbital process of the frontal	melon width	focusing the sound beam
6	Distance between the posterior end of the posterior process of the premaxilla and the anteriormost extension of the anteromedial sulcus of the premaxilla	melon length	focusing the sound beam
10	Length of the premaxillary sac fossa/plate + nasofrontal sac scars, from the premaxillary foramen to the posteriormost scar of the nasofrontal sac on the maxilla-nasal suture.	premaxillary sac length	sound directionality (Pilleri and Gihr, 1979)
12	Width of the premaxillary sac fossa/plate	premaxillary sac width	sound directionality (Pilleri and Gihr, 1979)
17	Distance between the posteriormost point of the posterolaterreal sulcus and the anteriorrmost point of the anteromedial suclcus	melon length	focusing the sound beam
18	Left nasal length, taken anteroposteriorly	bursae dimensions	sound producing
19	Right nasal length, taken anteroposteriorly	bursae dimensions	sound producing
22	Anteroposterior length of the dorsal opening of the bony naris	nasal passage	sound amplification
25	Maximun width of the dorsal opening of the bony naris on the median portion	nasal passage	air supply
26	Width of the dorsal opening of the bony naris on its posterior portion	nasal passage	air supply
27	Maximun anteroposterior extension of the air sinuses, from the anteriormost point of the anterior sinus scar on the maxilla/palatine to the posteriormost portion	air sinuses anteroposterior extension	isolation of sound (reception)

	of the posterior sinus excavation on the paraocciptal		
29	Length of the hamular process of the pterygoid	pterygoid air sinuses	isolation of sound (reception)
31	Maximun dorsaventral extension of the pterygoid sinuses, from the ventralmost point of the pterygoid hamular process to the optic infundibulum dorsally	pterygoid air sinuses	isolation of sound (reception)
35	Length of the orbit, distance from the anterorbital to the posterorbital process of the frontal	orbit size	vision

Table S4 - Results of Kruskal-Wallis analysis and post-hoc Man-Whitney test performed on PAST.

	3 environments			**2 environments**
n	Riverine *vs* coastal/estuarine	Riverine *vs* fully marine	Coastal/estuarine *vs* fully marine	Riverine *vs* marine
3	0.000004985	0.01756	0.9795	0.000005659
6	0.0002779	0.0000007197	0.001261	$p < 0.05$
10	-	-	-	-
12	0.0000779	0.03884	0.3645	$p < 0.05$
17	0,009745	0.00006281	0.01385	0.0004104
18	0,001339		0.08675	0.0003879
19	0.001531	0.00151	0.0613	0.0003996
22	$p < 0.05$	$p < 0.05$	-	-
25	0,00008414	0.1255	0.0495	0.0003069
26	-	-	-	-
27	na	na	na	0.00000606
29	na	na	na	0.0004041
31	na	na	na	0.0000002503
35	0.000000000006323	0.0005676	0,6221	0.00000000000454
18 D.I.	-	$p < 0.05$	$p < 0.05$	-

Table S5 - Specimens excluded from univariate analysis (specimens not utilized for each analysis).

Analysis	**description**	**riverine**	**coastal/estuarine**	**fully marine**
35 vs 3 (35 different by environments)	size of orbit	*Inia* sp. UNIRPVLM 005, *Ischyrorhinchus vanbenedeni* MLP 5-16.	*Australithax intermedia* MNHN PPI 65, *Piscolithax longirostris* MNHN SAS 933 *Pliopontos* MNHN PPI 193 *Pontoporia blainvillei* UFSC 1217, *Brachydelphis* (PPI 121) *Goniodelphis hudsoni* MCZ 3920 *Stenasodelphis russelae* CMMV 2234 *Odobenocetops peruvianus* USNM 488252, *Pontistes rectifrons* MACN 3190, *Atocetus iquensis* MNHN PPI 113, 114, 115, 127, *Neophocoena phocaenoides* USNM 240001-240003	*Brachydelphis mazeasi* SGO.PV 746, 748, 749, 968 *Brachydelphis* new form SGO.PV 972 *Pontistes* sp. SGO.PV 751, 1082
6 vs 35	melon length vs size of orbit	*Lipotes vexliffer* USNM 218293, *Inia geoffrensis* IDSM-Ig9515, *Sotalia fluviatilis* IDSM-Sf 9801, *Ischyrorhinchus vanbenedeni* MLP 5-16.	*Goniodelphis hudsoni* MCZ 3920 *Stenasodelphis russelae* CMMV 2234 *Brachydelphis mazeasi* MNHN PPI 124 Pontoporiidae indet. MPC 3037 *Pontoporia blainvillei* UFSC 1217, 1290 *Sotalia guianensis* UFSC 1208, 1219 *Australithax intermedia* MNHN PPI 65 *Lomacetus ginsburgi* MNHN PPI 104 *Atocetus iquensis* MNHN PPI 114	*Brachydelphis mazeasi* SGO.PV 746, 748, 749, 968 *Brachydelphis* new form SGO.PV 972 *Pontistes* sp. MPC 3052, SGO.PV 964, *Schyzodelphis* USNM 11977, *Kentriodon pernix* USNM 171077, *Lophocetus repenningi* USNM 205297, *Lomacetus* MPC 4.

35 i kruskal-wallis		*Lipotes vexliffer* USNM 218293, *Inia geoffrensis* IDSM-Ig9515, *Sotalia fluviatilis* IDSM-Sf 9801, *Ischyrorhinchus vanbenedeni* MLP 5-16, *Inia* sp. UNIRPVLM 005	*Goniodelphis hudsoni* MCZ 3920 *Stenasodelphis russelae* CMMV 2234 *Brachydelphis mazeasi* MNHN PPI 124 Pontoporiidae indet. MPC 3037 *Pontoporia blainvillei* UFSC 1217, 1290 *Pontistes rectifrons* MACN 3190, *Pliopontos littoralis* MNHN SAS 953, PPI 931 *Sotalia guianensis* UFSC 1208, 1219 *Australithax intermedia* MNHN PPI 65 *Lomacetus ginsburgi* MNHN PPI 104 *Atocetus iquensis* MNHN PPI 114 *Neophocoena phocaenoides* USNM 240001, *Odobenocetops peruvianus* USNM 488252	aff. *Piscolithax* MPC 229, *Pontistes* sp. SGO.PV 751, 1082
17 vs 3	kruskal wallis and comparison	*Inia geoffrensis* IDSM-Ig9515, *Sotalia fluviatilis* IDSM-Sf 9801, *Ischyrorhinchus vanbenedeni* MLP 5-16.	*Goniodelphis hudsoni* MCZ 3920, *Pontoporia blainvillei* UFSC 1217, 1290, *Pontistes rectifrons* MACN 3190, Pontoporiidae indet. MPC 3037, *Stenasodelphis russelae* CMMV 2234, *Brachydelphis mazeasi* MNHN PPI 121, 124, *Atocetus iquensis* MNHN PPI 114, 115	*Brachydelphis mazeasi* SGO.PV 746, 748, 749, 968 *Brachydelphis* new form SGO.PV 972 *Pontistes* sp. MPC 3052, SGO.PV 964, *Schyzodelphis* USNM 11977, *Kentriodon pernix* USNM 171077, *Lophocetus repenningi* USNM 205297,

				Lomacetus MPC 4.
17 Kruskal-wallis		*Inia geoffrensis* IDSM-Ig9515,	*Goniodelphis hudsoni* MCZ 3920, *Pontistes rectifrons* MACN 3190, *Stenasodelphis russelae* CMMV 2234, *Brachydelphis mazeasi* MNHN PPI 121, 124, *Pontoporia blainvillei* UFSC 1217, 1290, Pontoporiidae indet. MPC 3037, *Atocetus iquensis* MNHN PPI 113, 114, 115, 127	*Pontistes* sp. MPC 3052, SGO.PV 964, *Brachydelphis mazeasi* SGO.PV 746, 748, 749, 968, *Brachydelphis* new form SGO.PV 972 *Schyzodelphis* USNM 11977, *Kentriodon pernix* USNM 171077, *Lophocetus repenningi* USNM 205297, aff. *Lomacetus* MPC 4.
25 vs 26		*Sotalia fluviatilis* IDSM Sf 9801	*Brachydelphis mazeasi* MNHN PPI 121, 124, *Piscolithax longirostris* MNHN SAS 933 *Pontistes rectifrons* MACN 3190, *Atocetus iquensis* MNHN PPI 113, 114, 115 *Pliopontos littoralis* MNHN PPI 931, 193, SAS 953 *Lomacetus ginsburgi* MNHN PPI 104 *Australithax intermedia* MNHN PPI 65	*Kentriodon pernix* USNM 171077, aff. *Lomacetus* MPC 4, *Brachydelphis mazeasi* SGO.PV 748, puneadoazul, 749, 972, *Lophocetus repenningi* USNM 15985, 205297, *Pontistes* MPC 1082,
25 vs 24	anteriores +	*Sotalia fluviatilis* IDSM Sf 9801, *Platanista gangetica* USNM 172409	*Goniodelphis hudsoni* MCZ 3920, *Brachydelphis mazeasi* MNHN PPI 121, 124, *Piscolithax longirostris* MNHN SAS 933	*Brachydelphis mazeasi* SGO.PV 748, puneadoazul, 749, 972, *Pontistes* MPC

			Pontistes rectifrons MACN 3190, *Atocetus iquensis* MNHN PPI 113, 114, 115 *Pliopontos littoralis* MNHN PPI 931, 193, SAS 953 *Lomacetus ginsburgi* MNHN PPI 104 *Australithax intermedia* MNHN PPI 65	1082, *Kentriodon pernix* USNM 171077, *Lophocetus repenningi* USNM 15985, 205297, aff. *Piscolithax* MPC 229, aff. *Lomacetus* MPC 4,
2 environmental groups		riverine:	marine:	
17		*Inia geoffrensis* IDSM-Ig 9515, *Sotalia fluviatilis* IDSM-Sf 9801, *Ischyrorhinchus vanbenedeni* MLP 5-16.	*Goniodelphis hudsoni* MCZ 3920, *Pontistes rectifrons* MACN 3190, *Stenasodelphis russelae* CMMV 2234, *Brachydelphis mazeasi* MNHN PPI 121, 124, *Pontoporia blainvillei* UFSC 1217, 1290, Pontoporiidae indet. MPC 3037, *Pontistes* sp. MPC 3052, SGO.PV 964, *Brachydelphis mazeasi* SGO.PV 746, 748, 749, 968, *Brachydelphis* new form SGO.PV 972 *Schyzodelphis* USNM 11977, *Atocetus iquensis* MNHN PPI 114, 115, *Kentriodon pernix* USNM 171077, *Lophocetus repenningi* USNM 205297, aff. *Lomacetus* MPC 4.	na

SI. 3. References

Achurra, L. E. 2004. Cambios del nivel del mar y evolución tectónica de la cuenca neógena de Caldera, III Región. Unpublished M.S. thesis, Universidad de Chile, Santiago, Chile, 138 pp.

Achurra, L. E., J. P. Lacassie, J. P. Le Roux, C. Marquardt, M. Belmar, J. Ruiz-del-Solar, and S. E. Ishman. 2009. Manganese nodules in the Miocene Bahía Inglesa Formation, north-central Chile: Petrography, geochemistry, genesis and palaeoceanographic significance. Sedimentary Geology 217:128–139.

Allen, G. M. 1941. A fossil river dolphin from Florida. Bulletin of the Museum of Comparative Zoology at Harvard University 89:3-11.

Au, W.W.L., Kastelein, R.A., Rippe, T. & Schooneman, N.M. 1999. Transmission beam pattern and echolocation signals of a harbor porpoise (Phocoena phocoena). J. Acoust. Soc. Am. 106: 3699–3705.

Au, W. W. L., R. A. Kastelein, K. J. Benoit-Bird, T. W. Cranford, and M. F. McKenna. 2006. Acoustic radiation from the head of echolocating harbor porpoises (Phocoena phocoena). Journal of Experimental Biology 209:2726-2733.

Best, R. C., and V. M. F. da Silva. 1993. Inia geoffrensis. Mammalian Species 1.

Cione, A. L., J. R. Casciotta, M. Azpelicueta, M. J. Barla, and M. A. Cozzuol. 2005. Peces marinos y continentales del Mioceno del área mesopotámica argentina. Edad y relaciones biogeográficas. Historia 14:49 - 64.

Cozzuol, M. A. 1985. The Odontoceti of the Mesopotamiense of the Parana River ravines. Systematic review. Investigations on Cetacea VII:39-51, 2 plates.

Cozzuol, M. A. 1996. The record of aquatic mammals in southern South America. Munchner Geowissenschaftliche Abhandlungen 30321^342.

Cozzuol, M. A., and Silva, V. M. F. 1996. Un Registro de Inia sp fósil del Pleistoceno tardio-Holoceno del alto Rio Madeira, Rondonia, Brasil. In: 7° Reunión de Trabajos de Especialistas en Mamíferos Aquáticos de América del Sur, Resúmenes VII REUNION DE TRABAJOS DE ESPECIALISTAS EN MAMIFEROS ACUATICOS DE AMERICA DEL SUR Vinña del Mar, Chile.

Cozzuol, M. A. 2010. Fossil record and the evolutionary history of Iniodea; pp. 193–217 in M. Ruiz-Garcıa and J. Shostell (eds.), Biology Evolution and Conservation of River Dolphins within SouthAmer- ica andAsia. Nova Science Publishers, New York.

Cremer, M. J., and P. C. Simões-lopes. 2008. Distribution, abundance and density estimates of franciscanas, Pontoporia blainvillei (Cetacea: Pontoporiidae), in Babitonga bay, southern Brazil. Revista Brasileira De Zoologia 25:397-402.

Cremer, M. J., F. A. S. Hardt, A. J. J. Tonello, and P. C. Simões-lopes. 2011. Distribution and Status of the Guiana Dolphin. Zoological Studies 50:327-337.

Del Río, C.J. 1988. Bioestratigrafía y cronoestratigrafía de la Formación Puerto Madryn (Mioceno Medio). Provincia del Chubut-Argentina. Anales de la Acade- mia Nacional de Ciencias Exactas, Físicas y Naturales 40: 231-254.

Del Río, C.J. 2000. Malacofauna de las formaciones Paraná y Puerto Madryn (Mioceno marino, Argentina): su origen, composición y significado bioestratigráfico. In El Neógeno de Argentina (Aceñolaza, F.G.; Herbst, R.; editores). Serie Correlación Geológica 14: 77-101. Tucumán.

DeVries, T. J. 1998. Oligocene deposition and Cenozoic sequence boundaries in the Pisco Basin (Peru). Journal of South American Earth Sciences 11:217-231.

Heyning, J. E. and J. G Mead. 1990. Evolution of the nasal anatomy of cetaceans. Pp. 67-79 *in* J. Thomas and R. Kastelein (eds) *Sensory abilities of cetaceans*. Plenum, New York.

Hubert, N. y Renno, J.F. 2006. Historical biogeography of South American freshwater fishes. Journal of Biogeography 33: 1414-1436.

Herbst, R. y Zabert, L.L. 1987. Microfauna de la Formación Paraná (Mioceno Superior) de la cuenca Chaco-Paranaense (Argentina). Facena 7: 165-206.

Kirby, M. X. 2001. Differences in growth rate and environment between Tertiary and Quaternary Crassostrea oysters. Paleobiology 27:84-103.

May-Collado, L. J., and D. Wartzok. 2010. Sounds produced by the tucuxi (Sotalia fluviatilis) from the Napo and Aguarico rivers of Ecuador. Latin American Journal of Aquatic Mammals 8:131-136.

Morgan, G.S. 1994. Miocene and Pliocene marine mammal faunas from the Bone Valley formation of central Florida. Proc. San Diego Soc. Nat. Hist. 29:239-268

Muizon, C. D. 1983. Pliopontos littoralis un nouveau Platanistidae Cetacea du Pliocene de la cote peruvienne. C. R. Acad. Sc. Paris 296:1101-1104.

Muizon, C. D. 1984. Les vertebres fossiles de la formation pisco (perou), Deuxieme partie: Les Odontocetes (Cetacea, Mammalia) du Pliocene inferieur de Sud-Sacaco. Recherche Sur Les Civilisations 50.

Muizon, C. D. 1988. Les vertébrés fossiles de la Formation Pisco (Pérou). Troisième partie: Les odontocètes (Cetacea, Mammalia) miocènes. Travaux

De l'Institut Français d'É-tudes Andines 42:1–244.

Pilleri, G. E., and M. Gihr. 1977. Observations on the Bolivian (Inia boliviensis d'Orbigny 1834) and the Amazonean Bufeo (Inia geoffrensis de Blainville 1817), with description of a new subspecies (Inia geoffrensis humboldtiana). Investigations on Cetacea 10:11-76.

Pilleri, G. and M. Gihr. 1979. Skull, sonar field and swimming behaviour of *Ischyrorhynchus vanbenedeni* (Ameghino 1891) and taxonomical position of the genera *Ischyrorhynchus*, *Saurodelphis*, *Anisodelphis* and *Pontoplanodes. Investigations on Cetacea*, 10: 17-70.

Quadros, M.L., Rizzotto, G.J., Oliveira, J.G., & Castro, J.M. 2006. Depósitos Fluviais da Formação Rio Madeira, Pleistoceno Superior da Bacia do Abunã, Rondônia . *Simpósio de Geologia da Amazônia, IX, Anais, CD*

Sauerland, M., and G. Dehnhardt. 1998. Underwater audiogram of a tucuxi (Sotalia fluviatilis guianensis). The Journal of the Acoustical Society of America 103:1199-204.

Shirihai, H., and B. Jarret. 2009. Whales, Dolphins and Seals. A Guide to the Marine Mammals of the World. A&C Black Publishers, London, 384pp.

Simoes-Lopes P.C. (1988) Ocorreencia de uma populacao de Sotalia fluviatilis Gervais, 1853, (Cetacea, Delphinidae) no limite sul de sua distribuicao, Santa Catarina, Brasil. Biotemas 1, 57–62.

Thor, D. R. 1978. Depositional environments and paleogeo- graphic setting of the Santa Margarita Formation, Ventura County, California. In A. E. Fritsche, ed. Depositional environments of Tertiary rocks along Sespe Creek, Ventura Coun- ty, California. Pacific Coast Paleogeography FieldGuide 3:42– 59. Pacific Section, Society of Economic Paleontologists and Mineralogists, Los Angeles.

Visaggi, C. C., and S. J. Godfrey. 2010. Variation in composition and abundance of Miocene shark teeth from Calvert Cliffs, Maryland. Journal of Vertebrate Paleontology 30:26-35.

Von Fersen, L., Kamminga, L.C. & Seidl, A. 2000. Estudios preliminares sobre el comportamiento de un ejemplar de Franciscana (Pontoporia blainvillei) en Mundo Marino, Argentina. In: Report of the Third Workshop for Coordinated Research and Conservation of the Franciscana Dolphin (Pontoporia blainvillei) in the Southwestern Atlantic (UNEP/ CMS, ed), pp. 30–33. UNEP/CMS Secretariat, Bonn (in Spanish).

Ward, L. 2008 In gelogy and Paleontology of lee creek mine

Wedekin, L. L., F. G. Daura-Jorge, and P. C. Simões-Lopes. 2007. Seasonal variations in spatial usage by the estuarine dolphin, Sotalia guianensis (Cetacea, Delphinidae) at its southern limit of distribution. Brazilian Journal of Biology 67, 1–8.

Wedekin, L. L., F. G. Daura-Jorge, and P. C. Simões-Lopes. 2010. Habitat preferences of Guiana dolphins, Sotalia guianensis (Cetacea: Delphinidae), in Norte Bay, southern Brazil. Journal of the Marine Biological Association of the United Kingdom 90:1561-1570.

Tabla S1 - Taxa and specimens (skulls) classification of taxonomic, age and environmental groups.

Superfamily	Family	Species	Specimen type	Localidad	Formation	TL	Geologic age/ epoch/stage	Geological Age groups e group	second analysis	habitat preference/ paleoenvironment	Environmental grc	Sex	Acronimo	#	References
Platanistoidea	Platanistidae	*Platanista gangetica*	assigned in collections	Indus river, India	-		Holocene	0		riverine	riverine	IS	USNM	A23456	Reeves et al. 2002, Shirihai and Jarrett, 2006
Platanistoidea	Platanistidae	*Platanista gangetica*	assigned in collections	Indus river, India	-		Holocene	0		riverine	riverine	M	USNM	172409	Reeves et al. 2002, Shirihai and Jarrett, 2006
Platanistoidea	Platanistidae	*Platanista indi*	assigned in collections	Indus river, India	-		Holocene	0		riverine	riverine		BMNH	1646.a. 14.4134	Reeves et al. 2002, Shirihai and Jarrett, 2006
Platanistoidea	Platanistidae	*Platanista gangetica*	assigned in collections	R. Hughhi, near Botanical Gardens	-		Holocene	0		riverine	riverine		BMNH	1874.6.1.1 – 344b	Reeves et al. 2002, Shirihai and Jarrett, 2006
Platanistoidea	Platanistidae	*Platanista gangetica*	assigned in collections	Ganges river, India	-		Holocene	0		riverine	riverine		BMNH	1895.5.20.2	Reeves et al. 2002, Shirihai and Jarrett, 2006
Lipotoidea	Lipotidae	*Lipotes vexilliffer*	assigned in collections	Tung Ting Lake, China	-		Holocene	0		riverine	riverine	M	USNM	218293	Reeves et al. 2002, Shirihai and Jarrett, 2006
Lipotoidea	Lipotidae	*Lipotes vexliffer*	assigned in collections	Yang Tsé river, China	-		Holocene	0		riverine	riverine		BMNH	1922.b.22.1	Reeves et al. 2002, Shirihai and Jarrett, 2006
Inioidea	Stem-Inioidea	*Brachydelphis mazeasi*	assigned specimen (Gutstein et al. 2009)	Caldera, Región de Atacama, Chile	Bahía Inglesa Fm.		late Miocene	4		deep marine to shoreface	fully marine	IS	SGOPV	746	Achurra, 2004, Achurra et al. 2009
Inioidea	Stem-Inioidea	*Brachydelphis mazeasi*	assigned specimen (Gutstein et al. 2009)	Caldera, Región de Atacama, Chile	Bahía Inglesa Fm.		late Miocene	4		deep marine to shoreface	fully marine	IS	SGOPV	750	Achurra, 2004, Achurra et al. 2009
Inioidea	Stem-Inioidea	*Brachydelphis mazeasi*	assigned specimen (Gutstein et al. 2009)	Caldera, Región de Atacama, Chile	Bahía Inglesa Fm.		late Miocene	4		deep marine to shoreface	fully marine	IS	SGOPV	748	Achurra, 2004, Achurra et al. 2009
Inioidea	Stem-Inioidea	*Brachydelphis mazeasi*	assigned specimen (Gutstein et al. 2009)	Caldera, Región de Atacama, Chile	Bahía Inglesa Fm.	-	late Miocene	4		deep marine to shoreface	fully marine	IS	MPC	MPC S/N punt azu	Achurra, 2004, Achurra et al. 2009
Inioidea	Stem-Inioidea	*Brachydelphis mazeasi*	assigned specimen (Gutstein et al. 2009)	Caldera, Región de Atacama, Chile	Bahía Inglesa Fm.		late Miocene	4		deep marine to shoreface	fully marine	IS	SGOPV	747	Achurra, 2004, Achurra et al. 2009
Inioidea	Stem-Inioidea	*Brachydelphis mazeasi*	assigned specimen (Gutstein et al. 2009)	Caldera, Región de Atacama, Chile	Bahía Inglesa Fm.		late Miocene	4		deep marine to shoreface	fully marine	IS	SGOPV	968	Achurra, 2004, Achurra et al. 2009
Inioidea	Stem-Inioidea	*Brachydelphis mazeasi*	assigned specimen (Gutstein et al. 2009)	Caldera, Región de Atacama, Chile	Bahía Inglesa Fm.		late Miocene	4		deep marine to shoreface	fully marine	IS	SGOPV	749	Achurra, 2004, Achurra et al. 2009
Inioidea	Stem-Inioidea	*Brachydelphis mazeasi*	holotype	Cerro la Bruja, Ica, Perú	Pisco Fm.		middle Miocene	5		epicontinental sea	coastal/estuarine	IS	MNHN	PPI 121	Muizon 1983, DeVries, 1998
Inioidea	Stem-Inioidea	*Brachydelphis mazeasi*	paratype	Cerro la Bruja, Ica, Perú	Pisco Fm.		middle Miocene	5		epicontinental sea	coastal/estuarine	IS	MNHN	PPI 124	Muizon 1983, DeVries, 1998
Inioidea	Stem-Inioidea	*Brachydelphis new form*	assigned specimen (Gutstein et al. 2009)	Caldera, Región de Atacama, Chile	Bahía Inglesa Fm.		late Miocene	4		deep marine to shoreface	fully marine	IS	SGOPV	1109	Achurra, 2004, Achurra et al. 2009
Inioidea	Stem-Inioidea	*Brachydelphis new form*	assigned specimen (Gutstein et al. 2009)	Caldera, Región de Atacama, Chile	Bahía Inglesa Fm.		late Miocene	4		deep marine to shoreface	fully marine	IS	SGOPV	972	Achurra, 2004, Achurra et al. 2009
Inioidea	incertae sedis	*Goniodelphis hudsoni*	holotype	American Agricultural Chemical Company Mine, Polk Coun	Bone Valley Fm.		middle Miocene-e	5 – 3		epicontinental sea	coastal/estuarine	IS	MCZ	3920	Allen 1941, Morgan 1994, Cozzuol, 2010
Inioidea	Iniidae	*Ischyrorhynchus vanbenedeni*	assigned specimen (Burmeister, 1891, 1892, Pilleri and Gihr, 1979; Cozz	La Curtiembre, Entre Ríos, Argentina	Ituzaingó Fm.		late Miocene	4		fluvial system	riverine	IS	MLP	MLP 5- 16	Pilleri and Gihr, 1979, Cozzuol, 1996, Cione et al. 2005
Inioidea	Iniidae	*Ischyrorhynchus vanbenedeni*	assigned specimen (Burmeister, 1891, 1892, Pilleri and Gihr, 1979; Cozz	Entre Ríos, Argentina	Ituzaingó Fm.		late Miocene	4		fluvial system	riverine	IS	MACN	15135	Pilleri and Gihr, 1979, Cozzuol, 1996, Cione et al. 2005
Inioidea	Iniidae	*Inia* sp. nov.	assigned specimen (Cozzuol and Silva, 1996; Cozzuol, 2010)	Araras, Nova Mamoré, Rondonia, Brazil	Rio Madeira Fm.	-	Pleistocene	1		fluvial system	riverine	IS	UNIR-PLV-	M005	Quadros et al. 2006
Inioidea	Iniidae	*Inia geoffrensis*	assigned in collections	Praia do Pirarara	-	160 cm	Holocene	0		riverine, flooded forest	riverine	F	IDSM	Ig 9403	Shirihai and Jarrett, 2006, Best and da Silva, 1993, Pilleri and Gihr, 1977
Inioidea	Iniidae	*Inia geoffrensis*	assigned in collections	Comuidade do Jarauá	-	212 cm	Holocene	0		riverine, flooded forest	riverine	F?	IDSM	Ig 9301	Shirihai and Jarrett, 2006, Best and da Silva, 1993, Pilleri and Gihr, 1977
Inioidea	Iniidae	*Inia geoffrensis*	assigned in collections	Ressaca Iuirí (Mamirauá)	-	231 cm	Holocene	0		riverine, flooded forest	riverine	M	IDSM	Ig 9404	Shirihai and Jarrett, 2006, Best and da Silva, 1993, Pilleri and Gihr, 1977
Inioidea	Iniidae	*Inia geoffrensis*	assigned in collections	Lago de Tefé, Tefe, Amazonas, North Brazil	-	202 cm	Holocene	0		riverine, flooded forest	riverine	F	IDSM	Ig 9505	Shirihai and Jarrett, 2006, Best and da Silva, 1993, Pilleri and Gihr, 1977
Inioidea	Iniidae	*Inia geoffrensis*	assigned in collections	Lago de Tefé, Tefe, Amazonas, North Brazil	-	191 cm	Holocene	0		riverine, flooded forest	riverine	F	IDSM	Ig 9516	Shirihai and Jarrett, 2006, Best and da Silva, 1993, Pilleri and Gihr, 1977
Inioidea	Iniidae	*Inia geoffrensis*	assigned in collections	Parana de Tefé, Tefé, Amazonas, North Brazil	-	218 cm	Holocene	0		riverine, flooded forest	riverine	M	IDSM	Ig 2001-01	Shirihai and Jarrett, 2006, Best and da Silva, 1993, Pilleri and Gihr, 1977
Inioidea	Iniidae	*Inia geoffrensis*	assigned in collections	Lago Caruara, Tefé, Amazonas, North Brazil	-	200 cm	Holocene	0		riverine, flooded forest	riverine	M	IDSM	Ig 2002-01	Shirihai and Jarrett, 2006, Best and da Silva, 1993, Pilleri and Gihr, 1977
Inioidea	Iniidae	*Inia geoffrensis*	assigned in collections	Sao Jose do Urini Rosa, Tefé, Amazonas, North Brazil	-	12 palm	Holocene	0		riverine, flooded forest	riverine	IS	IDSM	Ig 2005-03	Shirihai and Jarrett, 2006, Best and da Silva, 1993, Pilleri and Gihr, 1977
Inioidea	Iniidae	*Inia geoffrensis*	assigned in collections	Comunidade do Caburini,Tefé, Amazonas, North Brazil	-	182,5 cr	Holocene	0		riverine, flooded forest	riverine	F	IDSM	Ig 9601	Shirihai and Jarrett, 2006, Best and da Silva, 1993, Pilleri and Gihr, 1977
Inioidea	Iniidae	*Inia geoffrensis*	assigned in collections	Juazinho RDSA, Tefé, Amazonas, North Brazil	-	150 cm	Holocene	0		riverine, flooded forest	riverine	?	IDSM	Ig 2005-01	Shirihai and Jarrett, 2006, Best and da Silva, 1993, Pilleri and Gihr, 1977
Inioidea	Iniidae	*Inia geoffrensis*	assigned in collections	Lago de Tefé, Tefe, Amazonas, North Brazil	-	133 cm	Holocene	0		riverine, flooded forest	riverine	F?	IDSM	Ig 9515	Shirihai and Jarrett, 2006, Best and da Silva, 1993, Pilleri and Gihr, 1977
Inioidea	Iniidae	*Inia geoffrensis*	assigned in collections	Boca do Igarapé Acú, Tefé, Amazonas, North Brazil	-	230 cm	Holocene	0		riverine, flooded forest	riverine	M	IDSM	Ig 2008-02	Shirihai and Jarrett, 2006, Best and da Silva, 1993, Pilleri and Gihr, 1977
Inioidea	Iniidae	*Inia geoffrensis*	assigned in collections	Boca do Igarapé Acú, Tefé, Amazonas, North Brazil	-	225 cm	Holocene	0		riverine, flooded forest	riverine	F?	IDSM	Ig 2006-01	Shirihai and Jarrett, 2006, Best and da Silva, 1993, Pilleri and Gihr, 1977
Inioidea	Iniidae	*Inia geoffrensis*	assigned in collections	Ponta do gato, proximo a calafate (RDSA), Tefé, Amazonas	-	205 cm	Holocene	0		riverine, flooded forest	riverine	F	IDSM	Ig 2007-06	Shirihai and Jarrett, 2006, Best and da Silva, 1993, Pilleri and Gihr, 1977
Inioidea	Iniidae	*Inia geoffrensis*	assigned in collections	Cano do lago Mamirauá, Tefé, Amazonas, North Brazil	-	202 cm	Holocene	0		riverine, flooded forest	riverine	F	IDSM	Ig 9602	Shirihai and Jarrett, 2006, Best and da Silva, 1993, Pilleri and Gihr, 1977
Inioidea	Iniidae	*Inia geoffrensis*	assigned in collections	Praia das conchas, Tefé, Amazonas, North Brazil	-	207 cm	Holocene	0		riverine, flooded forest	riverine	?	IDSM	Ig 2005-06	Shirihai and Jarrett, 2006, Best and da Silva, 1993, Pilleri and Gihr, 1977
Inioidea	Iniidae	*Inia geoffrensis*	assigned in collections	Rio San Fernando De Apure, Venezuela	-	142 cm	Holocene	0		riverine, flooded forest	riverine	F	USNM	395416	Shirihai and Jarrett, 2006, Best and da Silva, 1993, Pilleri and Gihr, 1977
Inioidea	Iniidae	*Inia geoffrensis*	assigned in collections	Formoso do Araguaia, Goias, Brasil	-	-	Holocene	0		riverine, flooded forest	riverine	IS	MCN-M	32-01	Shirihai and Jarrett, 2006, Best and da Silva, 1993, Pilleri and Gihr, 1977
Inioidea	Iniidae	*Inia geoffrensis*	assigned in collections	Formoso do Araguaia, Goias, Brasil	-	-	Holocene	0		riverine, flooded forest	riverine	M	MCN-M	89-01	Shirihai and Jarrett, 2006, Best and da Silva, 1993, Pilleri and Gihr, 1977
Inioidea	Iniidae	*Inia geoffrensis*	assigned in collections	Formoso do Araguaia, Goias, Brasil	-	-	Holocene	0		riverine, flooded forest	riverine	IS	MCN-M	152-01	Shirihai and Jarrett, 2006, Best and da Silva, 1993, Pilleri and Gihr, 1977
Inioidea	Pontoporiidae	*Pontistes* sp.	assigned specimen, Gutstein et al. 2008, Gutstein and Valenzuela-Toro (	Caldera, Región de Atacama, Chile	Bahía Inglesa Fm.		late Miocene	4		deep marine to shoreface	fully marine	IS	MPC	3052	Achurra, 2004, Achurra et al. 2009
Inioidea	Pontoporiidae	*Pontistes* sp.	assigned specimen, Gutstein et al. 2008, Gutstein and Valenzuela-Toro (	Caldera, Región de Atacama, Chile	Bahía Inglesa Fm.		late Miocene	4		deep marine to shoreface	fully marine	SI	SGOPV	964	Achurra, 2004, Achurra et al. 2009
Inioidea	Pontoporiidae	*Pontistes* sp.	assigned specimen, Gutstein et al. 2008, Gutstein and Valenzuela-Toro (	Caldera, Región de Atacama, Chile	Bahía Inglesa Fm.		late Miocene	4		deep marine to shoreface	fully marine	SI	SGOPV	1082	Achurra, 2004, Achurra et al. 2009
Inioidea	Pontoporiidae	*Pontistes* sp.	assigned specimen, Gutstein et al. 2008, Gutstein and Valenzuela-Toro (	Caldera, Región de Atacama, Chile	Bahía Inglesa Fm.		late Miocene	4		deep marine to shoreface	fully marine	SI	SGOPV	751	Achurra, 2004, Achurra et al. 2009
Inioidea	Pontoporiidae	*Pontistes rectifrons*	holotype	Entre Ríos, Argentina	Paraná Fm.		late Miocene	4		shallow marine tidally influenced	coastal/estuarine	IS	MACN	3190	Cozzuol, 1996, Cozzuol 1987; Herbst y Zabert (1987), Del Rio et al 1988, 2001; Hubert and Reno 2006, Cione et al. 2005

Skull measurements

Skull measurements

Inioidea	**Pontoporiidae**	*Pliopontos littoralis*	paratype	Sud Sacaco, Ica, Perú	Pisco Fm.		early Pliocene	3		epicontinental sea	coastal/estuarine	IS	MNHN	SAS953	Muizon 1983, 1984
Inioidea	**Pontoporiidae**	*Pliopontos littoralis*	holotype	Sud Sacaco, Ica, Perú	Pisco Fm.		early Pliocene	3		epicontinental sea	coastal/estuarine	IS	MNHN	PPI931	Muizon 1983, 1984
Inioidea	**Pontoporiidae**	*Pliopontos littoralis*	paratype	Sud Sacaco, Ica, Perú	Pisco Fm.		early Pliocene	3		epicontinental sea	coastal/estuarine	IS	MNHN	PPI193	Muizon 1983, 1984
Inioidea	**Pontoporiidae**	*Pliopontos* sp.	asigned specimen, Gutstein et al. 2008, Gutstein and Valenzuela-Toro (a	Caldera, Región de Atacama, Chile	Bahía Inglesa Fm.		late Miocene	4		deep marine to shoreface	fully marine	IS	MPC	302	Achurra, 2004, Achurra et al. 2009
Inioidea	**Pontoporiidae**	*Pliopontos* sp.	asigned specimen, Gutstein et al. 2008, Gutstein and Valenzuela-Toro (a	Caldera, Región de Atacama, Chile	Bahía Inglesa Fm.		late Miocene	4		deep marine to shoreface	fully marine	IS	MPC	3034	Achurra, 2004, Achurra et al. 2009
Inioidea	**Pontoporiidae**	*Pontoporidae* indet.	asigned specimen, Gutstein et al. 2008, Gutstein and Valenzuela-Toro (a	Caldera, Región de Atacama, Chile	Bahía Inglesa Fm.		late Miocene	4		deep marine to shoreface	fully marine	IS	MPC	3037	Achurra, 2004, Achurra et al. 2009
Inioidea	**Pontoporiidae**	*Stenasodelphis russelae*	holotype	Litle Cove Point, Maryland, USA	Saint Marys Fm.		early late Miocene	4		marine shelf to tidally influenced	coastal/estuarine	IS	CMM	V2234	Barnes and Godfrey 2008, Kidwell 1997, Visaggi and Godfrey 2010, Ward 2008
Inioidea	**Pontoporiidae**	*Pontoporia blainvillei*	asigned in collections	praia Mocambique, Florianopolis, SC – South Brazil	-	127 cm	Holocene	0		coastal, estuarine, bay	coastal/estuarine	F	UFSC	1290	Shirihai and Jarrett, 2006, Cremer and Simoes-Lopes, 2005
Inioidea	**Pontoporiidae**	*Pontoporia blainvillei*	asigned in collections	Cabo de santa marta grande, Laguna, SC – South Brazil	-	156 cm	Holocene	0		coastal, estuarine, bay	coastal/estuarine	F	UFSC	1217	Shirihai and Jarrett, 2006, Cremer and Simoes-Lopes, 2005
Inioidea	**Pontoporiidae**	*Pontoporia blainvillei*	asigned in collections	Cachoeira do Bom Jesus, Florianopolis, SC – South Brazil	-	-	Holocene	0		coastal, estuarine, bay	coastal/estuarine	F	UFSC	1310	Shirihai and Jarrett, 2006, Cremer and Simoes-Lopes, 2005
Inioidea	**Pontoporiidae**	*Pontoporia blainvillei*	asigned in collections	Cabo de santa marta, Laguna, SC – South Brazil	-	102 cm	Holocene	0		coastal, estuarine, bay	coastal/estuarine	M	UFSC	1215	Shirihai and Jarrett, 2006, Cremer and Simoes-Lopes, 2005
Inioidea	**Pontoporiidae**	*Pontoporia blainvillei*	asigned in collections	Cabo de santa marta, Laguna, SC – South Brazil	-	139 cm	Holocene	0		coastal, estuarine, bay	coastal/estuarine	F	UFSC	1216	Shirihai and Jarrett, 2006, Cremer and Simoes-Lopes, 2005
Inioidea	**Pontoporiidae**	*Pontoporia blainvillei*	asigned in collections	Praia de Mocambique, Florianopolis, SC – South Brazil	-	-	Holocene	0		coastal, estuarine, bay	coastal/estuarine	IS	UFSC	1046	Shirihai and Jarrett, 2006, Cremer and Simoes-Lopes, 2005
Inioidea	**Pontoporiidae**	*Pontoporia blainvillei*	asigned in collections	Cabo de santa marta, Laguna, SC – South Brazil	-	136 cm	Holocene	0		coastal, estuarine, bay	coastal/estuarine	M	UFSC	1214	Shirihai and Jarrett, 2006, Cremer and Simoes-Lopes, 2005
Inioidea	**Pontoporiidae**	*Pontoporia blainvillei*	asigned in collections	Praia dos Ingleses, Florianopolis, SC – South Brazil	-	-	Holocene	0		coastal, estuarine, bay	coastal/estuarine	IS	UFSC	1037	Shirihai and Jarrett, 2006, Cremer and Simoes-Lopes, 2005
Delphinoidea	Kentriodontidae	*Kentriodon sp.*	asigned specimen (Muizon 1988)	Westmorelandi County, Virginia, USA	Calvert Fm.		early-middle Mioc	6 – 5		shallow marine to neritic	fully marine	IS	USNM	317882	Ward 2008, Visaggi and Godfrey 2010
Delphinoidea	Kentriodontidae	*Kentriodon pernix*	asigned specimen (present work)	Virginia, USA	Calvert Fm.		early-middle Mioc	6 – 5		shallow marine to neritic	fully marine	IS	USNM	171077	Ward 2008, Visaggi and Godfrey 2010
Delphinoidea	Kentriodontidae	*Delphinodon dividum*	holotype	Calvert County, Maryland, USA	Calvert Fm.		early-middle Mioc	6 – 5		shallow marine to neritic	fully marine	IS	USNM	V7278	Ward 2008, Visaggi and Godfrey 2010
Delphinoidea	Kentriodontidae	*Lophocetus repenningi*	holotype	California, USA	Santa Margarita Fm.		early late Miocene	4		shallow fully marine	fully marine	IS	USNM	V23886	Barnes, 1978, Kirby, 2001
Delphinoidea	Kentriodontidae	*Lophocetus repenningi*	Lophocetus repenningi Mitchell	Calvert County, Maryland, USA	Calvert Fm.		early-middle Mioc	6 – 5		shallow marine to neritic	fully marine	IS	USNM	205297	Ward 2008, Visaggi and Godfrey 2010
Delphinoidea	Kentriodontidae	*Lophocetus pappus*	holotype	Calvert County, Maryland, USA	Calvert Fm.		early-middle Mioc	6 – 5		shallow marine to neritic	fully marine	IS	USNM	15985	Ward 2008, Visaggi and Godfrey 2010
Delphinoidea	Kentriodontidae	*Lophocetus calvertensis*	holotype	Calvert County, Maryland, USA	St. Mary's Fm.	c	early late Miocene	4		marine shelf to tidally influenced	coastal/estuarine	IS	USNM	V16314	Barnes, 1978, Kidwell 1997, Ward, 2008, Visaggi and Godfrey 2010
Delphinoidea	Kentriodontidae	*Hadrodelphis calvertensis*	holotype	Dawson 1996	Calvert Fm.		early-middle Mioc	6 – 5		shallow marine to neritic	fully marine	IS	CMM	V11	Ward 2008, Visaggi and Godfrey 2010
Delphinoidea	Kentriodontidae	*Schyzodelphis?*	Schyzodelphis crassangulum (Case)	Calvert County, Maryland, USA	Calvert Fm.		early-middle Mioc	6 – 5		shallow marine to neritic	fully marine	IS	USNM	V11977	Ward 2008, Visaggi and Godfrey 2010
Delphinoidea	Kentriodontidae	Kentriodontidae indet.	preguntar NICK o DAVE		missing data on catalog			?					USNM	547211	missing data on catalog
Delphinoidea	Kentriodontidae	*Atocetus iquensis*	holotype Muizon 1988	Cerro la Bruja, Ica, Perú	Pisco Fm.		middle Miocene	5	de vries ~10my	epicontinental sea	coastal/estuarine	SI	MNHN	PPI 113	Muizon, 1988
Delphinoidea	Kentriodontidae	*Atocetus iquensis*	asigned specimen (present work)	Cerro la Bruja, Ica, Perú	Pisco Fm.		middle Miocene	5	de vries ~10my	epicontinental sea	coastal/estuarine	SI	MNHN	PPI 127	Muizon, 1988
Delphinoidea	Kentriodontidae	*Atocetus iquensis*	paratype Muizon 1988	Cerro la Bruja, Ica, Perú	Pisco Fm.		middle Miocene	5	de vries ~10my	epicontinental sea	coastal/estuarine	SI	MNHN	PPI 115	Muizon, 1988
Delphinoidea	Kentriodontidae	*Atocetus iquensis*	paratype Muizon 1988	Cerro la Bruja, Ica, Perú	Pisco Fm.		middle Miocene	5	de vries ~10my	epicontinental sea	coastal/estuarine	SI	MNHN	PPI 114	Muizon, 1988
Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	Baia Norte, Florianopolis, SC – South Brazil	-	194 cm	Holocene	0		coastal	coastal/estuarine	M	UFSC	1083	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011
Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	Cabeceira da Ponte, Florianopolis, SC – South Brazil	-	188 cm	Holocene	0		coastal	coastal/estuarine	F	UFSC	1079	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011
Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	Estreito, Florianopolis, SC – South Brazil	-	181 cm	Holocene	0		coastal	coastal/estuarine	F	UFSC	1208	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011
Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	Gov Celso Ramos, SC – South Brazil	-	175 cm	Holocene	0		coastal	coastal/estuarine	F	UFSC	1289	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011
Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	Baia Norte, Cabeceira da Ponte. Florianopolis, SC – South	-	165,2 cr	Holocene	0		coastal	coastal/estuarine	F	UFSC	1104	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011
Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	Ilha de Anhatomirim, Gov. Celso Ramos, SC – South Brazil	-	99,5 cm	Holocene	0		coastal	coastal/estuarine	M	UFSC	1223	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011
Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	Cacupé, Florianopolis, SC – South Brazil	-	203,2 cr	Holocene	0		coastal	coastal/estuarine	F	UFSC	1180	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011
Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	Gov Celso Ramos, SC – South Brazil	-	131 cm	Holocene	0		coastal	coastal/estuarine	M	UFSC	1226	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011
Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	Costeira de Pirajubae, Florianopolis, SC – South Brazil	-	148 cm	Holocene	0		coastal	coastal/estuarine	F	UFSC	1219	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011
Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	Praia dos Currais, Gov Celso Ramos, SC – South Brazil	-	157,5 cr	Holocene	0		coastal	coastal/estuarine	F	UFSC	1130	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011
Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	Praia Itaguacu, Florianopolis, SC – South Brazil	-	175 cm	Holocene	0		coastal	coastal/estuarine	F	UFSC	1321	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011
Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	Praia Barreiros, Sao Jose, Florianopolis, SC – South Brazil	-	185,5 cr	Holocene	0		coastal	coastal/estuarine	F	UFSC	1329	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011
Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	Cacupé, Florianopolis, SC – South Brazil	-	190 cm	Holocene	0		coastal	coastal/estuarine	M	UFSC	1336	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011
Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	APA Anhatomirim, Gov, Celso Ramos, SC – South Brazil	-	199 cm	Holocene	0		coastal	coastal/estuarine	M	UFSC	1291	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011
Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	Proc, Caieira do Norte, Gov, Celso Ramos, SC – South Bra	-	189 cm	Holocene	0		coastal	coastal/estuarine	M	UFSC	1297	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011
Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	Proc, Jardim Atlantico, Florianopolis, SC – South Brazil	-	154 cm	Holocene	0		coastal	coastal/estuarine	M	UFSC	1333	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011
Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	Sambaqui, Florianopolis, SC – South Brazil	-	110,5 cr	Holocene	0		coastal	coastal/estuarine	M	UFSC	1174	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011
Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	Sao Francisco do Sul, Florianopolis, SC – South Brazil	-	197 cm	Holocene	0		coastal	coastal/estuarine	M	UFSC	1175	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011
Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	Estreito, Florianopolis, SC – South Brazil	-	175,3 cr	Holocene	0		coastal	coastal/estuarine	M	UFSC	1312	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011
Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	Praia da Daniela, Florianopolis, SC – South Brazil	-	145,5 cr	Holocene	0		coastal	coastal/estuarine	M	UFSC	1307	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011

Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	Ilha de Anhatomirim, Gov. Celso Ramos, SC – South Brazil	-	131 cm	Holocene	0	coastal	coastal/estuarine	M	UFSC	1296	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011
Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	Ponte do Rio Sambaqui, Florianopolis, SC – South Brazil	-	147,3 cr	Holocene	0	coastal	coastal/estuarine	M	UFSC	1178	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011
Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	Baia Norte, Cabeceira da Ponte, Florianopolis, SC – South	-	140 cm	Holocene	0	coastal	coastal/estuarine	M	UFSC	1239	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011
Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	Praia de Fora, Palhoca, SC – South Brazil	-	-	Holocene	0	coastal	coastal/estuarine	M	UFSC	1354	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011
Delphinoidea	Delphinidae	*Sotalia guianensis*	assigned in collections	Serraria, Florianopolis, SC – South Brazil	-	192 cm	Holocene	0	coastal	coastal/estuarine	M	UFSC	1352	Shirihai and Jarrett, 2006; Simoes-Lopes 1988; Wedekin et al. 2007, 2010, Cremer et al. 2011
Delphinoidea	Delphinidae	*Sotalia fluviatilis*	assigned in collections	Igarape BACABA, Lago Amana, Tefe, Amazonas, North Br	-	147 cm	Holocene	0	riverine	riverine	IS	IDSM	Sf 2008-01	Shirihai and Jarrett, 2006
Delphinoidea	Delphinidae	*Sotalia fluviatilis*	assigned in collections	Ponta da Maloca Lago Amana, Tefe, Amazonas, North Bra	-	146 cm	Holocene	0	riverine	riverine	F	IDSM	Sf 2005-04	Shirihai and Jarrett, 2006
Delphinoidea	Delphinidae	*Sotalia fluviatilis*	assigned in collections	Ponta do Jauari, Tefe, Amazonas, North Brazil	-	152 cm	Holocene	0	riverine	riverine	M	IDSM	Sf 2005-03	Shirihai and Jarrett, 2006
Delphinoidea	Delphinidae	*Sotalia fluviatilis*	assigned in collections	Boa esperanca, Tefe, Amazonas, North Brazil	-	146 cm	Holocene	0	riverine	riverine	F	IDSM	Sf 2004-01	Shirihai and Jarrett, 2006
Delphinoidea	Delphinidae	*Sotalia fluviatilis*	assigned in collections	Lago de Tefé, Tefe, Amazonas, North Brazil	-	147 cm	Holocene	0	riverine	riverine	F	IDSM	Sf 9702	Shirihai and Jarrett, 2006
Delphinoidea	Delphinidae	*Sotalia fluviatilis*	assigned in collections	Comunidade Barroso, Tefe, Amazonas, North Brazil	-	154 cm	Holocene	0	riverine	riverine	F	IDSM	Sf 2004-02	Shirihai and Jarrett, 2006
Delphinoidea	Delphinidae	*Sotalia fluviatilis*	assigned in collections	Lago de Tefé, Tefe, Amazonas, North Brazil	-	75,3 cm	Holocene	0	riverine	riverine	M	IDSM	Sf 9801	Shirihai and Jarrett, 2006
Delphinoidea	Delphinidae	*Sotalia fluviatilis*	assigned in collections	Marajai, Tefe, Amazonas, North Brazil	-	115 cm	Holocene	0	riverine	riverine	F	IDSM	Sf 2001-01	Shirihai and Jarrett, 2006
Delphinoidea	Delphinidae	*Sotalia fluviatilis*	assigned in collections	Nogueira, Tefe, Amazonas, North Brazil	-	110 cm	Holocene	0	riverine	riverine	M	IDSM	Sf 9514	Shirihai and Jarrett, 2006
Delphinoidea	Delphinidae	*Sotalia fluviatilis*	assigned in collections	Lago de Tefé, Tefe, Amazonas, North Brazil	-	144 cm	Holocene	0	riverine	riverine	F	IDSM	Sf 9503	Shirihai and Jarrett, 2006
Delphinoidea	Delphinidae	*Sotalia fluviatilis*	assigned in collections	Lago de Tefé, Tefe, Amazonas, North Brazil	-	153,5 cr	Holocene	0	riverine	riverine	F	IDSM	Sf 2006-04	Shirihai and Jarrett, 2006
Delphinoidea	Delphinidae	*Sotalia fluviatilis*	assigned in collections	Guariba (rio Solimoes), Tefe, Amazonas, North Brazil	-	140,5 cr	Holocene	0	riverine	riverine	F	IDSM	Sf 2007-03	Shirihai and Jarrett, 2006
Delphinoidea	Delphinidae	*Sotalia fluviatilis*	assigned in collections	Bom Jesus do Baré, Tefe, Amazonas, North Brazil	-	150 cm	Holocene	0	riverine	riverine	F	IDSM	Sf 2005-06	Shirihai and Jarrett, 2006
Delphinoidea	Delphinidae	*Sotalia fluviatilis*	assigned in collections	Ponta da Maloca/Amana, Tefe, Amazonas, North Brazil	-	152 cm	Holocene	0	riverine	riverine	M	IDSM	Sf 2005-05	Shirihai and Jarrett, 2006
Delphinoidea	Delphinidae	*Sotalia fluviatilis*	assigned in collections	Lago Amana, Tefe, Amazonas, North Brazil	-	117 cm	Holocene	0	riverine	riverine	M	IDSM	Sf 2006-05	Shirihai and Jarrett, 2006
Delphinoidea	Delphinidae	*Sotalia fluviatilis*	assigned in collections	Lago Amana, Tefe, Amazonas, North Brazil	-	150 cm	Holocene	0	riverine	riverine	?	IDSM	Sf 9509	Shirihai and Jarrett, 2006
Delphinoidea	Phocoenidae	*Piscolithax longirostris*	holotype	Sud Sacaco, Ica, Perú	Pisco Fm.	-	early Pliocene	3	epicontinental sea	coastal/estuarine	SI	MNHN	SAS 933	Muizon, 1983, 1984
Delphinoidea	Phocoenidae	*Australithax intermedia*	holotype	El Jahuay, Ica, Peru	Pisco Fm.	-	late Miocene	4	epicontinental sea	coastal/estuarine	SI	MNHN	PPI 65	Muizon, 1988
Delphinoidea	Phocoenidae	*Lomacetus ginsburgi*	holotype	Aguada de Lomas, Ica, Peru	Pisco Fm.	-	late Miocene	4	epicontinental sea	coastal/estuarine	SI	MNHN	PPI 104	Muizon, 1988
Delphinoidea	Phocoenidae	*aff. Lomacetus*	Gutstein y Valenzuela-Toro accepted	Caldera, Región de Atacama, Chile	Bahía Inglesa Fm.	-	late Miocene	4	deep marine to shoreface	fully marine	IS	MPC	MPC4	Achurra, 2004, Achurra et al. 2009
Delphinoidea	Phocoenidae	*aff. Piscolithax*	Gutstein y Valenzuela-Toro submitted	Caldera, Región de Atacama, Chile	Bahía Inglesa Fm.	-	late Miocene	4	deep marine to shoreface	fully marine	IS	MPC	229	Achurra, 2004, Achurra et al. 2009
Delphinoidea	Phocoenidae	*Neophocaena phocaenoides*	assigned in collections	Woosung, Shangai, China	-	-	Holocene	0	[illegible]	coastal/estuarine	M	USNM	240002	Reeves et al. 2002, Shirihai and Jarrett, 2006
Delphinoidea	Phocoenidae	*Neophocaena phocaenoides*	assigned in collections	Woosung, Shangai, China	-	-	Holocene	0	[illegible]	coastal/estuarine	F	USNM	240001	Reeves et al. 2002, Shirihai and Jarrett, 2006
Delphinoidea	Phocoenidae	*Neophocoena phocaenoids*	assigned in collections	Woosung, Shangai, China	-	-	Holocene	0	[illegible]	coastal/estuarine	IS	USNM	240003	Reeves et al. 2002, Shirihai and Jarrett, 2006
Delphinoidea	Phocoenidae	*Phocoena phocoena*	assigned in collections	Assateague Island, ¼ Mile South of Dune Crossing, Worce	-	145 cm	Holocene	0	coastal	coastal/estuarine	M	USNM	571358	Reeves et al. 2002, Shirihai and Jarrett, 2006
Delphinoidea	Phocoenidae	*Phocoena phocoena*	assigned in collections	Nags Head, Opposite Colony House Cinema, Milepost 10.5	-	165 cm	Holocene	0	coastal	coastal/estuarine	F	USNM	504757	Reeves et al. 2002, Shirihai and Jarrett, 2006
Delphinoidea	Phocoenidae	*Phocoena phocoena*	assigned in collections	Rodanthe, About 1 Mi N of Hatteras Island Pier, Dare, Nortl	-	102 cm	Holocene	0	coastal	coastal/estuarine	F	USNM	504543	Reeves et al. 2002, Shirihai and Jarrett, 2006
Delphinoidea	Phocoenidae	*Phocoena phocoena*	assigned in collections	Assateague Island, 1,5 Mi S of Visitor Center On S End of I	-	153 cm	Holocene	0	coastal	coastal/estuarine	F	USNM	504606	Reeves et al. 2002, Shirihai and Jarrett, 2006
Delphinoidea	Phocoenidae	*Phocoena phocoena*	assigned in collections	Samoa Peninsula, Ca. 4 Mi. W. Of Arcata, N. End of Penins	-	150 cm	Holocene	0	coastal	coastal/estuarine	IS	USNM	550152	Reeves et al. 2002, Shirihai and Jarrett, 2006
Delphinoidea	Odobenocetopsidae	*Odobenocetops peruvianus*	holotype	Sud Sacaco, Ica, Perú	Pisco Fm.		early Pliocene	3	epicontinental sea	coastal/estuarine	IS	USNM	488252	Muizon, 1993, Muizon and Domning, 2002

Capítulo 4

New Toothed Whales (Inioidea, Odontoceti) from the Neogene of the South-East Pacific (Atacama Region, Chile) and North Atlantic (North Carolina, U.S.A.): implications to river dolphins distribution and facial morphology

CAROLINA S. GUTSTEIN
STEPHEN J. GODFREY
MARIO A. COZZUOL
PAULO SIMOES-LOPES
MAURICIO CANALS L.

Capítulo 4

New Toothed Whales (Inioidea, Odontoceti) from the Neogene of the South-East Pacific (Atacama Region, Chile) and North Atlantic (North Carolina, U.S.A.): implications to river dolphins distribution and facial morphology

CAROLINA S. GUTSTEIN[1], STEPHEN J. GODFREY[2], MARIO A. COZZUOL[3], PAULO SIMOES-LOPES[4], MAURICIO CANALS L.[1,5]

[1]Laboratorio de Ecofisiología, Departamento de Ciencias Ecologicas, Facultad de Ciencias, Universidad de Chile, Las Palmeras 3425, Ñuñoa, Santiago, Chile. sgcarolina@gmail.com

[2]Calvert Marine Museum, P.O. Box 97, Solomons, Maryland, U.S.A. 20688

Godfresj@co.cal.md.us

[3]Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte, MG, Brazil

[4]Laboratório de Mamíferos Aquáticos, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, 88040-970, Florianópolis, Santa Catarina, Brazil, lamaqsl@ccb.ufsc.br

[5]mcanals@uchile.cl

Key Words: Inioid, Neogene, Bahia Inglesa Formation, Eastover Formation, Atacama Region Chile, North Carolina U.S.A.

VIII.1. ABSTRACT

Two new monotypic genera of Neogene (Miocene) odontocetes are named on the basis of two partial skulls (SGO-PV.21605 and CMM-V-4061). The South American species, SGO-PV.21605, was recovered from the "Las arenas" locality (Atacama Region, Chile) and derives from the Bahia Inglesa Formation. The type specimen of the North American species, CMM-V-4061, was found on the riverbed of the Meherrin River and is believed to derive from the Eastover Formation (North Carolina, U.S.A.). Synapomorphies of these genera include: anteriorly retracted premaxillae and maxillae; wide exposure of the frontal on the external surface of the cerebro-nasal plate; nearly symmetrical vertex; large dorsal infraorbital foramen level with the posterior margin of the external bony nares; and a pocket on the lateral face of the frontal below and behind the postorbital process of the frontal. A symplesiomorphy that they retain are two small but pronounced concavities on the cerebral face of the frontal/mesethmoid that are presumed to have held olfactory bulbs in life.

Both genera are tentatively assigned to the Inioidea; a significant addition to this taxonomically small but growing group of mostly western hemisphere odontocetes. The unusual configuration of the facial region in these two species might reflect differences in the distribution of the facial organs and associated musculature. They evidence additional osteological permutations, and consequently new complexity in the way in which odontocete skulls telescoped.

VIII.2. INTRODUCTION

The extant South American river dolphins are traditionally grouped in the superfamily Inioidea (Cetacea, Odontoceti), (sensu Muizon, 1988a); a conclusion with which more recent work is in agreement (Arnason and Guldberg, 1996; Yang and Zhou, 1999; Geisler and Sanders, 2003; Geisler et al., 2011, 2012). Extant Inioidea comprises two mono-generic families (considering the extant record only), Iniidae and Pontoporiidae. *Inia* is a strictly freshwater form that includes two living species; *Inia geoffrensis* (Blainville, 1817) found within the Orinoco and Amazon River basins and *Inia boliviensis* (Banguera-Hinestroza et al, 2002) within the Beni-Mamoré River basin. *Pontoporia* is monotypic (*P. blainvillei* (Gervais and d'Orbigny, 1844)) and inhabits shallow marine environments along the southeastern coast of South America, with some entrance into proximal riverine systems including Babitonga Bay, Southern Brazil (Cremer and Simoes-Lopes 2005) and the La Plata estuary of Argentina and Uruguay (Casinos) (Secchi, 2010).

In recent reviews of the Inioidea Cozzuol (2010) concluded that it consisted of the Brachydelphidae (elevating the pontoporiid subfamily Brachydelphininae to family status, and therefore the family name should reflect that; the Brachydelphinidae; but see Geisler et al., (2012)), Pontoporiidae, Iniidae, and possibly Lipotidae. Cozzuol's (2010) entirely extinct Brachydelphinidae ranges in age from the Middle Miocene to the Late Pliocene. This family includes *Brachydelphis mazeasi* Muizon, 1984, from the Pisco Formation in Peru; *Brachydelphis* sp. from Peru and Chile (Cozzuol, 2010); *Protophocaena minima* Abel 1905 from Europe (i.e., Belgium and The Netherlands (Lambert and Post, 2005)); and *Stenasodelphis russellae* Godfrey and Barnes, 2008 from the St. Mary's Formation/late Miocene of Maryland, U.S.A. By the other hand the incorporation of all genus (except *Goniodelphis* and *Pontistes*) on Geisler *et al.*, (2012) analysis, the Inioidea was defined to consist of two families, the Pontoporiidae (which retains *Brachydelphis*) and the Iniidae, to the exclusion of the Lipotidae (consisting of the more stem-ward *Lipotes vexillifer* and its sister taxa *Parapontoporia* spp.).

Currently, the Pontoporiidae Gill, 1871 (sensu Geisler et al., in press) is known from the late middle Miocene (if *Brachydelphis* is removed from the family it would be from the late Miocene) to the present time. Extinct pontoporiids include *Pontistes rectifrons* Burmeister, 1885 from the Parana Formation/late Miocene of Argentina (Cozzuol, 1985, 1996, 2010); *Pontistes* from the Bahia Inglesa Formation in Chile (Canto et al., 2002; Cozzuol, 2010), unnamed forms from Denmark (Pyenson and Hoch, 2007); *Pliopontos littoralis* Muizon, 1983 from the Pisco Formation/Early Pliocene of Peru (Muizon, 1983, 1984), *Auroracetus bakerae* Gibson and Geisler, 2009 from the Yorktown Formation/Early Pliocene of North Carolina, U.S.A. (Gibson and Geisler, 2009), and additional unnamed forms from Florida (Morgan, 1994) and North Carolina (Whitmore, 1994).

Extinct iniids are now known from Argentina (*Ischyrorhynchus vanbenedeni* (Ameghino, 1891) Ituzaingo Formation/Late Miocene Cozzuol (1985), (1996); *Saurocetes argentinus* Burmeister, 1871 and *Saurocetes gigas* Cozzuol, 1988, Ituzaingo Formation/Late Miocene Cozzuol (1988), (1996); *Plicodontinia mourai* Miranda Ribeiro, 1938, (a taxon that is based on very fragmentary remains which are not diagnostic) and *Inia* sp. nov., both from the Pleistocene of Brazil Cozzuol (2010); and the U.S.A. (*Meherrinia isoni* Geisler *et al.* 2012, from North Carolina Eastover Formation/Upper Miocene, Messinian), and by the enigmatic and poorly known *Goniodelphis hudsoni* Allen, 1941, Florida Palmetto Fauna, Bone Valley Formation/late Miocene (Morgan, 1994).

The systematic discrimination between Asian and South American river dolphins is mostly accepted since Gray (1863), who placed *Platanista* and *Inia* into separate monotypic families, Platanistidae and Iniidae, respectively. This was the first work to propose a systematic arrangement for the 'river' dolphins (*Lipotes* had not yet been described). *Pontoporia* (=*Stenodelphis*), however, was placed by Gray in the family Delphinidae. In the mean time, many specialists considered it as a distinct group within the marine true dolphins (Kellogg 1928, Miller 1923). Flower (1867) also proposed a systematic scheme for the "river dolphins" dividing the family Platanistidae into two subfamilies, the Platanistinae containing only *Platanista*, and the Iniinae, containing *Inia* and provisionally *Pontoporia*. This is the first and only reference until Muizon (1985) considering *Inia* and *Pontoporia* as close related groups. Miller (1923) followed Gray in recognizing separate families Platanistidae and Iniidae (including *Lipotes*) and placing *Pontoporia* into the Delphinidae. Since Miller's (1918) description, the taxonomic relationship between *Inia* and *Lipotes* has been generally supported. Fraser and Purves (1960) found 32 features of the cetacean ear to be identical in *Inia* and *Lipotes,* based on outer and middle ear morphologic characters of 37 species, including the four living genera of river dolphins. Kasuya (1973) based on comparative analysis of the tympano-periotic bone also recognized *Inia* and *Lipotes* as the two modern members of the Iniidae. While the overall resemblance (particularly in skull morphology) and shared ecological habit encouraged the grouping of *Inia* + *Lipotes*, the rarity of specimens and paucity of scientific attention left considerable room for revision.

Phylogenetic studies confirmed both the separation of Platanistidae from Iniidae and Pontoporiidae and the closer relationship of *Lipotes,* to the last two, sometimes placed in its own family or even superfamily (Lipotidae or Lipotoidea). The description of new related taxa (mostly pontoporiids) as *Auroracetus bakerae* (Gibson and Geisler, 2009), *Stenasodelphis russellae* (Godfrey and Barnes 2008), and other new records and reevaluation of known specimens inside and outside South America *Brachydelphis mazeasi* Muizon

1988 (see also Gutstein et al., 2009), *Protophocoena minima* (Lambert and Post, 2005), cf. *Pontistes* (Pyenson and Hoch, 2007), *Goniodelphis hudsoni* Allen (see also Cozzuol 2010), is shedding new light on the Inioidea diversity and has certainly great implications in phylogeny, although it has not been fully understood yet.

The Inioidea has increased in species diversity and distribution in the last 20 years. Nevertheless, with the exception of *Brachydelphis mazeasi* the new species (i.e. *Stenasodelphis* and *Auroracetus*) are very similar in general morphology to the modern genera *Pontoporia* and *Inia* and the fossil *Ischyrorhynchus*. Having this in mind, we can define three morphotypes of Inioidea: the *Inia-Ischyrorhynchus-Meherrinia* morphotype (where the vertex is formed by a well developed knob like process of the frontals); the *Pontoporia-Pliopontos-Pontistes* morphotype (a low-plane vertex and entire dorsal profile) and; the *Brachydelphis* morphotype (relatively short snouted, brachycephalic, mediolaterally expanded dorsal skull profile).

The purpose of this effort is to add to the growing number of inioids known from the fossil record by naming and describing two new genera and species as well as describing an entirely new facial morphology arrangement. Odontocetes already present a dizzying array of cranial morphologies; the forms described here only add to that diversity. They evidence additional osteological permutations, and consequently new complexity in the way in which odontocete skulls telescoped.

VIII. 2. 1. Institutional Abbreviations—CMM-V-, Calvert Marine Museum fossil vertebrate collection, Solomons, Maryland, U.S.A.; **SGO.PV**, Area Paleontología, Museo Nacional de Historia Natural de Santiago, Santiago, Chile.

VIII. 2. 2. Materials and methods

Comparisons with every other inioid except for *Protophocoena minima*) only by literature) as well as other delphinidans and odontocetes in general. We performed a phylogenetic analysis considering the matrix proposed by Geisler et al. 2011 and emended for Inioidea taxa in Geisler et al (2012) (with 6 extra characters and 5 extra taxa: *Auroracetus bakerae, Ischyrorhynchus vanbenedeni, Meherrinia isonia, Protophocoena minima, Stenasodelphis russelae*)). The matrix used here is the one of Geisler et al. 2012 with one extra character, considered diagnostic for Iniidae (sensu Cozzuol 2010), nevertheless we perform a minuciuos revision of the character coding specially in the south american specimens that we had access and not very commonly described in the literature (i.e. *Ischyrorhynchus*). The complete description of characters as well as the changes in character coding (Table S1) are detailed in the Supplementary online information 1.

The phylogenetic analysis comprised the use of new technology search in TNT, running simultaneouemmended combining the results of heuristic search, Rachet parsimony, drift and tree fusing, all of which considering implied weighting (Goloboff, 1993, Goloboff et al., 2008a, b). The main difference between the present analysis and the one performed in Geisler *et al.* (2012) is that all the character were considered non-additive, a decision we based on the poorly known and mostly unstable phylogenetic data there is for odontocetes that could serve as a base for the ordering of the characters. The tree stability it was performance by reordering method of Jacknife.

VIII. 3. SYSTEMATIC PALEONTOLOGY

CETACEA Brisson, 1762

ODONTOCETI Flower, 1867

DELPHINIDA de Muizon, 1984

INIOIDEA de Muizon, 1988

SGO-PV.21605 new genus

(Figs. 1–2)

SGO-PV.21605 Gutstein, Godfrey, Cozzuol, Simoes-Lopes and Canals new genus

Type species— SGO-PV.21605, new species.

Diagnosis of genus—As for the type and only species.

SGO-PV.21605, new species

Hypodigm—The holotype and only know specimen is a partial skull SGO-PV.21605 (Fig. 2) , from the "Las arenas" locality recovered from the Bahía Inglesa Formation (middle Miocene to late Pliocene, Achurra, 2004; Achurra et al., 2009).

Diagnosis—Odontocetes that differ from *Archaeodelphis*, *Xenorophus*, *Agorophius*, *Patriocetus*, *Albertocetus*, *Simocetus* and other stem-odontocetes by not having: a parietal exposed behind the frontal; a well developed nuchal crest, and the nasals not roofing the fully retracted external bony nares. They differ from Physeteroidea, Platanistoidea, Ziphioidea, and Delphinida, by having the cerebral nasal plate of the frontal widely exposed between the nuchal crest and the posterior most extension of the ascending processes of the maxillae which are thick at the posterior level of the external bony nares. Consequently, the posterior margin of the maxilla does not extend much beyond the posterior-most margin of the nasals. Generic autapomorphies include: anteriorly retracted premaxillae and maxillae; wide exposure of the frontal on the external surface of the cerebro-nasal plate; symmetrical vertex; dorsal maxillary opening of the large dorsal infraorbital foramen level with the posterior margin of the external bony nares; and a pocket on the lateral face of the frontal below and behind the postorbital process of the frontal. Convex nasal portion of premaxillae instead of a premaxillary sac fossa of most odontocetes; behind each premaxillary foramen, an accessory premaxillary foramina is present immediately adjacent to the narial opening; premaxillae retracted rostrally to about the anteroposterior midpoint in length of external nares; nasals show curved ridge on anterodorsal face; nasals triangular and anteroposteriorly elongated; width of frontal portion of vertex does not exceed width of nasal portion; anteroposteriorly elongate and elevated sagittal margins of frontals, all of which suggest Inioidea affinities; base of frontal contribution to vertex strongly bilaterally compressed; vertex of *MPC-222* shows intermediate condition between that of Pontoporiidae and Iniidae, being elongate like in Pontoporiidae, yet elevated in relationship to facial plane, but not so upturned as in Iniidae where the vertex forms a knob-like structure.

Locality and Age—The Bahía Inglesa Formation is already known to preserve a diverse and abundance vertebrate fauna (Fig.1). Most of the reported records (all fossil dolphins) are from the bone bed layer, well exposed at the "Mina Fosforita" locality (Gutstein et al., 2008; 2009; Walsh and Hume, 2001; Walsh and Naish, 2000; called Bonebed Member by Walsh and Suárez, 2005). The site where SGO-PV.21605 was collected was from an exposure on the outskirts of the town of Caldera. Unfortunately, the quarry is no longer accessible because of town/urban expansion. Although the site remains poorly known, it preserves an intriguing fauna including the first manatee (Trichechidae) recovered from the southeast Pacific coast (Bianucci et al., 2006).

Sr-Sr isotopic analysis of overlying beds (Achurra, 2004; Suarez y Marquardt, 2003; Achurra et al., 2009) yields a minimum age of Late Miocene for other localities (e.g. El Morro) interpreted to be above the horizon where SGO-PV.21605 was collected (Suarez y Marquardt, 2003). Studies of the shark-tooth fauna concur that the assemblage is Late Miocene in age (Suarez y Marquardt, 2003; Bianucci et al., 2006). Unfortunately, no more precise date is available for the recovery horizon and stratigraphic correlation is obscured by numerous faults and discontinuity with the rest of the Bahia Inglesa Formation.

VIII. 3. 1. Description of SGO-PV.21605

Skull—The specimen of SGO-PV.21605 (Fig. 2) consists of the facial region of a partial skull including the vertex, nasal passages, and premaxillary plate, with an associated partial occipital shield preserving the condyles. This specimen presents a unique configuration of the maxilla, premaxilla, nasal, and frontal. The most remarkable feature of this specimen is the anteriorly-retracted posterior margin of the maxillae exposing a wide swath of the frontal (i.e., the frontal nasal plate) lateral to the vertex.

Premaxilla—The ascending process of the premaxillae are preserved. The processes are especially inflated in the narrow band of bone between the premaxillary foramina and the nares, forming the premaxillary plate, as in other

Inioidea (Fig. 2). Neverthless, the premaxilla reach only a little posterior to the mid-length of the bony nares. The premaxillary foramen bears an anteromedial and a posterolateral sulcus as in Pontoporiidae *sensu lato* (including *Brachydelphis*). Behind each premaxillary foramen, there is an accessory premaxillary foramina, without sulci, lying just anterior to the nasal passage.

Maxilla—The maxillae ascending processes have no contact with the nuchal crest nor do they participate in the formation of the vertex (Fig. 2). Posterolateral to the premaxillae and nares, the maxillae appear inflated. The maxilla-frontal sutures are retracted rostrally such that the posterior margins of the maxillae do not reach beyond the posterior level of the nasal-frontal sutures. The maxilla-frontal suture and the posteriormost portion of the maxillae are deeply interdigitating. Lateral to the nares and lying adjacent to the aforementioned suture is the posterior maxillary foramen (i.e., the dorsal infraorbital foramen). At 9 mm in diameter, this foramen is unusually large; reminiscent of the condition in *Inia* and *Ischyrorhynchus*.

Nasal—The nasals are fairly robust elements forming a nearly straight transverse posterior margin of the external nares (Fig. 2). From this point, at which they are at their maximum width, they taper posteriorly onto the vertex. Beginning at the anterolateral corner of the nasals, a sharp ridge curves posteromedially on the anterodorsal face of the nasals, becoming less pronounced towards the posterior extremity of the bone. Between these ridges is a shallow elongate concavity extending the full length of the nasals. The nasals attain their maximum length just lateral to their common suture on the mid-line of the symmetrical vertex. The nasal-frontal suture passes anteroventrally from the mid-point in the length of the vertex. The back of the nasals also marks the narrowest point of the vertex.

The nasals are massive which resembles the primitive condition in Delphinida, but triangular and smoothly inclined, sloping from the more elevate frontal to meet the upwardly projected mesethmoid, resembling that of Pontoporiidae. Nevertheless, in SGO-PV.21605 the nasals are even more massive than in *Pontistes* (Fig. 2 and 4).

Frontal—The frontals exhibit a moderately high medial elevation; a thick rostro-caudally elongate crest that forms most of the vertex. From its highest elevation at the level of the nuchal crest, the vertex is smoothly inclined anteroventrally. Because the maxillae are withdrawn rostrally, wide dorsal exposures of the frontals occupy much of the facial/frontal shield posterior and posterolateral to the nares. Medially along the vertex, the frontal-frontal suture exhibits innumerable folded ridges. These folds are interpreted as *ossa suturata* (Simões-Lopes 2008), very common in artiodactyls skull sutures, mainly present in the frontal and maxilla.

This configuration of the vertex, i.e., one that is formed only by the frontals and nasals, medially restricted, and abruptly raised, is diagnostic of Iniidae, although in SGO-PV.21605 it is not squared in its dorsal outline, nor is it as elevated as it is in other members of the family.

Ventral View—The basicranium is not preserved, consequently only the roof of the braincase is visible in ventral view (Fig. 2). The skull is preserved up to the point of the basisphenoid-presphenoid fissure, showing both the foramina rotundum and optic canals. Above this area is the cribriform plate which lies within the mesethmoid which occupies almost half of the preserved anterodorsal wall of the braincase. The mesethmoid/cribriform plate is well developed with more foramina than in most Delphinida. Posterodorsally, the highly folded frontals are visible (Fig. 2). There is no sign of an interparietal in SGO-PV.21605. A small broken portion of the parietal is preserved, forming the lateral edges of the braincase.

Lateral View—In lateral view, mostly we can observe the inclined position of the nasals and frontals on the vertex. Also jumps in the sight the differences in height from the medial (sagital) portion of the frontals and lateral most preserved part of the frontals. The posterior dorsal infraorbital foramen lyes at the indented maxilla-frontal suture is wide open and visible in lateral view (because the lateral side is incomplete). The maxilla-frontal suture reaches at its medial portion the level of the nasal posterior limit and laterally lyes more anteriorly reaching the posterior limit of the external bony nares. The parietal is visible in the ventral portion of the skull. It shows a deeply excavated posterior posteroorbital sinus fossa, even more conspicuous than modern dolphins and porpoises, just posterior to the optic canal and foramen rotundum ventral exposition. The premaxilla posterior limit ends mid-length the external bony nares antero-posterior extension. The nasals shows a small excavation which marks the postromedial end of the premaxillary sac attachment which extends from just posterior the second premaxillary foramen. Interestingly, they are quite symmetric as in Inioidea and differently from Delphinoidea. No orbitosphenoid-basisphenoid limit can be observed.

It makes it a species with such contrasting features as deeply excavated post orbital pterygoid sinus (derived) and the maxilla not reaching the nuchal crest (primitive).

CETACEA Brisson, 1762
ODONTOCETI Flower, 1867
DELPHINIDA de Muizon, 1984
INIOIDEA de Muizon, 1988
(Fig. 3)

CMM-V-4061, new species

Type species— CMM-V-4061, new species.

Diagnosis—Premaxillae strongly retracted anteriorly; robust nasals, sub-rectangular in dorsal view; ventrolateral edges of nasals deeply imbedded into corresponding troughs in frontals; supernumerary ossification present between frontals on vertex (*may be individually variable); apex of vertex formed by frontals and supernumerary ossification (*); vertex elevated and bilaterally compressed. (Primitive feature: olfactory bulb fossae present as are the numerous foramina that pierce the frontal/cribriform plate). Another inioid, *Meherrinia isoni* Geisler, Godfrey, and Lambert 2012, is also known from the same locality. The vertices of these two taxa are very distinct and no one would confuse *CMM-V-4061 CMM-V-4061* for *Meherrinia isoni. CMM-V-4061 CMM-V-4061* shares the following characteristics with *SGO-PV.21605*: rostrally retracted premaxillae and maxillae, large posterior maxillary foramen lateral to nares,

It differs from *SGO-PV.21605* by the nasal morphology which is smooth in the dorsal surface, not showing the ridges which individualize the naso-frontal sac fossa to the lateral sides of both nasals as observed in *SGO-PV.21605.*

Hypodigm—CMM-V-4061, type and only known specimen.

Type Locality—The holotype, CMM-V-4061, was recovered by R. Ison from the riverbed of the Meherrin River a tributary of the Chowan River, Murfreesboro, Hertford County, North Carolina, U.S.A. (North 36°, 27', 18.8": West 77°, 2', 36.8").

Formation and Age—the specimen was not found in situ. It was collected from the riverbed of the Meherrin River, Murfreesboro, Hertford County, North Carolina. Unfortunately, the specimen was devoid of entombing sediment. Nevertheless, it is considered to have been locally derived, probably from the Cobham Bay Member of the Eastover Formation (upper Miocene, Messinian), (Ward, pers. comm., November 30, 2009). Because it was not collected in situ, it is possible that it could have come from the Pliocene, Yorktown Formation (in ascending order from the Sunken Meadow, Rushmere, or Morgarts Beach Member of this formation), but according to Ward (pers. comm., November 30, 2009), these derivations are less likely because of where the specimen was recovered. A further argument (which we admit is not a weighty one) in favor of its derivation from the Eastover Formation is the observation that *CMM-V-4061* has not been found in the Yorktown Formation, for which a rich marine mammal fauna has been described (Ray et al., 2008). *Auroracetus bakerae* Gibson and Geisler, 2009 is currently the only known inioid from the Yorktown Formation.

VIII. 3. 2. Description of CMM-V-4061

Skull—The holotype specimen of *CMM-V-4061* (CMM-V-4061, Fig. 3) consists of the posterior facial region of a partial skull including the vertex, posterior margin of the nares, and a partial supraoccipital. Ventrally, part of the vomer/mesethmoid complex is also preserved.

Maxilla—Only the posterior-most parts of the maxillae adjacent to the nares and nasals are preserved. As in *SGO-PV.21605*, the maxillae are retracted anteriorly such that they do not overlap the frontals immediately adjacent to the vertex. Admittedly, the posterolateral margins of the maxillae are not complete, so the precise extent to which the maxillae covered the frontals is not known (Fig. 3). Deep interdigitating sutures bind the maxillae and frontals (Fig. 3C). A shallow trough present on the anterior extremity of the preserved segment of the right maxilla is interpreted as the area that held the posterior extent of the now-missing premaxillae in life (Fig. 3A). This trough is not thought to be the posterolateral sulcus from the premaxillary foramen for two reasons: the premaxillae are not preserved in this specimen and the posterolateral sulcus is never that close to the medial margin of the nares. If we have correctly appraised the nature of this trough, it would strongly suggest that the premaxillae were retracted rostrally to at least the same extent as seen in SGO-PV.21605 (Fig. 2). The thickened posteromedial margin of the maxillae broadly contacts and underlies the lateral margin of the nasals (Fig. 3A & C).

Nasals—Both nasals are well preserved in CMM-V-4061. They present as blocky elements each being sub-rectangular in outline in both dorsal and lateral views. In dorsal view, their anterior margin forms an essentially straight border for the posterior margin of the external nares. From this their combined widest point, they taper gradually before turning abruptly towards the apex of the vertex. The pronounced undercut below the anterior margin of the nasals (Fig. 3C) may have held the now-missing part of the ethmoid that formed the nasal septum. The frontals or a combination of the frontals and a supernumerary ossification are wedged between the posteromedial end of the nasals.

Frontal—The frontals are the largest bones preserved in CMM-V-4061, including most of the area from the temporo-orbital plate to the back of the vertex (Fig. 3). Immediately medial to the orbital margin of the frontal is a conspicuous trough that would have opened as the posterior-most dorsal infraorbital foramen. As in *SGO-PV.21605*, the trough is larger than in any other comparably-sized odontocete. Behind the thickened maxillae, the frontals gain wide exposure as they form the lateral face of the elevated vertex. Together with the supraoccipital, the frontals form the narrow, pointed, and nearly symmetrical vertex. A supernumerary bone or an interparietal ossification contributes to the formation of the vertex. It is visible both in photos of the partial skull and in CT-scans of CMM-V-4061(Fig. 3A & D). The CT images seem to indicate that it is a separate ossification, distinct from the frontals, but lack of clarity engenders caution; it may simply be a folded portion of the left frontal masquerading as a supernumerary ossification.

Ventrally, the frontals preserve the endocranial cavity (Fig. 3F). Ethmoid foramina pass from the anterior face of the cranial cavity anterolaterally towards the orbits. Dorsomedial to the ethmoid foramina are two small ovoid depressions, the long axis of which has an anteroventral-posterodorsal orientation. They are believed to have held the olfactory bulbs in life. Extending dorsomedially from each of these depressions is a channel that merges medially. The two olfactory bulb depressions and confluent channels exhibit multiple perforations that pass through the bone to the mesethmoid side of the nasal passages (Fig. 3B & F). These small foramina are interpreted as remnants of the cribriform plate which conducted olfactory nerves and vessels to whatever olfactory receptor tissue existed within the narial passages.

Supraoccipital—A robust supraoccipital is wedged deeply between and behind the frontals (Fig. 3). It under laps the frontals posteromedially where its ventral margin becomes increasingly ridge-like posteriorly. This ventral supraoccipital ridge separated the cerebral hemispheres posteriorly.

Vomer—The anterior-most part of CMM-V-4061 consists of a small section of the vomer that separated the internal nares (Fig. 3). Here, a trough-like portion of the vomer would have held the ethmoid – only part of which remains intact.

VIII. 3. 3. Implications for Inioidea facial morphology

These new species brings diversity on the facial morphology of the Inioidea. While they have Inioidea characters as the elevated vertex formed mostly by the frontals (differing from Delphinoidea that have an elevated vertex formed by the frontals, nasals and maxilla in conjunction), they also present a retraction of the maxilla up to the level of the posterior dorsal infraorbital foramina on both sides. Nevertheless, a slight retraction of the maxilla, which do not contact the occipital in the medial portion, is also observed in adult individuals of *Inia* and *Ischyrothynchus*. Interestingly in juvenile individuals the maxilla go further posterior than in the adults. In SGO-PV.21605 and CMM-V-4061 the maxilla is also thickened probably a subproduct of the retraction of this bone, where the maxillonasolabialis attaches. This unusual morphology, not observed in any other taxa within Odontoceti, creates a concave region on the posterior facial surface. As observed in *Inia* (Fig. 4), where there is a concave surface on the maxilla but in the same position of that of SGO-PV.21605 and CMM-V-4061, this space is filled by the big expansion of the vestibular sac (not attached to the bone) which is expanded and surrounds the elevated vertex (Fig. 4). We interpret this condition to be present in *Ischyrorhynchus* due to the virtually identical morphology of the face with *Inia* and hypothesized a similar facial tissue morphology for both new genera.

The vestibular sac is also enlarged in the related extant *Pontoporia* (Fig. 4) but it has not the half-moon shape of *Inia* and as it do not present an elevated vertex, the vestibular do not surround it as well. Instead the vestibular sac morphology of *Pontoporia* is rather oval in shape, being more anteroposteriorly elongate than the ones in Delphinoidea as *Sotalia guianensis* and *Cephalorhynchus eutropia* and *Phocoena phocoena* (Fig. 4).

Given this antero-posteriorly elongated vestibular sac which can be observed for both extant species and inferred in the extinct species, as expected they also present a much enlarged posterior dorsal infraorbital foramina, more pronounced on the species which present the concave surface of the posterior facial region (*Ischyrorhynchus*, *Inia*, SGO-PV.21605 and CMM-V-4061), which would have enervate and fed (the foramina the enlarged soft tissue facial structures in life. These enlarged vestibular sac may work as acoustic concave mirrors, generating a more focused echolocation beam. This morphology is convergent with the one observed in the extant *Platanista* (Indian river dolphin) which has also a concave acoustic mirror but formed by the pterygoid sinus expansion in the unusual developed maxillary crest (Mead and Fordyce 2009). As for the other valid inioids (see **Redefining Inioidea)** described for the North Hemisphere (*Goniodelphis*, *Stenasodelphis*, *Meherinia*, *Brachydelphis*, *Pontistes*) it is possible to observe the enlarged posterior dorsal infraorbital foramina and the slightly elevated vertex formed only for the frontals, which is concordant with the interpretations described above. Nevertheless, the fragmentary or poorly preserved nature of the specimens prevent better intrepretation of the facial soft tissues. In the case of *Goniodelphis* the foramina are not visible, because it is not preserved (broken) on the right side and covered with sediment in the left side, nevertheless it is possible to observe a very large excavation on this region, since it is broken on the right side, which suggest the expansion of the foramina as well.

VIII. 3. 4. Redefining Inioidea

We propose here a series of characteristics to redefine Inioidea, since some confusion on this topic has been generated in more comprehensive phylogenetic analysis (Geisler and Sanders 2003, Geisler *et al.* 2011, 2012).

To access the inioids phylogenetic relationships and test the group monophyly we performed a phylogenetic analysis based on previously published matrix (Geisler *et al.* 2011, 2012). We eliminate basal taxa and its characters (not related with inioid definition) and reviewed and modified (when pertinent) the inioid character definition and coding (see SI 1). Particularly, some character we find to be miss-interpreted in the earlier analysis (Geisler *et al.* 2011, 2012) which are listed in table 1, mainly in *Ischyrohynchus* coding.

The phylogenetic analysis results recovered one most parsimonious tree (Fit=144.19) were it can be appreciate the main odontocete clades, as the Delphinida, Delphinoidea and Inioidea. In the jackknife reordering these clades were not recovered as stable. The latter can be considered a monophyletic group in its strict sense, formed by *Inia* + *Pontoporia* and all its descendants (node 80) by the following characters: mandibular symphisis fusion (character 40), position of the posterior end of premaxilla (character 89), supraocciptal at same level of the frontals and/or nasals (character 128), falciform process of the squamosal poorly developed (character 176), posterior portion of periotic fossa with a deep large fossa posteriorly (character 187), length of of anterior process of the periotic very short (character 203), shape of cross section through anterior process at midlength (character 208) and dorsal edge of sigmoid process does not articulate with squamosal or periotic (character 260).

Atocetus and *Albireo* are also close related, as sister groups, with Inioidea in this analysis, the characters that unite *Atocetus* with *Albireo* and Inioidea (9, 29, 285) and *Albireo* with Inioidea (character 68 and 122).

Within Inioidea there is two clades that would correspond to Iniidae (*Inia*, *Meherrinia*, *Ischyrorhynchus*) defined by the low lateral margin of posterolateral sulcus (character 309) and the presence of a deep sagittal sulcus on middle occiput (character 310) and Pontoporiidae (*Pontoporia*, *Pliopontos*, *Brachydelphis*, *Protophocoena*, *CMM-V-4061*, *SGO-PV.21605*, *Auroracetus* and *Stenasodelphis*) lacrimal wraps around anterior edge of supraorbital process of frontal and slightly overlies its anterior end (character 51), presence of two infraorbital foramina (character 64), longitudinal profile of floor of squamosal fossa slightly sigmoidal, concave in the posterior part (character 147), presence of stylomastoid fossa, situated on posterior face of pars cochlearis posterodorsal to stapedial muscle fossa (character 224), dorsal edge of posterior process of periotic contributes to the posterior process of petrosal (character 247), posterior process of periotic with horizontal plate and very thin for most of its length (character 248), medial portion of maxilla, situated on either side of the vertex, faces mainly dorsally (character 307).

In the present analysis *Ischyrorhynchus* was recovered as an Iniidae, which was supported several synapomorphies for Iniidae as follows: supraorbital processes of frontal slopes laterodorsally away from vertex (character 46), posterior-most end of ascending process of premaxilla located posterior to anterior edge of the floor of the squamosal fossa (character 74), nasal anteroposteriorly compressed into a nearly vertical plate with fossa on ventrolateral surface for posterior nasal sac (caudal sac of Cranford *et al.*, 1996) (character 117), Frontals higher than nasals (character 124), frontals posterior to nasals and between the premaxillae wider than maximum transverse width across nasals (character 125).

Based on the study of the specimens and comparisons with ontogeny and variation on fossil *Brachydelphis* and living *Pontoporia* (Gutstein *et al.* 2009) we propose here to invalidate *Auroracetus*, and assign the specimen to *Stenasodelphis* sp. since its morphological proximity and when submitted to cladistic analysis also results in a sister group relationship. This is supported also for the fact there is no valid diagnostic character, since most of the ones cited on *Auroracetus* description can be addressed with its juvenile condition (probably a neonate, which is evident from the loose sutures observed in every cranial bone of the holotype and only specimen; Fig. 5, see also Gutstein *et al.*, 2009). On the other hand, *Protophocoena* do not show any diagnostic character that cannot be considered individual variation observed in *Brachydelphis* (Gutstein *et al.* 2009) and also in agreement with the probable presence of this genus in the tortonian of the northern sea (cf. *Brachydelphis*, Pyenson and Hoch, 2007). As for *Stenasodelphis* some characters are also shared with *Brachydelphis*, specially the new form described recently for Chile and Peru (Gutstein *et al.* 2009). A more extensively review and morphometric assessment of the morphology of this new form is needed to decide about it position and the possibility that it can be referred to *Stenasodelphis*.

The specimens here described were recovered as a derived group of Pontoporiidae, nevertheless this phylogenetic position has to considered important morphological changes, as the retraction of the maxilla, being an additional reversion.

VIII. 4. Discussion

SGO-PV.21605 and *CMM-V-4061* differ from *Archaeodelphis, Xenorophus, Agorophius, Patriocetus*, *Albertocetus*, *Simocetus* and other stem-odontocetes by not having: a parietal exposed behind the frontal; a well developed nuchal crest, and nasals that do not roof over the fully retracted external bony nares. They differ from Physeteroidea, Platanistoidea, Ziphioidea, and Delphinida by having the cerebral nasal plate of the frontal widely exposed between the nuchal crest and the posterior most extension of the ascending processes of the maxillae which are thick at the posterior level of the external bony nares. Consequently, the posterior margin of the maxilla does not extend much beyond the posterior-most margin of the nasals. Synapomorphies of SGO-PV.21605 and *CMM-V-4061* include: anteriorly retracted premaxillae and maxillae; wide exposure of the frontal on the external surface of the cerebro-nasal plate; essentially symmetrical vertex (in both SGO-PV.21605 and *CMM-V-4061*, the right frontal on the vertex is more deeply concave than is the left side); large opening of the maxillary foramen (dorsal infraorbital foramen) level with the posterior margin of the external bony nares; and a pocket on the lateral face of the frontal below and behind the postorbital process of the frontal. Both genera differ from other inioids in that their nasals are robust and collectively wide anteriorly so that the posterior margin of nares is much wider than it is in other inioids.

VIII. 4. 1. Relationships of the new species within Inioidea

The premaxillary sac plate (*sensu* Gutstein *et al.* 2009) inflated surface on the premaxilla and smoothly excavated surface on the maxilla in SGO-PV.21605 is in an intermediate position between *Pontoporia* and *Inia.*

CMM-V-4061 differs from all other odontocetes, fossil and Recent. Given the fragmentary condition of the holotype, a definitive taxonomic assignment is admittedly tentative. CMM-V-4061 exhibits several features that suggest inioid affinities.

The sister-group relationship of *Atocetus* and *Albireo* with Inioidea is an unusual position for these taxa, usually related to Delphinoidea (Fordyce 1994, Geisler *et al.* 2011, 2012).

The Inioidea was most recently defined by Geisler *et al.*, (2011) as the last common ancestor of *Inia* and *Pontoporia* and all its descendents, these include; the posterior ends of its premaxillae are retracted so that they do not contact the nasals, and as in *Stenasodelphis*, *Meherrinia*, and *Inia*, the anterior margin of the supraoccipital is deeply wedged between the frontals on the vertex. Another classifications (Cozzuol, 2010) recognize 3 families within Inioidea:

Brachydelphidae, Iniidae and Pontoporiidae. Within Inioidea 2 monophyletic clades were recovered, one including *Inia* (Iniidae) and the other *Pontoporia* (Pontoporiidae).

In the present analysis the late Miocene south american *Ischyrorhynchus* is confirmed to be an Iniidae as suggested (Cozzuol 1996, 2010) and debated elsewhere, alternatively also grouped with the asiatic river dolphins, Platanistidae (Pilleri and Gihr, 1977, Geisler *et al.*, 2012). Nevertheless, the characters that have grouped *Ischyrorhynchus* with the platanistids were mainly related to teeth, mandibular and rostrum morphology (known as homoplasic from molecular data, Nikaido *et al.* 2001 and detected as convergence in the total evidence analysis of Geisler *et al.* 2011) and others were following all interpretation erroneous classified. As we were able to review personally the specimen, there were three characters that were unknown and we were able to code it here. Nevertheless, the main differences are nevertheless observed even running the matrix without the 1/3 ordered specimen as performed in Geisler *et al.* (2011, 2012)

CMM-V-4061 like *Inia* also has an elevated vertex, however in the former it tapers dorsally whereas in *Inia* it generally forms a chunky bulbous prominence, called knob-like process by some authors. In CMM-V-4061 and MPC-222 as in *Inia*, the apex of the vertex is mostly centered in a mid-line ridge along the supraoccipital, only gently skewed to the left but nothing like the asymmetric position observed in Delphinoidea taxa, for example.

VIII. 4. 2. Implications to Inioidea taxa distribution and affinities

Traditionally the Iniidae family was considered an endemic family of South Hemisphere given the extant species distribution and the most long therm known fossils (e.g. *Saurocetes* and *Ischyrorhynchus*). However, this interpretation has proven to be inaccurate giving the last decade studies which show a wide range of geologic age span, morphological and probably ecological diversity as well as the mentioned wider geographic distribution. Changing from a restricted riverine occurrence with a more or less precise evolutionary and biogeographic trend, shifting from a marine ancestor within the middle to late Miocene to a restricted riverine habitat with 3 acknowledged genera only (Cozzuol, 2010) to a diverse family with more than double specious rate (7 genera) distributed in the Atlantic and Pacific oceans. The same shift in the literature has happened before with the several new records of Pontoporiidae into the same oceans, making these results more consistent and valid for the whole Inioidea group. Nevertheless, this new diversity brings more uncertainty in the definition of both families, making it easier to refer to these taxa as Inioidea, which seems to be more trustable across different authors phylogenetic hypothesis and taxonomy (Muizon, 1988, Nikaido et al. 2001, Cozzuol, 2010, Geisler et al. 2011, 2012).

North Hemisphere inioids now include: *Goniodelphis hudsoni* Allen, 1941, *Stenasodelphis russellae Godfrey and Barnes, 2008; Brachydelphis* sp. (present work, former *Auroracetus bakerae* Gibson and Geisler, 2009); *Meherrinia isoni* Geisler, Godfrey, and Lambert 2012, and CMM-V-4061 (present work).

VIII. 5. Conclusions

The overall configuration of SGO-PV.21605 may reflect a difference in the pattern and distribution of the facial organs and musculature. Consequently, cranial telescoping in odontocetes could be more complex than previously thought.

The fossil record, much extended with this new genus, seems to reveal that the morphological diversity was greater in the neogene a tendency also observed in the species diversity at this epoch, particularly in the case of the Inioidea.

Studies on the echolocation physiology and the morphofunctional correlation of the anatomic structures related to sound generation and reception are cornerstone to interpret this paleobiologic aspect of the neogene dolphins. The fossil record, much extended with this new genus, seems to reveal that the morphological diversity was greater in the neogene a tendency also observed in the species diversity at this epoch, particularly in the case of the Inioidea.

VIII. 6. Acknowledgments

We express our deepest gratitude to R. Ison for collecting and donating the specimen *CMM-V-4061* of the Calvert Marine Museum. N. Pyenson (USNM), D.J. Bohaska (USNM), and C. Potter (USNM) are gratefully acknowledged for encouraging access to the collections of fossil and modern odontocetes in their care. For reviews of our manuscript, we are grateful to J. Pojeta (USNM) provided liberal access to his lab where CMM-V-4061 was whitened with sublimed ammonium chloride; many thanks. This work was made possible with funding from the Citizens of Calvert County, the Board of Calvert County Commissioners, MD, and the Clarissa and Lincoln Dryden Endowment for Paleontology at the Calvert Marine Museum.

VIII. 7. References

Achurra, L., 2004. Cambios del nivel del mar y evolución tectónica de la cuenca Neógena de Caldera, III Región. [Master´s thesis]: Santiago, Chile, Departamento de Geología de la Universidad de Chile, 138 p.

Achurra, L. E., J. P. Lacassie, J. P. Le Roux, C. Marquardt, M. Belmar, J. Ruiz-del-Solar, and S. E. Ishman. 2009. Manganese nodules in the Miocene Bah´ıa Inglesa Formation, north-central Chile: petrography, geochemistry, genesis and palaeoceanographic significance. Sedimentary Geology 217:128–139.

Banguera-Hinestroza, E., Cardenas, H., Ruiz-García, M., García, Y.F., Marmontel, M., Gaitán, E., Vásquex, R., and García-Vallejo, F. 2002. Molecular identification of evolutionarily significant units in the Amazon River Dolphin *Inia* sp. (Cetacean Iniidae). The Journal of Heredity 93:321-322.

Brisson, M. J. 1762. Le regnum animale in classes IX distributum, sive synopsis methodica sistens generalem animalium distributionem in classes IX, & duarum primarum classium, quadrupedum scilicet & cetaceorum, particularem dibvisionem in ordines, sectiones, genera & species. T. Haak, Paris, 296 pp.

Canto J., J. Yanez, and M.A. Cozzuol. 2002. Mamíferos marinos neógenos de la

Formación Bahía Inglesa, Caldera, III Región, Chile. In *Primer Congreso Latinoamericano de Paleontologia de Vertebrados, Resumenes Primer Congreso Latinoamericano de Paleontologia de Bertebrados. Santiago de Chile,* 2002:22-23.

Cassens, I., Vicario, S., Waddell, V. G., Balchowsky, H., Van Belle, D., Ding, W., Chen, F., Mohan, R. S. L., Simoes-Lopes, P. C., Bastida, R., Meyer, A., Stanhope, M. J., and Milinkovitch, M. C. 2000. Independant adaptation to riverine habitats allowed survival of ancient cetacean lineages. Proceedings of the National Academy of Sciences 97:11343-11347.

Cozzuol, M. A. 1985. The Odontoceti of the "Mesopotamiense" of the Parana River ravines. Systematic review. Investigations on Cetacea 7:39–53.

Cozzuol, M.A. 1996. The record of the aquatic mammals in southern South America. *In*: G. Arratia, (ed.). *Contributions to southern South America to Vertebrate Paleontology*, Münchner Geowissenschaftliche Abhandlungen, Reihe A, Geologie und Paläontologie 30: 321-342.

Cozzuol, M.A. 2010. Fossil record and the evolutionary history of Iniodea. pp. 193-217. *Chapter 10 in*: M. Ruiz-García, and J. Shostell, (eds.). *Biology,* *Evolution and Conservation of River Dolphins within South America and Asia.* Nova Science Publishers, New York.

Flower, W. H. 1867. Description of the skeleton of *Inia geoffrensis* and of the skull of *Pontoporia blainvillei*, with remarks on the systematic position of these animals in the order Cetacea. Transactions of the Zoological Society of London 6:87-116.

Fordyce, R. E. 1981. Rhabdosteid dolphins (Mammalia: Cetacea) from the Middle Miocene, Lake Frome area, South Australia.

Fordyce, R. E. and Muizon, C. de. 2001. Evolutionary history of Cetaceans: a review. Secondary adaptation of Tetrapods to Life in Water, J. -M Mazin & V de Buffrénil (eds): 169-132. 1174.

Geisler;, J. H., S. J. Godfrey, and O. Lambert. 2012. A new genus and species of late Miocene inioid (Cetacea, Odontoceti) from the Meherrin River, North Carolina. Journal of Vertebrate Paleontology 37-41.

Gibson, M. L. and J. H. Geisler. 2009. A new Pliocene dolphin (Cetacea: Pontoporiidae), from the Lee Creek Mine, North Carolina. Journal of Vertebrate Paleontology 29:966-971

Godfrey, S. J. and L. G. Barnes. 2008. A new genus and species of Late Miocene pontoporiid dolphin (Cetacea: Odontoceti) from the St. Marys Formation in Maryland. Journal of Vertebrate Paleontology 28:520–528.

Godfrey, S. J., J. H. Geisler, and O. Lambert. 2009 A new genus and species of Pliocene dolphin (Cetacea: Odontoceti: Inioidea) from North Carolina, U.S.A. Journal of Vertebrate Paleontology 29(3, Supplement):106A.

Kasuya, T. 1973. Systematic consideration of recent toothed whales based on the morphology of tympano-periotic bone. *The Scientific Report of the Whales Research Institute* 25: 1-104.

Muizon, C. de. 1988c. Les relations phylogénétiques des Delphinida (Cetacea; Mammalia). Annales de Paléontologie (Vert.-Invert.). *Editions Recherche sur les civilizations* 74(4): 159-227.

Muizon, C. de. 1988b. Les vertébrés fossiles de la Formation Pisco (Pérou) III: Les Odontocètes (Cetacea: Mammalia) du Miocène. *Editions Recherche sur les Civilizations* Paris. 244pp.

Nikaido, M., Matsuno, F., Hamilton, H., Brownell Jr, R., Cao, Y., Ding, W., Zuoyan, Z., Shedlock, A., Fordyce, R., Hasegawa, M., Okada, N., 2001. Retroposon analysis of major cetacean lineages: The monophyly of toothed whales and the paraphyly of river dolphins. Proceedings of the National Academy of Sciences of the United States of America 98, 7384-7389.

Pyenson, N. D. and E. Hoch. 2007. Tortonian Pontoporiid Odontocetes from the Eastern North Sea. Journal of Vertebrate Paleontology 27:757–762. doi: 10.1671/0272-4634(2007)27[757:TPOFTE]2.0.CO;2

Ray, C. E., Bohaska, D. J., Koretsky, I. A., Ward, L.W., and Barnes, L. G. (eds.). 2008. *Geology and Paleontology of the Lee Creek Mine, North Carolina, IV. Virginia Museum of Natural History Special Publication 14.* Virginia Museum of Natural History Press: Martinsville, Virginia.

Secchi, E. R. 2010. Life history and ecology of Franciscana, Pontoporia blainvillei (Cetacea, Pontoporiidae); pp. 301–322, Chapter16 in M. Ruiz-García, and J. Shostell, (eds.), Biology, Evolution and Conservation of River Dolphins within South America and Asia. Nova Science Publishers, New York.

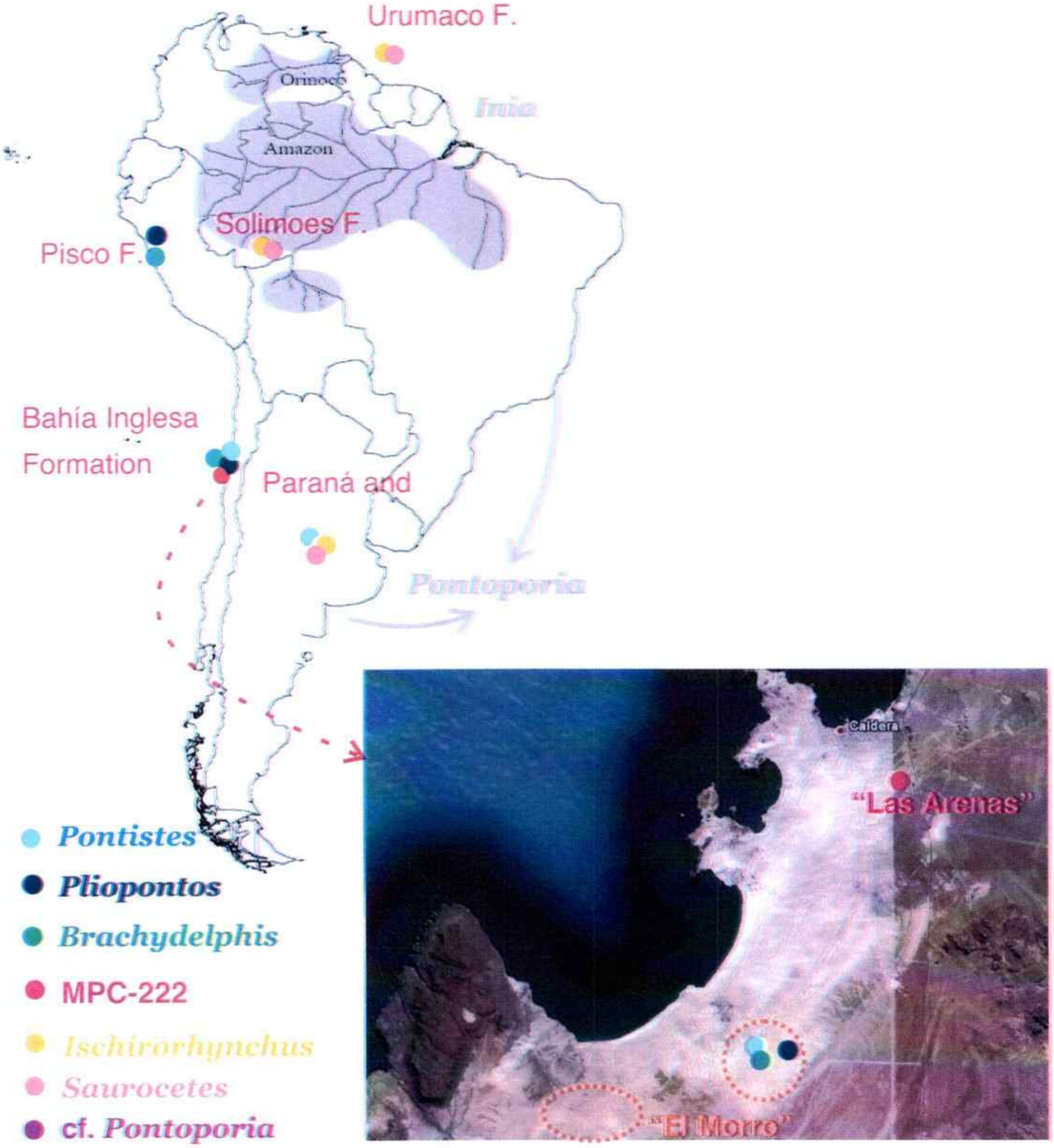


Figure 1. The distribution of south american Inioidea from the neogene to the present. In detail of the localities of the Bahía Inglesa Formation diverse and abundance vertebrate fauna.

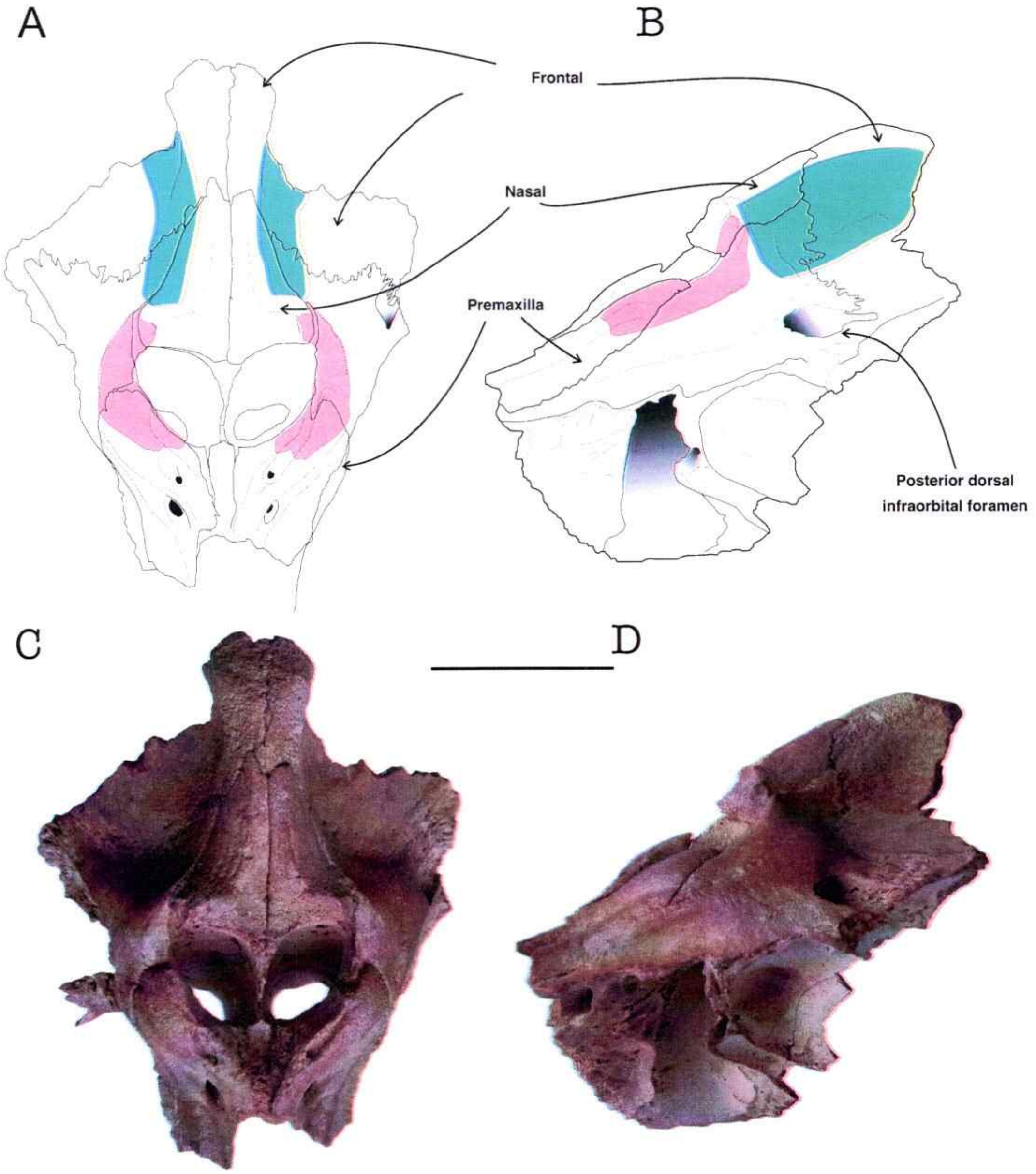


Figure 2. *MPC-222* (nov. gen. et sp.). A, C) dorsal view and C and D) lateral view. The green shape in the line-drwaws (A and B) correspond to surface of contact with the cranial bones of the vestibular sac and in light red to the nasoforntal and premaxillary sac together once it was not possible to trace the limit between these sacs. Scale bars equal 50 mm.

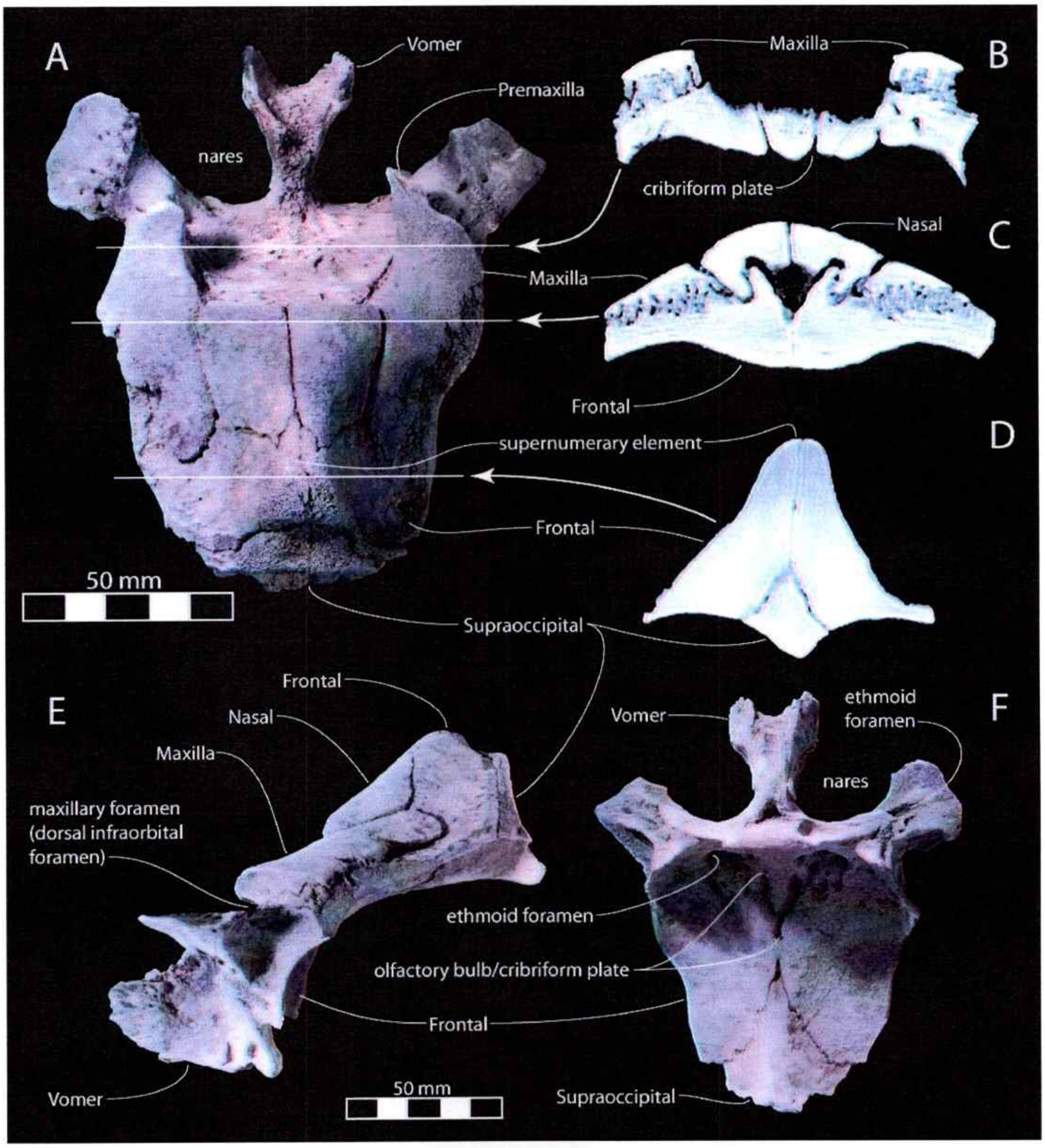


Figure 3. *CMM-V-4061* (nov. sp.). A, CMM-V-4061 in dorsal view. B, single CT-scan image through CMM-V-4061 as indicated by the transverse white line in A to which the corresponding arrow is pointing. C, single CT-scan image through the anterior part of the nasals as indicated by the white line in A. D, single CT-scan image through the vertex showing the supernumerary ossification between the frontals, as indicated by the white line in A. Scale bars equal 50 mm.

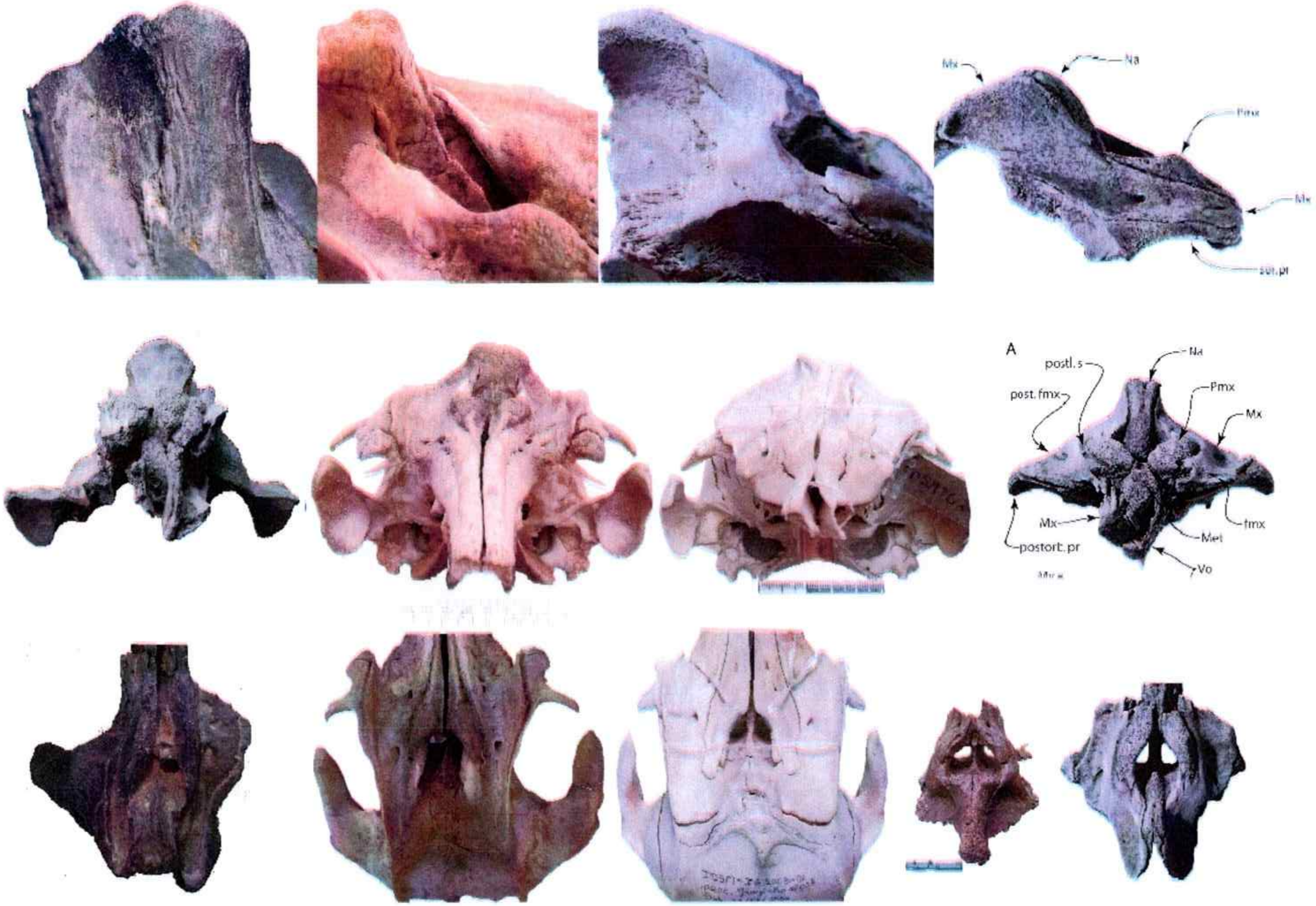


Figure 4 - Direct morphological comparison of selected Inioidea skulls in dorsolateral, frontal and dorsal view, from above to bellow. **A**) *Ischyrorhynchus vanbenedeni* (MACN 15135) B) adult specimen of *Inia geoffrensis* (IDSM Ig-9301); C) neonate specimen of *Inia geoffrensis* (IDSM Ig-2005-1), C); CMM-V-4061, E) SGO-PV.21605, F) *Pontoporia blainvillei* (UFSC 1290). All skulls are scaled to represent the same vertex size (from the anterior end of bony naris to supracocciptal crest). Scale bars = 5 cm.

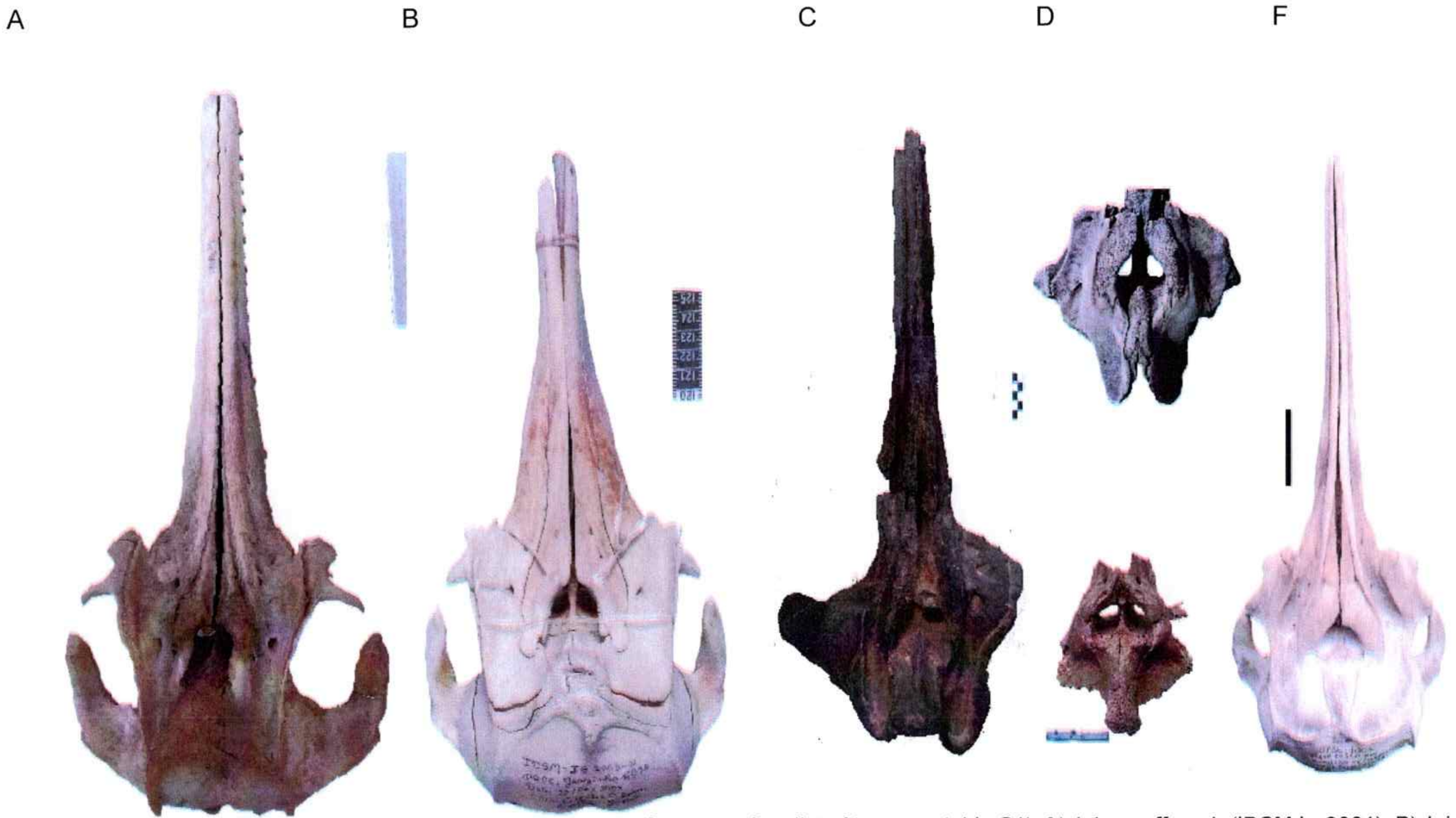


Figure 5 – Dorsal views of skulls of selected taxa in the dataset (for a complete list of taxa see table S1). **A**) *Inia geoffrensis* (IDSM Ig-9301); B) *Inia geoffrensis* (IDSM Ig-2005-1), C) *Ischyrorhynchus vanbenedeni* (MACN 15135); D) CMM-V-4061, E) SGO-PV.21605, F) *Pontoporia blainvillei* (UFSC 1290). All skulls are scaled to represent the same vertex size (from the anterior end of bony naris to supracocciptal crest). Escale bars = 5 cm.

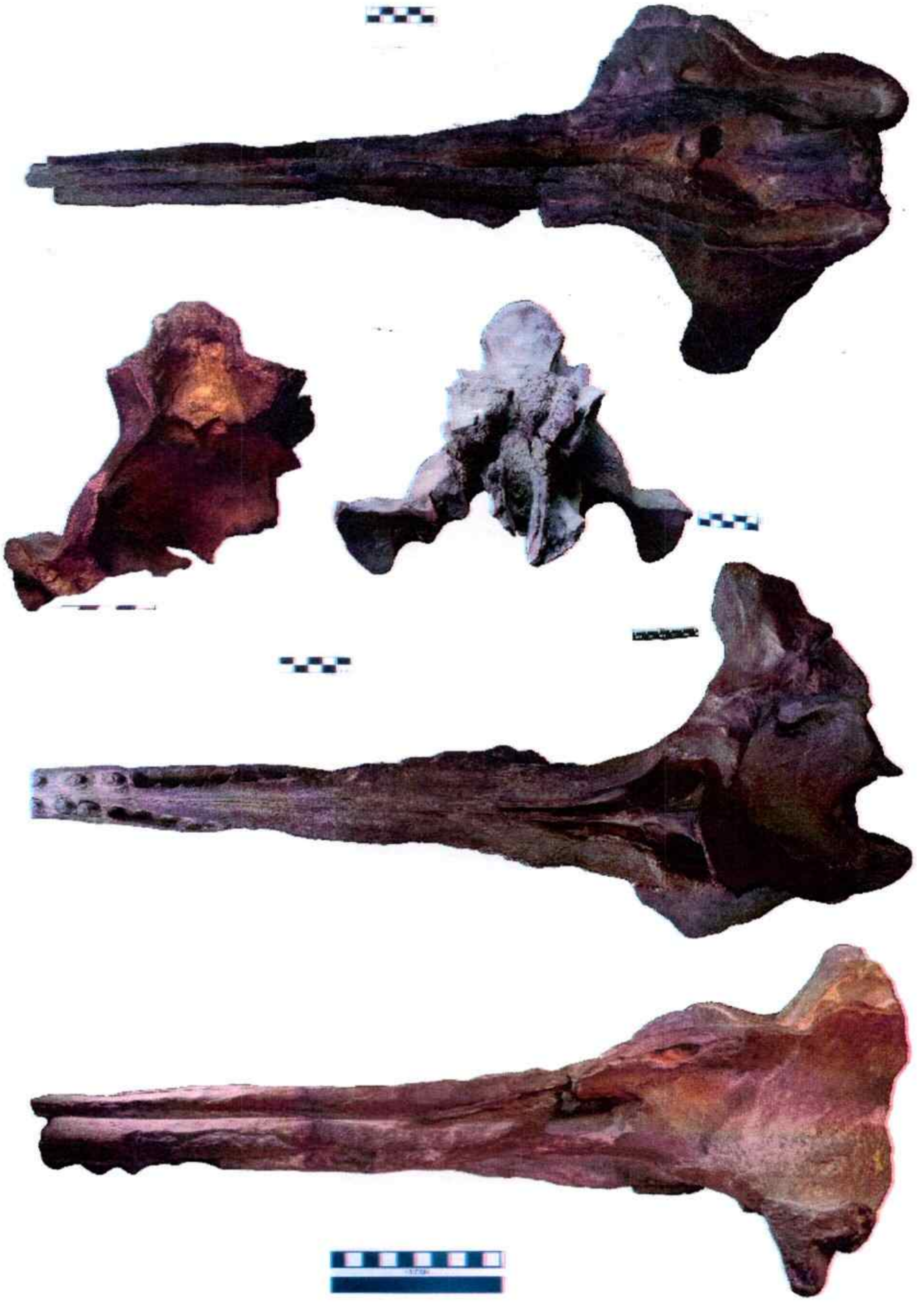


Figure 6 – Skull of the only argentinean river dolphin argentinean from the late miocene *Ischyrorhynchus vanbenedeni* (MACN 15135). A) Dorsal view, B) Occiptal view, C) frontal view of another referred specimen (MLP 5-16), D) ventral view and E) lateral view.

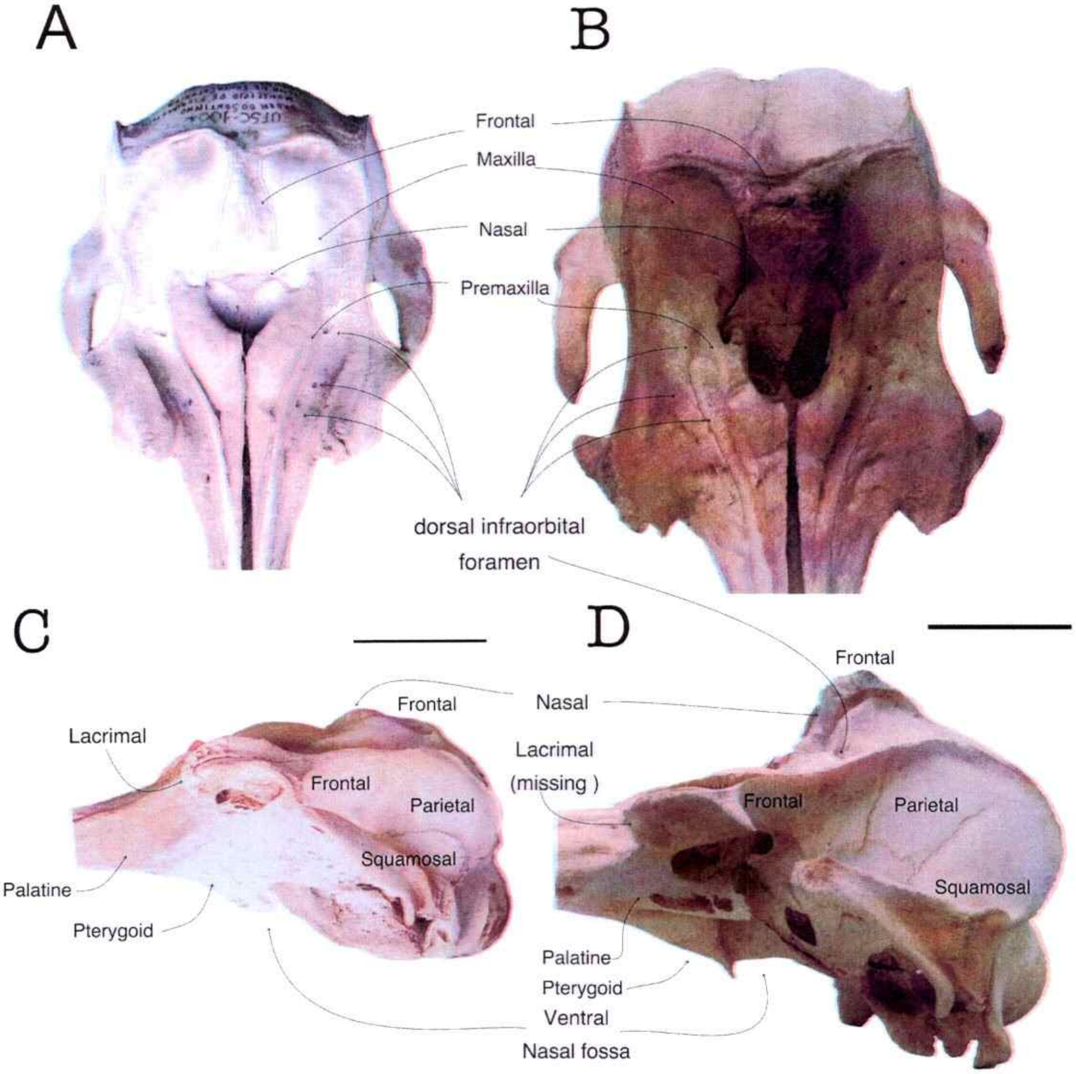


Figure 7 – A) dorsal and B) lateral view of the skull of *Inia geoffrensis* (MCN-M-32) subadult specimen and C) dorsal and Lateral view of the skull of *Pontoporia bainvillei* (UFSC 1290). Scale bar = 5cm

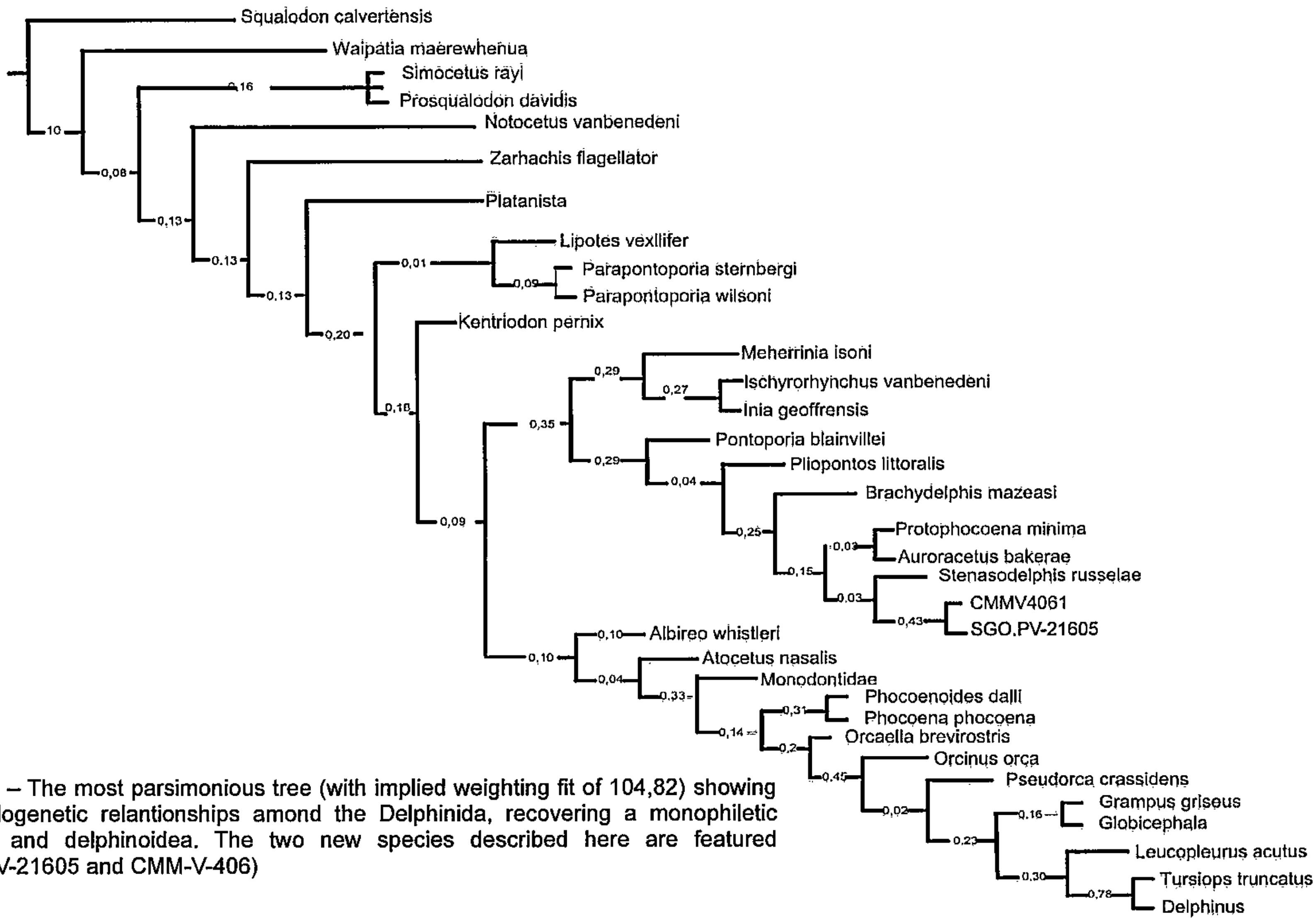


Figure 8 – The most parsimonious tree (with implied weighting fit of 104,82) showing the phylogenetic relantionships amond the Delphinida, recovering a monophiletic Inioidea and delphinoidea. The two new species described here are featured (SGO.PV-21605 and CMM-V-406)

Supplementary Information – Capítulo 4

I) Character list based on Geisler et al. (2012) morphologic sub-matrix:

The complete morphological matrix and coding of Geisler et al. (2011, 2012) was reviewed, there were three characters that were redefined or reinterpreted in the present work (47, 74, 77). The complete list of morphologic characters as it was used here, is presented. The matrix used here includes a total of 35 taxa including all Delphinida, Platanistoidea and outgroups (*Squalodon calvertensis, Waipatia maerewheua, Simocetus rayi)*. The characters that were not relevant in the reduced matrix were deactivated using the tools for recognizing homoplasic characters in TNT.

1. *Baleen.*—Absent (0); present (1) (Miller, 1923).

2. *Rostrum.*—Narrows in width anteriorly or anterior half approximately the same width as posterior half (0); anterior part widened transversely (1) (Muizon, 1994).

3. *Length of rostral portion of maxilla* (ordered).—Short, rostral portion of maxilla < 43% of condylobasal length excluding the premaxillae (0); intermediate, rostral portion between 48 and 70% of modified condylobasal length (1); elongate,

rostral portion > 73% modified condylobasal length (2) (modified from Barnes, 1985).

4. *Anterior half of maxilla.*—Its lateral edge in cross section forms an angle of 60° to 45° (0); highly acute angle with flattened maxilla (1) (modified from Barnes, 1990).

5. *Vomerine trough, or mesorostral canal.*—Open, vomer in cross section is V-shaped or U-shaped (0); partially or completely filled in with bone, becomes solid rod of bone (1) (Moore, 1968).

6. *Rostral constriction well anterior to antorbital notch.*—Absent (0); present (1) (Barnes, 1985).

7. *Width of rostrum at antorbital notch* (ordered).—Wide, rostral width > 92% the width across of middle of orbits (0); fairly wide, between 82% and 72% the width across orbits (1); narrow, between 68% and 46% the orbital width (2); very narrow, between 32% and 29% the orbital width (3).

8. *Premaxilla in dorsal view.*—Portion adjacent to and anterior to nasal opening narrows or remains the same width anteriorly (0); widens at anterior end (1).

9. *Premaxillae on anterior two thirds of rostrum* (ordered).—With skull in dorsal view, contact along midline for most or entire length (0); sporadic contact along rostrum (1); separated by a narrow fissure for entire length (2); clear separation although mesorostral gutter still has a partial roof (3); very wide separation, mesorostral gutter is completely open along entire length (4) (modified from Muizon, 1988a; Fordyce, 1994; Messenger and McGuire, 1998).

10. *Suture between maxilla and premaxilla on rostrum* (ordered).—Suture fused along most of rostrum (0); anterior quarter of rostrum fused with remaining portions unfused (1); unfused along entire rostrum but articulation tight (2); suture is unfused and marked by a deep grooved (3) (modified from Fordyce, 1994; Messenger and McGuire, 1998).

11. *Posterior region of rostral edge* (ordered).—Lateral margin is straight or gently concave with skull in dorsal view (0); slightly bowed outward causing a V-shaped antorbital notch (1); bowed far outward forming a deep U-shaped antorbital notch (2); lateral margin of maxilla nearly contact lacrimal and jugal resulting in the opening of the notch being a narrow slit (3).

12. *Posterodorsal portion of maxilla*.—Sutured to frontal (0); not sutured, separated from frontal by a distinct gap, which is situated between the maxilla anterodorsal and the frontal ventrally (1) (McLeod et al., 1993).

13. *Steep face on anterolateral edge of zygomatic process of maxilla clearly separating it from rostral portion of maxilla* (ordered).—Absent (0); present but low (1); present and well developed (2).

14. *Posterior end of ascending process of maxilla.*—Tapers to a point (0); end is squared-off (1). Cannot be scored for taxa with maxilla covering most of supraorbital processes of the frontal.

15. *Posterior wall of antorbital notch.*—Maxilla (0); lacrimal and jugal (1).

16. *Palatal surface of rostrum.*—Flat or gently concave (0); bears pronounced longitudinal keel along the midline of the rostrum (1) (McLeod et al., 1993). The keel is formed by vomer and medial edges of maxillae

17. *Palatal surface of maxilla.*—Bears few vascular foramina, those that are present are small (0); bears many, large vascular foramina that open laterally and anterolaterally into long sulci (1); bears numerous small vascular foramina that lack sulci (2).

18. *Posterior end of palatal surface of rostrum at the suture between palatine and maxilla* (ordered).—Concave to flat, depth of rostrum, measured as the

dorsoventral distance from the level of the lateral edge of rostrum to the ventral-most part of rostrum, is < 8% the width of rostrum at antorbital notches (0); convex, depth between 11% and 25% the rostral width (1); highly convex, rostral depth > 27% the rostral width (2). The convexity of the rostrum is a part of characters included by Barnes (1985) and Fordyce (1994).

19. *Palatine.*—Sutured to maxilla and suture visible (0); fused to maxilla (1) (Messenger and McGuire, 1998).

20. *Palatine/Maxilla suture.*—In ventral view, suture between both palatines and both maxillae is straight transversely or bowed anteriorly (0); maxillae have posterior

processes that separate palatines anteriorly, suture around midline is V-shaped and points posteriorly (1).

21. *Teeth in females.*—Erupt in adulthood (0); do not erupt in adulthood but remain in the crypt (1) (Moore, 1968).

22. *Tooth rows.*—Separated and diverge posteriorly (0); left and right sides adjacent to the midline and thus close together, are nearly parallel (1) (Zhou, 1982).

23. *Number of double-rooted teeth in maxilla* (ordered).—None (0); 1 or 2 (1); 4 (2); 5 (3); 6 (4); 7 (5); 8 or more (6). The primitive state for Cetacea and Artiodactyla is probably state —3‖; however, the character was coded with no teeth as state —0‖ in order to implement the ordering of states in the phylogenetic analyses. Muizon (1987, 1991, 1994) noted that the absence of all double-rooted teeth is a synapomorphy of Platanistidae plus Squalodelphinidae.

24. *Number of teeth with alveoli completely enclosed in the maxilla* (ordered).—None, 1, 2, or 3 (0); 7 to 8 (1); 9 to 10 (2); 11 to 13 (3); 15 to 17 (4); 21 to 23 (5); 26 to 29 (6); 32 to 39 (7); 50 to 60 (8) (modified from Messenger and McGuire, 1998). State —1‖ is probably the primitive condition for Cetacea and Artiodactyla; however, the character was coded with no teeth as state —0‖ in order to implement the ordering of states in the phylogenetic analyses. Barnes (1985) listed extreme polydonty as a synapomorphy of the genus *Parapontoporia*.

25. *Large diastemata between posterior buccal teeth.*—Absent (0); present (1).

Teeth Morphology

26. *Tooth enamel.*—Smooth (0); bears reticulating striae (1); nodular (2) (Zhou, 1982).

27. *Lower anterior mandibular teeth.*—Conical (0); spatulate (1); laterally compressed (2) (Messenger and McGuire, 1998). Heyning (1989b) described state —1‖ and Moore (1968) described state —2‖.

28. *Lower anterior teeth.*—Deeply rooted with at least half of tooth forming root (0); not deeply rooted (1) (Flower, 1872; Moore, 1968).

29. *Accessory shelf on posterior teeth.*—Present (0); absent (1) (Flower, 1867; Messenger and McGuire, 1998).

30. *Posterior buccal teeth* (ordered).—High peg-shaped teeth, crown base is < 37% the crown height (0); nearly an equilateral triangle, crown base is between 100% to 148% the crown height (1); wide low teeth, crown base is > 180% the crown height (2).

31. *Buccal teeth ectocingulum.*—Absent (0); present (1).

32. *Buccal teeth entocingulum.*—Present (0); absent (1).

33. *Buccal teeth.*—Bear accessory cusps (0); cusps absent (1) (Kellogg, 1923b).

34. *Central cusp as compared to denticles.*—Much larger (0); subequal (1). Cannot be scored for taxa that lack denticles.

Mandibular

35. *Anterior-most mandibular teeth* (ordered).—Oriented anteriorly (0); vertical (1); inclined posteriorly (2) (Moore, 1968; Messenger and McGuire, 1998).

36. *Anterior-most mandibular teeth* (ordered).—Smaller than posterior teeth (0); approximately same size as posterior teeth (1); greatly enlarged (2) (modified from Flower, 1872; Heyning, 1989; Muizon, 1991; Messenger and McGuire, 1998).

37. *Number of teeth number in lower jaw* (ordered).—None (0); 1 (1); 2 (2); 8 to 9 (3); 11 to 12 (4); 13 to 14 (5); 20 to 23 (6); 24 to 27 (7); 28 to 34 (8); more than 40 teeth (9) (modified from Messenger and McGuire, 1998). State —3‖ is probably the primitive condition for Cetacea and Artiodactyla; however, the character was coded with no teeth as state —0‖ in order to implement the ordering of states in the phylogenetic analyses.

38. *Mandible in lateral view.*—Straight (0); arched dorsally (1) (McLeod et al., 1993).

39. *Length of mandibular symphysis* (ordered).—Short, mandibular symphysis forms less than 28% of the total mandibular length (0); long, symphysis length between 33% and 40% of the mandibular length (1); very long, symphysis forms more than 48% of the length of the mandibles (2) (modified from Heyning, 1989; Barnes, 1990).

40. *Mandibular symphysis* (ordered).—Fused (0); sutured but unfused (1); not sutured, connected by ligaments (2) (Fordyce, 1994). Barnes (1990) listed a loose mandibular symphysis as a synapomorphy of Mysticeti. State —1‖ is probably the primitive condition for Cetacea and Artiodactyla; however, the fused condition was designated as state —0‖ in order to implement the ordering of states in the phylogenetic analyses.

41. *Longitudinal groove on underside of mandible*.—Absent (0); present (1) (Miller, 1923).

42. *Mandible* (ordered).—Bowed medially (0); straight (1); slightly bowed laterally, a line drawn from the posterior-most to anterior-most points stays within body of mandible (2); strongly bowed outward, line from anterior to posterior points does not entirely lie within body of mandible (3) (Miller, 1923; Sanders and Barnes, 2002).

43. *Mandibular fossa.*—Small or absent (0); present and large, forms a large cavity posterior to mandibular foramen (1) (Barnes, 1990).

44. *Shape of coronoid process* (ordered).—Long and low, height of mandible at coronoid process < 89% the length of coronoid (0); height of mandible between 100% and 177% the length of coronoid (1); short and high, height between 203% and 300% coronoid length (2); very high and short, height > 450% the length of coronoid (3).

45. *Dorsal surface of condyle.*—Elevated above dorsal edge of the rest of mandible, not counting coronoid process (0); at same level as rest of mandible (1) (Sanders and Barnes, 2002).

Orbit

46. *Supraorbital processes of frontal.*—Are horizontal or gradually slope lateroventrally away from vertex of skull (0); abruptly depressed at base to a level noticeably below that of dorsal surface of interorbital region (1); slope laterodorsally away from vertex (2) (Miller, 1923; Messenger and McGuire, 1998).

47. *Dorsal edge of orbit relative to lateral edge of rostrum* (ordered).—Below the level of the edge of rostrum (0); orbit low, either in line with edge of rostrum or

slightly above it, height of orbit < 46% the height of rostral base, both heights measured relative to the lateral edge of rostrum (1); orbit low, height of dorsal edge of orbit between 50% and 92% the rostral height (2); orbit high, height between 100% and 128% the rostral height (3); orbit elevated well above rostrum, orbital height > 163% the rostral height (4).

48. *Frontal/Maxilla suture.*—With skull in lateral view, suture is approximately horizontal, and lateral exposure of frontal over the orbit does not thicken posteriorly (0); angled posterodorsally at and angle of 50° to 70° from axis of rostrum, lateral exposure of frontal thickens posteriorly (1) (Miller, 1923). This character cannot be scored for taxa that lack overlap of the maxilla onto the frontal.

49. *Anterior edge of the supraorbital process* (ordered).—Oriented anteromedially (0); oriented slightly anterolaterally, forms an angle < 30° with sagittal plane (1); oriented anterolaterally, forms an angle between 35° and 60° (2); oriented anterolaterally or laterally, forms and angle between 68° and 90° degrees (3); oriented posterolaterally, forms an angle between 107° and 120° (4); oriented posterolaterally, forms an angle > 142° (5). The anterior edge of the supraorbital process participates in the formation of the antorbital notch. An antorbital notch opening anteriorly was listed by Barnes (1990) as a synapomorphy of Odontoceti.

50. *Lacrimal*.—Forms small bone on anterior edge of orbit with small orbital portion (0); enlarged both posteromedially and anterolaterally paralleling anterior edge of supraorbital process of frontal, shaped like a thick rod (1).

51. *Lacrimal* (ordered).—Restricted below supraorbital process of frontal (0); wraps around anterior edge of supraorbital process of frontal and slightly overlies its anterior end (1); greatly expanded posterodorsally and covering much of lateral side of supraorbital process of frontal (2) (modified from Miller, 1923; Kellogg, 1923a).

52. *Lacrimal foramen or groove*.—Present (0); absent (1).

53. *Lacrimal and jugal*.—Separate (0); fused (1) (Miller, 1923; Heyning, 1989).

54. *Jugal and lacrimal*.—Jugal and lacrimal contact each other externally (0); lacrimal excluded from edge of skull, jugal directly contacts anterior edge of frontal (1) (modified from Miller, 1923).

55. *Combined anteroposterior length of the lacrimal and jugal exposure that is posterior to antorbital notch* (ordered).—With skull in ventral view, exposure is small and combined length forms < 31% of anteroposterior distance from

antorbital notch to postorbital ridge (0); intermediate, forms between 50% and 92% of that distance (1); large, forms between 62% and 69% that distance (2); very large, forms > 77% of that distance (3). The postorbital ridge is a curved ridge that extends from the postorbital process to the orbital foramen (Fordyce, 2002). It follows much of the course of the orbital nerve and demarcates the separation between the orbital and postorbital regions of the skull.

56. *Jugal.*—Thick and sturdy (0); thin splint or incomplete or absent (1) (Miller, 1923).

57. *Dorsolateral edge of internal opening of infraorbital foramen.*—Formed by maxilla (0); formed by maxilla and lacrimal and/or jugal (1); formed by lacrimal and/or jugal (2); formed by frontal (3) (modified from Miller, 1923).

58. *Ventromedial edge of internal opening of infraorbital foramen* (ordered).—Formed by maxilla (0); formed by maxilla and palatine and/or pterygoid (1); formed by palatine and/or pterygoid (2) (modified from Miller, 1923).

59. *Maxillary infraorbital plate.*—Absent (0); present but small (1), present and large (2) (Miller, 1923). The infraorbital plate of the maxillary is the posterior part of the maxilla underlying the orbit.

60. *Anterior-most point on the posterior edge of the supraorbital process* (ordered).—The anterior-most point is at the lateral edge of postorbital process (0); located laterally, between 70% and 74% of transverse distance from sagittal plane to the lateral edge of postorbital process (1); positioned approximately midway, located between 42% and 61% of that distance (2); medially positioned, located at a point < 34% of that distance (3).

61. *Postorbital process.*—Long and projects posterolaterally and slightly ventrally (0); short and directed ventrally (1).

62. *Postorbital ridge.*—Present, forms well-defined curved ridge on posterior edge of sulcus for optic nerve (0); no well-defined ridge, region is gently convex (1).

Facial Region

63. *Facial region of skull, skull in lateral view* (ordered).—Concave (0); flat (1); moderately arched dorsally (2); greatly arched dorsally (3) (Miller, 1923; Heyning, 1989; Messenger and McGuire, 1998).

64. *Infraorbital foramina* (ordered).—Single (0); two (1); three or more (2) (Barnes, 1984).

65. *Rostral basin.*—Absent or poorly defined (0); present, situated medial to antorbital notch and anterior to supraorbital process of frontal, best developed medially and ventrally where lateral edge of maxilla is very thin (1).

66. *Transverse distance between lateral edges of right and left premaxillae at antorbital notches* (ordered).—Small, distance < 48% the width of rostrum at antorbital notches (0); intermediate, distance between 52% and 64% the antorbital width (1); wide, distance > than 78% the antorbital width (2).

67. *Premaxillae immediately anterior to external bony nares* (ordered).—Widely separate with skull in dorsal view, gap between medial edges of premaxillae > 63% the maximum width of external bony nares (0); narrow separation, gap between premaxillae between 56% and 32% the width of external nares (1); separation absent or nearly so, gap < 28% the nares width (2).

68. *Premaxillae anterior to nasal openings* (ordered).—Are flat or concave, form a premaxillary sac fossa (spiracular plate) (0); convex transversely (1); form distinct bosses or ―premaxillary eminencies‖ with steep posterior faces on anterior edges of nasal openings (2) (Muizon, 1988a; Barnes, 1990). This character was split into two characters by Messenger and McGuire (1998). They are combined here because a taxon with bosses cannot simultaneously have a fossa.

69. *Premaxillary foramina* (ordered).—Absent (0); present and one on right side (1); two on right side (2); three on right side (3) (modified from Barnes, 1990).

70. *Premaxillary foramen size* (ordered).—Right and left subequal (0); left larger than right (1); left much larger than right (2) (modified from Messenger and McGuire, 1998).

71. *Position of premaxillary foramen.*—Far anterior of antorbital notch and anterior edge of supraorbital process (0); approximately medial to or posterior to antorbital notch region, which is at the junction of supraorbital process with rostrum (1).

72. *Posterolateral sulcus from premaxillary foramen* (ordered).—Sulcus very short or absent (0); present and short (1); present and extends to level equivalent to middle of nasal openings (2) (modified from Muizon, 1988a).

73. *Premaxillae.*—Restricted to medial position adjacent to mesorostral canal and nasal opening (0); extended laterally covering much of the supraorbital process (1). The maxilla in turn overlies the premaxilla (Kellogg, 1923a).

74. *Posterior-most end of ascending process of premaxilla* (ordered).—Located just anterior to or in a transverse line with anterior edge of supraorbital process of the frontal (0); in line with anterior half of supraorbital process of frontal or halfway point, anteroposteriorly, of supraorbital process (1); in line with posterior half of supraorbital process or postorbital process of frontal (2); in line with gap between postorbital process and anterior tip of zygomatic process of the squamosal or in line with anterior tip of the latter process (3); in line with space between anterior tip of zygomatic process of squamosal and anterior edge of floor of the squamosal fossa or in line with anterior edge of floor of the squamosal fossa (4); located posterior to anterior edge of floor of the squamosal fossa (5).

75. *Maxillary foramen.*—Absent (0); present and one, situated over supraorbital process of frontal (1); two (2); foramina absent because roof of canal that carries posterior branches of internal maxillary artery and the maxillary division of infraorbital nerve is unossified (3) (modified from Barnes, 1990). The maxillary foramen (or foramina) is distinct from the facial opening(s) of the infraorbital canal.

76. *Maxilla* (ordered).—Abuts anterior edge of supraorbital process of frontal (0); partially covers supraorbital process (1); covers almost entire surface (2) (Miller,

1923; Fordyce, 1994). Fordyce erected state —1ll for *Archaeodelphis* (Allen, 1921).

77. *Posterior-most edge of the ascending process of maxilla* (ordered).—Situated well anterior to anterior edge of orbit (0); in transverse line with anterior half of supraorbital process of frontal or in line with the halfway point, anteroposteriorly, of supraorbital process (1); in line with posterior half of supraorbital process or in line with postorbital process of frontal (2); in line with gap between postorbital process and the anterior tip of zygomatic process of squamosal or in line with anterior tip of the latter process (3); in line with space between anterior tip of zygomatic process of squamosal and anterior edge of floor of squamosal fossa or in line with anterior edge of the floor of squamosal fossa (4); posterior to anterior edge of floor of squamosal fossa (5).

78. *Anterolateral corner of maxilla overlying supraorbital process of frontal*.—Thin and equal in thickness to parts posteromedial (0); thickened with thinner maxilla in posteromedial direction (1). The thickened maxilla plus other nearby elevated structures (e.g. nasal opening, supraoccipital), delimit the edges of a broad fossa for the insertion of the maxillonasolabialis muscle.

79. *Maxillary ridge* (ordered).—Absent (0); present (1); form transversely compressed and high crest (2); crest arches over and encloses a cavity for the

melon (3) (modified from Miller, 1923; Muizon, 1987). Messenger and McGuire (1998) split this into two characters; however, this results in scoring the absence of the crests twice.

80. *Anterior edge of nasals* (ordered).—In transverse line with incisors, canines, or intervening diastema (0); in line with P1 (1); in line with P2 or about 18% of the total rostral length towards anterior edge of rostrum (2); just anterior to or in line with anterior edge of supraorbital process of frontal (3); in line with anterior half of supraorbital process of frontal or in line with the halfway point, anteroposteriorly, of supraorbital process (4); in line with posterior half of supraorbital process or in line with postorbital process of frontal (5); in line with gap between postorbital process and the anterior tip of zygomatic process of squamosal or in line with the anterior tip of the latter process (6); in line with space between the anterior tip of zygomatic process of squamosal and anterior edge of the floor of squamosal fossa or in line with anterior edge of the floor of squamosal fossa (7); posterior to the anterior edge of the floor of the squamosal fossa (8).

81. *Anterior edge of nasal openings.*—V-shaped, premaxillae gradually converge anteriorly to the midline (0); U-shaped, premaxillae abruptly converge anteriorly to the midline (1) (Muizon, 1988a). Muizon (1988a) described state —0‖ as heart-shaped.

82. *Maxillae* (ordered).—In region anterior to nasal openings, maxillae are exposed lateral to premaxillae (0); maxillae are exposed at posterior end of roof of

mesorostral gutter, medial to the premaxillae and nearly converge on midline (1); same as 1 except maxilla also exposed on anterior edge of nasal openings (2) (Muizon, 1988a).

83. *Ossicles.*—Absent (0); present, occur in anteromedial corners of nasal openings, probably a derivative of the maxilla (1) (Muizon, 1988a).

84. *Right premaxilla* (ordered).—Posterior edge approximately in line with posterior edge of left premaxilla (0); right premaxilla extended distinctly farther than left (1); right extended much farther than left (2) (modified from Barnes, 1990; Messenger and McGuire, 1998).

85. *Transverse width of right premaxilla immediately anterior to external bony nares* (ordered).—Distinctly narrower than left premaxilla (0); subequal, width of right premaxilla within 10% of the width of left premaxilla (1); right wider, width is between 130% and 145% the width of the left (2); right much wider, width > 167% the width of the left (3)..

86. *Right premaxilla.*—Portion posterior to nasal openings wider than portion anterior to opening, with nasal septum angled anteriorly and to the right (0); portion anterior wider than portion posterior to nasal opening, septum angled anteriorly and to the left (1). Cannot be scored for taxa that lack extension of the premaxilla posterior to the nasal openings or those that lack asymmetrical widening of the right premaxilla.

87. *Osseous external nasal openings.*—Left and right are the same size (0); left is twice or more the size of the right (1) (Barnes, 1990).

88. *Supracranial basin.*—Absent (0); present (1) (Heyning, 1989).

89. *Posterior end of premaxilla.*—Posterior end adjacent to lateral edge of nasal opening (0); angled slightly laterally resulting in the following sequence, from lateral to medial, in one transverse plane: premaxilla, maxilla, anterior edge of nasals or mesethmoid (1) (Muizon, 1988a; Heyning, 1989).

90. *Angle of premaxillae anterior to external bony nares, skull in lateral view (ordered).*—Low angle, premaxillae form an angle < 28° with the lateral edge of rostrum (0); intermediate angle, form an angle between 30° and 40° (1); high angle, form an angle > 45° (2) (modified from Moore, 1968).

91. *Premaxillae adjacent to nasal opening* (ordered).—Thin dorsoventrally and porous internally (0); pachyostotic, in direction perpendicular to face, and pachyosteosclerotic but nasals and premaxillae equally project dorsally and anteriorly (1); extreme pachyostosis, premaxillae adjacent to nasals project farther outward, anteriorly and dorsally (2) (modified from Moore, 1968).

92. *Proximal ethmoid region.*—Not visible in dorsal view, roofed over by nasals (0); exposed dorsally (1) (Miller, 1923).

93. *Mesethmoid.*—Forms T-shaped bone with median plate separating right and left nasal passages, not all of the dorsal part is divided by median plate (0); bears expanded posterodorsal plate which is not divided by median plate, median plate situated more ventrally (1) (modified from Muizon, 1984; Muizon, 1988a). This bone may include parts of the cribiform and perpendicular plates of the ethmoid.

Facial Soft Tissue

94. *Shape of soft tissue external nares.*—Crescent with apices pointed anteriorly (0); crescent with apices pointed posteriorly, might be skewed (1); rectangular (2); a longitudinal slit, might be slightly sigmoidal or angled (3); comma-shaped (4) (modified from Messenger and McGuire, 1998).

95. *Soft tissue nasal passages distal to bony external nares* (ordered).—Separate with two separate soft tissue external nares (0); separate for most of length but confluent just proximal to blowhole (1); confluent (2) (Heyning, 1989; Messenger and McGuire, 1998).

96. *Orientation of right soft tissue nasal passages.*—Oriented anterodorsally (0); oriented dorsally (1) (Messenger and McGuire, 1998). Cannot be scored for taxa that have little soft tissue in the facial area. In those taxa the bony and soft tissue external nares are in the same position.

97. *Right posterior dorsal bursa.*—Small (0); hypertrophied to form the spermaceti organ (1) (Cranford et al. 1996).

98. *Melon* (ordered).—Absent (0); small (1); hypertrophied (2) (Heyning and Mead, 1990).

99. *Distal sacs.*—Absent (0); present, situated immediately distal to museau de singe (1) (modified from Heyning, 1989). The vestibular sacs are considered homologous to the distal sacs of the right nasal passage of physeterids.

100. *Left and right distal sacs.*—Equal in size (0); right larger, includes physeterid condition of no distal sac on the left nasal passage (1) (Mead, 1975; Heyning, 1989).

101. *Blowhole ligament.*—Absent (0); present (1) (Heyning, 1989).

102. *Right posterior nasal sac* (ordered).—Present and elongate, in some cases it reaches osteological vertex (0); reduced and short, never reaches osteological vertex (1); absent (2). This is the same as the frontal sac of physeterids.

103. *Nasofrontal sacs* (ordered).—Absent (0); portions posterior to nasal passage present (1); same as previous state except that sacs extend anterodorsally around, and then in front of, the nasal passages; in dorsal view both nasofrontal sacs form a horseshoe shape (2) (Heyning, 1989).

104. *Inferior vestibule.*—Absent (0); present, forms a diverticulum of nasal passages posterior to blowhole ligament (1) (Heyning, 1989).

105. *Premaxillary sacs.*—Absent (0); present, form the most proximal diverticulum of nasal passages; they extend anteriorly adjacent to dorsal surfaces of premaxillae (1) (Heyning, 1989).

106. *Accessory sac.*—Absent (0); present, forms a small diverticulum of inferior vestibule and extends anterolaterally around the attachment of blowhole ligament to premaxilla (1) (Mead, 1975).

Vertex and Area Adjacent to Nares

107. *Inflection of ascending process of premaxilla.*—Gradual with premaxilla in dorsal view smoothly tapering as premaxilla shifts from a horizontal to a mostly vertical position (0); abrupt with an anterior splint of maxilla that emarginates the posterior edge of premaxilla and splits it into a posterolateral plate and posteromedial splint (1) . The inflection point is where the premaxilla shifts from a primarily horizontal position, mainly on the rostrum, to a more vertical position, mainly adjacent and posterior to the nasal openings (derived from Fordyce, 1994).

108. *Position of inflection of premaxilla* (ordered).—In transverse line with P1 (0); in line with P2 or about 18% of total rostral length towards anterior edge of rostrum (1); just anterior to or in line with anterior edge of supraorbital process of frontal (2); in line with anterior half of supraorbital process of frontal or in line with the halfway point, anteroposteriorly, of supraorbital process (3); in line with posterior half of supraorbital process or in line with postorbital process of frontal (4); in line with gap between postorbital process and the anterior tip of zygomatic process of squamosal or in line with the anterior tip of the latter process, space

is absent in some taxa (5); in line with space between the anterior tip of zygomatic process of squamosal and anterior edge of the floor of squamosal fossa or in line with anterior edge of the floor of squamosal fossa (6); posterior to anterior edge of the floor of squamosal fossa (7).

109. *Premaxillary cleft.*—Absent (0); present, posterior part of ascending process of premaxilla bears a distinct cleft that originates from at posterior edge of the premaxilla and continues anteriorly dividing the premaxilla in two (1); present but cleft is shallow (2). In odontocetes, the cleft begins at the anterior splint of the maxilla and helps divide the posterolateral plate from the posteromedial splint.

110. *Premaxillae adjacent to and at posterior edge of the nasal opening* (ordered).—Do not clearly overhang maxillae (0); premaxillae overhang maxillae (1); premaxillae greatly enlarged laterally, region between lateral edge of the right premaxilla and supraoccipital is partially enclosed (2) (Muizon, 1991).

111. *Narial pit* (new term).—Absent (0); present, an anterior extension of nasal passage and forms a blind pocket in the maxilla just dorsal to maxilla/palatine suture; medial wall of pocket is formed by vomer (1). This character is usually not visible in complete skulls.

112. *Posterior end of ascending process of premaxillae* (ordered).—Face anterolaterally (0); face anteriorly (1); face anteromedially (2) (modified from Moore, 1968).

113. *Nasal bones* (ordered).—Two (0); one (1); none (2) (Heyning, 1989).

114. *Suture between right and left nasals and right and left frontals* (ordered).—Shifted towards right side (0); situated on midline (1); shifted towards left side (2) (Barnes, 1985). Character state ―1‖ is probably the primitive condition for Cetacea and Artiodactyla; however, the character was coded with suture on the right side as state ―0‖ in order to implement the ordering of states in the phylogenetic analyses.

115. *Dorsoventral thickness of anterior edge of nasal* (ordered).—Very thin, nasal thickness < 82% of the anterior nasal width (0); thick, nasal thickness between 100% and 173% of the nasal width (1); very thick, > 200% the nasal width (2). Measurement taken approximately five millimeters from anterior edge.

116. *Both nasals in dorsal view.*—Anterior edges are straight in one transverse plane (0); with point on midline and a gap on each side between premaxilla and nasal (1) (Moore, 1968). The shape of the nasals is based on the dorsal surface. In some cases the nasals may come to a point medially but at a more ventral position adjacent to the mesethmoid plate (state 0), (e.g. *Inia* AMNH 93412).

117. *Nasal* (ordered).—Elongate anteroposterior plate or blocky (0); anteroposteriorly compressed into a nearly vertical plate with fossa on ventrolateral surface for

posterior nasal sac (caudal sac of Cranford et al., 1996) (1); fossa well excavated with boss delimiting dorsal edge (2) (modified from Muizon, 1988a; Messenger and McGuire, 1998).

118. *Nasals*.—Medial portions roughly in same horizontal plane as lateral portions or higher (0); medial portions greatly depressed forming a median trough immediately posterior to nasal openings (1) (Muizon, 1988a, 1991). This character appears in some ziphiids and also some kentriodontids where it is called the internasal fossa by Muizon (1988a).

119. *Maximum transverse width of both nasals* (ordered).—Very narrow, < 37% of the maximum width of the external bony nares (0); narrow, width between 55% and 89% of the nares width (1); within 10% of the nares width (2); wide, width between 123% and 140% the nares width (3); very wide, between 152% and 160% the nares width (4); extremely wide, width > 188% the width of external bony nares (5).

120. *Combined width of posterior edge of nasals* (ordered).—Wide, width > 150% the maximum width of external bony nares (0); subequal to external nares, width between 85% and 135% the nares width (1); narrow, width between 79% and 50% the nares width (2); very narrow, width between 44% and 39% the nares width (3); extremely narrow, width < 31% the nares width (4). The combined width can only be measured where the nasals meet on the midline. In some taxa there is a more posterior point where the width is wider, but the nasals, in such cases, are separated medially by the frontals.

121. *Nasal/Frontal suture.*—Approximately straight transversely (0); frontal has anterior wedge between posterior ends of nasals (1) (Muizon, 1988a).

122. *Position of posterior-most edge of nasals* (ordered).—Just anterior to or in a transverse line with anterior edge of supraorbital process of frontal (0); in line with anterior half of supraorbital process of frontal or in line with the halfway point, anteroposteriorly, of supraorbital process (1); in line with posterior half of supraorbital process or in line with postorbital process of frontal (2); in line with gap between postorbital process and the anterior tip of zygomatic process of squamosal or in line with the anterior tip of the latter process (3); between anterior the tip of zygomatic process of squamosal and anterior edge of the floor of squamosal fossa or in line with anterior edge of the floor of squamosal fossa (4); posterior to the anterior edge of the floor of the squamosal fossa (5). The

length of the nasal is determined by the positions of its anterior and posterior edges; therefore, its length is not scored as a separate character.

123. *Height of posterior portions of nasals relative to lateral edge of maxilla* (ordered).—Approximately equal to height of the base of rostrum (see character 58 for a description of measurement used); nasal height between 92% and 139% the rostral height (0); elevated above rostrum, height of nasals between 156% and 203% the rostral height (1); very elevated, height of nasals between 229% and 282% the rostral height (2); extremely elevated, height of nasals between 354% and 420% the rostral height (3); nasals tower above facial part of skull, height of nasals > 548% the rostral height (4) (modified from Heyning, 1989).

124. *Frontals* (ordered).—Lower than nasals (0); same height as nasals (1); higher than nasals (2) (Muizon, 1988a). Messenger and McGuire (1998) coded the presence of

the frontal protuberance as a separate character; however, taxa with a frontal protuberance always have the frontals higher than the nasals.

125. *Frontals posterior to nasals and between the premaxillae* (ordered).—Wider than maximum transverse width across nasals (0); same width as nasals (1); narrower than nasals, maxillae expanded medially posterior to the nasals (2)

(Muizon, 1988a). Cannot be scored for taxa that lack maxillae posterior to the nasal bone.

126. *Dorsal exposure of frontals.*—Fairly flat with separation between right and left frontal obscure (0); frontals are nodular with distinct separating sulcus on midline (1) (Fordyce, 1994).

127. *Anterodorsal wall of braincase.*—Formed by frontal (0); mostly formed by maxilla (1) (Schulte, 1917; Miller, 1923).

128. *Supraoccipital* (ordered).—Below frontals and/or nasals, whichever is higher (0); at same level as frontals and/or nasals (1); higher than frontals and/or nasals (2) (modified from Moore, 1968).

129. *Maxilla on dorsal surface of skull.*—Does not contact supraoccipital posteriorly, maxilla separated by frontal and/or parietal (0); contact present (1) (Muizon, 1991, 1994).

Temporal Fossae, Zygoma, Occiput

130. *Temporal crest.*—Dorsal surface adjacent to crest is nearly horizontal, crest appears to be directed laterally (0); dorsal surface is concave and surface of temporal fossa

below crest faces almost entirely laterally, crest appears to be oriented dorsolaterally (1) (Muizon, 1988a).

131. *Temporal crest* (ordered).—In posterior position, frontal roofs over the anterior third or more of temporal fossa (0); on posterior edge of supraorbital process of frontal (1); lateral end of temporal crest on dorsal surface of supraorbital process (2); entire crest on dorsal surface of supraorbital process (3) (modified from Heyning, 1989).

132. *Roof of temporal fossa.*—Frontal (0); frontal but with large opening through which maxilla and/or premaxilla is exposed; margins of the window are formed by a frontal ring (1). This can only be scored in taxa that have a posterior position of the temporal crest.

133. *Frontal/parietal suture in lateral view.*—Vertical or slightly angled posteroventrally (0); dorsal portion of suture pointed and extended far anterior so that the anteriormost point of parietal is anterior to the posterior-most point of premaxilla (1) (Miller, 1923).

134. *Parietals in dorsal view.*—Contact each other on the midline or are separated by an interparietal (0); are in place in the skull roof but are visible only as small triangular areas at edges of the intertemporal constriction, supraoccipital overlaps median portions of parietals and obscures them (1); are

completely absent in the skull roof (2); visible only as triangular areas dorsolateral to supraoccipital, supraoccipital does not overlap parietals but separates and contacts them along an irregular suture (3) (Whitmore and Sanders, 1977; Barnes 1990).

135. *Interparietal.*—Present (0); absent or fused so that it is not distinguishable from parietals and frontals (1).

136. *Cross-section through intertemporal region, including parietals* (ordered).—Ovoid cross-section with sagittal crest (0); ovoid but sagittal crest absent (1); pinched ventrally and dorsal part expanded laterally, expanded part is rounded-over in cross-section (2); dorsal part is greatly expanded, overhangs more ventral portions, and lateral edge of dorsal surface is a sharp ridge (3).

137. *Length of intertemporal region, ventral view of skull roof with basicranium removed* (ordered).—Intertemporal region absent or short, canal in frontals that contained olfactory stem and bulbs is < 10% of the length from posterior edge of dorsal nasal sinuses to posterior edge of skull (0); long, canal is between 18% and 35% of that length (1); very long, canal > 44% of that length (2).

138. *Dorsoventral thickness of intertemporal region* (ordered).—Thin, thickness is < 25% the maximum height of skull, as measured from intercondylar notch to

dorsal-most point of the supraoccipital (0); thick, thickness between 30% and 43% of the skull height (1); very thick, thickness > 54% of the skull height (2).

139. *Anterior-most point of the supraoccipital, in dorsal view* (ordered).—In transverse line with space between posterior edge of skull and anterior edge of the floor of squamosal fossa (0); in line with space between anterior edge of the floor of squamosal fossa and the anterior tip of zygomatic process of squamosal (1); in line with gap between anterior edge of zygomatic process of squamosal and the anterior-most point along posterior edge of the supraorbital process of frontal (2); in line with supraorbital process of frontal (3); in line with or anterior to anterior edge of

supraorbital process of frontal; anterior edge of supraorbital process is taken at its medial-most point (4) (modified from Miller, 1923).

140. *Pronounced bulge anterior to alisphenoid exposure in temporal fossa.*—Absent (0); present (1).

141. *Alisphenoid.*—Broadly exposed laterally in temporal fossa (0); lateral surface is broadly overlapped by parietal so that only a narrow strip on the ventral edge of temporal fossa is visible in lateral view (1). This character is not applicable for taxa that lack a dorsally expanded alisphenoid.

142. *Zygomatic process of squamosal*.—Directed anteriorly (0); directed anterolaterally (1) (Sanders and Barnes, 2002).

143. *Dorsal edge of zygomatic process, skull in lateral view*.—Gently convex dorsally (0); near anterior end there is a distinct dorsal flange or process, flange usually articulates with frontal (1); concave dorsally (2).

144. *Emargination of posterior edge of zygomatic process by sternomastoid muscle fossa, skull in lateral view* (ordered).—Absent, posterior edge forms nearly a right angle with dorsal edge of zygomatic process of squamosal (0); slight emargination (1); deep emargination (2).

145. *Width of squamosal lateral to exoccipital, skull in posterior view* (ordered). — Narrow, exposed portion of squamosal < 14% the distance between sagittal plane and lateral edge of exoccipital (0); intermediate width, width between 16% and 35% of that distance (1); wide, width between 40% and 55% of that distance (2); very wide, width > 129% the distance between sagittal plane and lateral edge of exoccipital (3).

146. *Depth of squamosal fossa* (ordered).—Absent or very shallow, depth of fossa < 52% the horizontal distance from dorsal edge of zygoma to the point above deepest part of squamosal fossa (0); shallow, depth between 55% and

91% that distance (1); deep, depth between 98% and 168% that distance (2); very deep, depth greater than 180% that distance (3) (derived from Barnes, 1985). The depth of the fossa is measured relative to the dorsal edge of the zygomatic process, which forms the lateral border of the fossa.

147. *Longitudinal profile of floor of squamosal fossa.*—Highly sigmoidal, concave posteriorly in region of a secondary squamosal fossa (*sensu* Sanders and Barnes, 2002) but convex anteriorly (0); slightly sigmoidal, posterior part concave but does not form a discrete pit (1); flat (2); convex (3).

148. *Floor of squamosal fossa.*—Same dorsoventral thickness anteriorly and posteriorly (0); thickens posteriorly (1).

149. *Squamosal prominence.*—Absent (0); present, forms a medial projection on crest that forms the lateral edge of squamosal fossa, is continuous with a dorsoventral ridge on lateral wall of the squamosal fossa (1) (Sanders and Barnes, 2002).

150. *Ventral edge of zygomatic process of squamosal in lateral view* (ordered). —Concave ventrally (0); straight (1); convex ventrally (2). Geisler and Sanders (2003) treated this as an unordered character.

151. *Postglenoid process in lateral view* (ordered).—Tapers ventrally to a point (0); anterior and posterior sides nearly parallel with squared-off ventral end (1); same as state —1ll except anteroposterior diameter of postglenoid process is very wide (2).

152. *Anterior edge of supraoccipital in dorsoposterior view* (ordered).—Triangular, pointed anteriorly (0); semicircular (1); rectangular (2) (Barnes, 1985).

153. *Lambdoidal crests of supraoccipital.*—Horizontal and directed laterally, overhanging temporal fossae (0); directed dorsolaterally, not or only slightly overhanging temporal fossae (1); very low and not directed either way (2).

154. *Posteromedial wall of temporal fossa.*—Visible in dorsal view (0); hidden in dorsal view by lateral edges of supraoccipital (1). Cannot be scored for taxa where the anterior-most point of supraoccipital is posterior to the level of the anterior edge of the floor for the squamosal fossa.

155. *Occipital shield.*—Smoothly convex or concave (0); bears distinct sagittal crest (1) (Sanders and Barnes, 2002).

156. *Dorsal condyloid fossa* (ordered).—Absent (0); present, situated anterodorsal to dorsal edge of condyle (1); present and forms a deep pit (2) (Sanders and Barnes, 2002).

Anterior Basicranium

157. *Anterior sinus* (ordered).—Absent (0); present but short (1); elongate with corresponding trough on maxilla (2) (Fraser and Purves, 1960). *Inia* has a very elongate anterior sinus; however, its corresponding trough on the maxilla is absent. All other taxa that have an elongate sinus also have a well-defined trough.

158. *Palatine.*—Relatively thin, floors posterior part of nasal cavity (0); thick, forms part of the anterior wall of the nasal cavities (1) (Miller, 1923).

159. *Palatines* (ordered).—Exposed ventrally (0); partially covered by pterygoid dividing it into medial and lateral exposures (1); ventral surfaces covered completely by pterygoids (2) (Miller, 1923; Muizon, 1987).

160. *Palatine* (ordered).—Ventral surface flat or convex (0); bears fossa for anterior end of pterygoid sinus (1); fossa well developed, divides palatine into medial and lateral laminae (2) (Muizon, 1988a, 1991).

161. *Lateral lamina of palatine.*—Free from or sutured to maxilla (0); fused to maxilla (1) (Muizon, 1988a).

162. *Pterygoid/palatine suture in ventral view* (ordered).—Angled anterolaterally (0); nearly transverse, pterygoid forms a substantial part of subtemporal crest (1); angled anteromedially (2).

163. *Pterygoid sinus fossa* (ordered).—Absent or cannot be distinguished from anterior part of fossa for cavum tympani (0); present, anterior edge approximately in line with anterior edge of foramen ovale (1); present and extended well anterior to foramen ovale (2); extended anterior to anterior edge of orbit (3) (modified from Fraser and Purves, 1960).

164. *Lateral lamina (outer plate or external duplication) of pterygoid.*—Present (0); partial, restricted to region lateral to the hamular process (1); absent (2) (Miller, 1923; Fraser and Purves 1960).

165. *Subtemporal crest.*—Present on alisphenoid and/or pterygoid, marks lateral edge of pterygoid fossa (0); subtemporal crest absent, pterygoid fossa extended laterally into orbital region (1) (derived from Fordyce, 1994).

166. *Inferior lamina of pterygoid*.—Absent or restricted to extreme anterior edge of pterygoid sinus cavity (0); present and floors most of sinus cavity (1) (modified from Fraser and Purves, 1960).

167. *Superior lamina of pterygoid* (ordered).—Present and covers most of ventral exposure of alisphenoid (0); absent from the sphenoidal region but present in orbital region (1); partially absent from orbital region (2); completely absent from orbital region (3) (Miller, 1923; Fraser and Purves, 1960).

168. *Posterior part of pterygoid sinus fossa, region immediately anterior to exit for mandibular branch of trigeminal nerve* (ordered).—One single fossa (0); split into a smaller and shallower posterior fossa and a much larger anteriorly extended deeper fossa by a low ridge (1); same as state —1‖ except divided by a high ridge (2).

169. *Preorbital lobe of pterygoid sinus* (ordered).—Absent (0); present but small (1); present and enlarged (2); enlarged and forms distinct excavation anterior to optic foramen (3); enlarged and extended posterodorsally over frontals to be roofed by maxilla (4) (Fraser and Purves, 1960).

170. *Postorbital lobe of pterygoid sinus* (ordered).—Absent (0); present but small (1); present and enlarged (2); enlarged and forms prominent fossa on

ventral surface of supraorbital process of frontal posterior to optic foramen (3) (Fraser and Purves, 1960).

171. *Coalescence of pre-orbital and post-orbital lobes of pterygoid sinus dorsal to optic nerve.*—Absent (0); present (1) (Fraser and Purves, 1960).

172. *Hamular process of the pterygoid.*—Splint like (0); solid, long and subconical (1); hollow and excavated by pterygoid sinus, lateral side highly concave, may or may

not have lateral and inferior laminae (2); form thin horizontal plates (3); absent (4) (modified from Fraser and Purves, 1960).

173. *Hamular processes of pterygoids.*—Rounded over in ventral view (0); bear anteroposterior keels (1) (Muizon, 1988a).

174. *Posterior-most point of hamular process of pterygoid, or medial part of pterygoid if the hamular process is absent* (ordered).—In transverse line with the middle of orbit (0); in line with postorbital process (1); in line with anterior edge of zygomatic process of squamosal (2); in line with middle of zygomatic process (3); in line with the postglenoid process (4).

Posterior Basicranium

175. *Fossa for pterygoid sinus on alisphenoid posterior to groove for mandibular branch of trigeminal nerve* (ordered).—Absent, bone is flat or not ossified because of enlarged internal foramen ovale (0); shallow fossa (1); deep subcircular fossa (2) (modified from Fordyce, 1994).

176. *Falciform process of squamosal.*—Plate-like with a wide, anteroposteriorly, base (0); rod-like with narrow base (1); poorly-developed or absent (2).

177. *Falciform process of the squamosal.*—Medial surface sutured to lateral lamina of pterygoid (0); not sutured (1). Cannot be scored for taxa that lack a lateral lamina of the pterygoid.

178. *Tympanosquamosal recess* (ordered).—Absent (0); absent but a small rectangular fossa for sigmoid process of the tympanic present, its long axis is transverse, and it

is located medial to postglenoid process of squamosal (1); present and enlarged, forms a triangular fossa medial and anteromedial to postglenoid process (2); very large, forms large fossa that borders entire medial edge of glenoid fossa (3) (derived from Fraser and Purves, 1960).

179. *Lateral edge of middle sinus.*—Smooth (0); deckle-edged (1) (derived from Fraser and Purves, 1960).

180. *Position of alisphenoid/squamosal suture, skull in ventral view* (ordered).—Anterior to external foramen of foramen ovale or homologous groove (0); courses along groove for mandibular branch of trigeminal nerve, or just posterior to it (1); just medial to anterior edge of floor of squamosal fossa, foramen ovale, and/or groove situated entirely on alisphenoid (2).

181. *Groove for mandibular branch of trigeminal nerve*.—Directed laterally and is entirely posterior to pterygoid sinus fossa (0); lateral end of groove wraps laterally around the posterior end of the pterygoid sinus fossa and opens primarily anteriorly (1).

182. *Ventral part of squamosal posterior to postmeatic process* (ordered).—Large area of laminated bone, appears externally as multiple sutures (0); small area of laminated bone restricted to ventrolateral edge of squamosal (1); without laminated bone (2) (Kasuya, 1973).

183. *Cranial hiatus*.—Absent, petrosal contacts basioccipital medially or partially separated by narrow fissure (0); present but constricted, a medial projection of parietal partially divides fenestra (1); absent, parietal contacts basisphenoid and/or basioccipital dividing fenestra in two (2); present, wide space between basioccipital

and both petrosal and squamosal (3). The cranial hiatus is formed by a coalescence of the internal foramen ovale and the basicapsular fissure (modified from Heyning, 1989a and Luo and Gingerich, 1999).

184. *Periotic fossa* (sensu Fordyce 1994).— absent (0), anterior portion present, with the spinous process in its most anterior edge (1); posterior portion present, divided from the posterior portion by a trabercular ridge, it receives the Hook-like process (=sub-circular fossa of Muizon, 1987) (2). See discussion about this character and others (185, 186 and 187) bellow.

188. *Zygomatic process of squamosal* (ordered).—Very short, length of process < 92% of the maximum width of glenoid fossa (0); short, length between 103% and 162% of glenoid width (1); intermediate length, length between 171% and 189% of the glenoid width (2); long, length between 198% and 271% of glenoid width (3); very long, length > 300% of the width of glenoid fossa (4). State —3‖ or state —4‖ is probably the primitive condition for Cetacea and Artiodactyla; however, the character was coded with state —0‖ (short zygomatic processes) in order to implement the ordering of states in the phylogenetic analyses.

189. *External auditory meatus.*—Wide (0); narrow (1) (Fordyce, 1994).

190. *Vomer.*—Posterior edge terminates on or at anterior edge of basisphenoid (0); terminates on basioccipital covering basioccipital/basisphenoid suture ventrally (1) (Barnes, 1984).

191. *Basioccipital crest.*—Narrow transversely (0); wide and bulbous (1) (Sanders and Barnes, 2002).

192. *Rectus capitus anticus muscle fossa.*—Absent or poorly developed (0); present with a well-defined anterior edge (1). The anterior edge forms a curved ridge that joins the basioccipital crest laterally and curves posteromedially to join its counterpart at the sagittal plane.

193. *Posteroventralmost point of basioccipital crest.*—Rounded over (0); forms a closely appressed separate flange, a narrow crease separates it dorsally from rest of basioccipital crest (1); distinct flange that projects posteriorly (2); distinct but separated by a pronounced notch that interrupts basioccipital crest (3).

194. *Angle formed by the basioccipital crests in ventral view* (ordered).—Parallel with no angle formed (0); 15° to 40° (1); 45° to 68° (2); 74° to 90° (3); > 100° (4) (modified from Muizon, 1991).

195. *Hypoglossal foramen.*—Thick bone separating it from jugular foramen, or jugular notch (0); separating bone very thin or absent, in the latter case hypoglossal foramen becomes confluent with jugular foramen (1).

196. *Jugular notch, gap between paroccipital process and basioccipital crest.* —Open notch, opening and depth of the notch are roughly equal (0); narrow and almost slit-like, depth is much greater than width of opening (1).

197. *Paroccipital process, skull in ventral view* (ordered).—Angled posterolaterally, extends posterior to posterior-most edge of condyle (0); posterior edge in transverse line with posterior edge of condyle (1); posterior edge is well anterior to posterior edge of condyle (2).

Malleus

198. *Tuberculum of the malleus.*—Unreduced (0); highly reduced, almost indistinguishable from articular head (1) (Doran, 1876).

199. *Processus muscularis of malleus* (ordered).—Processus muscularis shorter than manubrium of malleus (0); subequal (1); processes muscularis longer than manubrium (2) (modified from Muizon, 1988a).

Petrosal (Periotic)

200. *Apex of anterior process of the petrosal*.—In ventral or dorsal view blunt or pointed (0); bears tubercle (1) (Luo and Marsh, 1996).

201. *Anterior process in lateral view*.—Anterior edge of anterior process squared-off (0); comes to a blunt apex (1); comes to a slender point (2) (modified from Muizon, 1988a).

202. *Apex of anterior process of the petrosal*.—At same level or dorsal to ventral edge of pars cochlearis (0); well ventral to ventral edge of the pars cochlearis, process appears to be ventrally deflected (1) (modified from Fordyce, 1994).

203. *Length of anterior process of the petrosal* (ordered).—Absent (0); present but very short, length < 36% of the length of pars cochlearis (1); short, length between 59% and 94% of the promontorial length (2); nearly the same as length of pars cochlearis, length between 100% and 134% of the promontorial length (3); long, length between 141% and 174% of the promontorial length (4); very long, length > 212% of the length of the pars cochlearis (5) (modified from the following: Muizon, 1988; Luo and Marsh, 1996; Geisler and Luo, 1996). The length of the pars cochlearis was measured from its anterior edge to the ventral edge of the fenestra rotunda.

204. *Anterior process in lateral view.*—Ventral edge convex ventrally or nearly flat (0); ventral edge clearly concave (1) (Muizon, 1988a). The fovea epitubaria, which articulates with the accessory ossicle of the tympanic, is greatly expanded anteriorly in state —1‖.

205. *Anteroexternal sulcus.*—Absent (0); present on lateral surface of anterior process of petrosal, oriented primarily anteroposteriorly but bowed ventrally (1) (modified from Fordyce, 1994).

206. *Sulcus for capsuloparietal emissary vein.*—Present, forms a dorsoventral groove on lateral side of anterior process immediately anterior to lateral tuberosity (0); absent (1) (derived from Geisler and Luo, 1998).

207. *Articulation of anterior process with squamosal* (ordered).—Extensive, most of lateral side contacts squamosal (0); large centrally-oriented ovoid region contacts squamosal, free around the edges (1); contact is very small (2); contact is absent, articulates via ligaments (3).

208. *Shape of cross section through anterior process at midlength* (ordered).—Highly elliptical, transverse diameter is < 36% the dorsoventral diameter (0); ovoid, transverse diameter is between 51% and 78% of the dorsoventral diameter (1); approximately circular, transverse diameter between 85% and

134% of the dorsoventral diameter (2); bulbous, transverse diameter > 141% of the dorsoventral diameter (3) (modified from Fordyce, 1994 and Luo and Marsh, 1996).

209. *Contact of anterior process of petrosal with portion of ectotympanic bulla anterior to accessory ossicle* (ordered).—Absent (0); present but no clear fossa for articulation on petrosal (1); anterior bullar facet present but shallow with poorly defined medial edge (2); present with well defined medial and lateral edges (3) (Fordyce, 1994). Cannot be scored for taxa in which the bulla is completely fused to the anterior process of the petrosal or in some taxa with very short anterior processes.

210. *Flange of anterior process of petrosal.*—Absent (0); present (1) (Geisler and Luo, 1996; Luo and Marsh, 1996). The flange is here redefined as part of the lateral tuberosity, specifically a horizontal shelf on its lateral and anterior sides that overhangs the anterior process.

211. *Lateral tuberosity* (ordered).—Absent (0); present, forms a bulbous prominence lateral to fossa for malleus (1); present and elongate, forms a lateral process that articulates dorsally with squamosal (2) (Muizon, 1991; Luo and Marsh, 1996; Geisler and Luo, 1996).

212. *Emargination of lateral edge of petrosal by hiatus epitympanicus.*—With petrosal in ventral view, emargination is narrow and is situated slightly posterior to base of

posterior process (0); emargination is wide and is approximately in line with gap between fenestrae ovalis and rotunda (1).

213. *Fossa incudis* (ordered).—Poorly defined or cannot be differentiated from rest of epitympanic recess (0); forms a clear circular fossa (1); circular fossa present on a short pedestal, the incudal process (2) (Luo and Marsh, 1996).

214. *Fossa for malleus.*—Present (0); absent or poorly developed (1) (Geisler and Luo, 1996).

215. *Ventrolateral ridge of petrosal* (ordered).—Absent (0); present (1); present and expanded (2) (Geisler and Luo, 1996).

216. *Lateral side of petrosal* (ordered).—Entire side of petrosal contains pitted and rugose bone (0); all but anterior process is rugose (1); lateral side of posterior process of petrosal is pitted and rugose, remaining portions are smooth (2); entire side of petrosal is smooth (3).

217. *Origin of tensor tympani muscle* (ordered).—Deep, pocket-like fossa with anterior groove (0); anterior groove only (1); broad, poorly defined origin without a clear groove (2) (Luo and Marsh, 1996; Geisler and Luo, 1998).

218. *Angle between anterior process of petrosal and anterior edge of pars cochlearis* (ordered).—Obtuse, pars cochlearis appears transversely compressed (0); nearly 90 degrees, pars cochlearis looks rectangular or semicircular in ventral view (1); acute, pars cochlearis looks globular (2). Covers part of character 18 of Luo and Marsh (1996).

219. *Anteromedial corner of pars cochlearis.*—Rounded (0); angular (1) (Muizon, 1987; Fordyce, 1994).

220. *Pars cochlearis.*—Most convex part is on ventrolateral surface (0); most convex part is on medial surface. Area of greatest convexity begins anteromedial to fenestra rotunda and extends anterodorsally on the medial face. With petrosal in dorsal view, there is a wide expanse of bone medial to internal acoustic meatus (1).

221. *Ridge on anterolateral side of pars cochlearis, petrosal in ventral view* (ordered).— Present and high, forms an anteroposterior ridge that also forms

the medial edge of a trough for tensor tympani muscle (0); present and low (1); absent (2) (Luo and Marsh, 1996).

222. *Fenestra rotunda.*—Oval (0); shaped like a teardrop with a fissure directed towards the perilymphatic foramen (1) (Fordyce, 1994).

223. *Posterodorsal edge of stapedial muscle fossa.*—Ventral to or in line with dorsal edge of fenestra rotunda (0); well dorsal to fenestra rotunda (1).

224. *Stylomastoid fossa* (ordered).—Absent (0); present, situated on posterior face of pars cochlearis posterodorsal to stapedial muscle fossa (1); enlarged dorsally and medially, covers much of posterior face of pars cochlearis (2); enlarged posterolaterally onto posterior process of the petrosal (3) (Geisler and Luo, 1996).

225. *Caudal tympanic process of the petrosal.*—Prominent, its ventral and posterior edges form a right angle in medial view (0); low, its ventral and posterior edges are joined by a smooth curve (1).

226. *Caudal tympanic process of petrosal in posteromedial view.*—Well separated from crista parotica, no division between stapedial muscle fossa and

stylomastoid foramen (0); narrow separation or contact, clear separation of stapedial muscle fossa and stylomastoid foramen (1).

227. *Perilymphatic foramen* (ordered).—Smaller than endolymphatic foramen (0); approximately the same size (1); much larger with narrow posterior edge (2) (modified from Muizon, 1987 and Fordyce, 1994).

228. *Distance between perilymphatic foramen and fenestra rotunda* (ordered).—No distance, both apertures are confluent (0); narrow, distance < 89% of the distance between fenestra ovalis and fenestra rotunda (1); wide, distance between 96% and 122% of the space between fenestrae ovalis and rotunda (2); very wide, distance > 146% (3) (modified from Geisler and Luo, 1996).

229. *Distance between endolymphatic foramen and fenestra rotunda* (ordered). —Very narrow, distance < 112% of the distance between fenestra ovalis and fenestra rotunda (0); narrow, distance between 121% and 185% (1); wide, distance between 192% and 211% (2); very wide, distance > 222% the distance between fenestra ovalis and fenestra rotunda (3).

230. *Elongation of pars cochlearis towards cranial cavity, dorsally and medially.* —Absent (0); present, inner porous bone expanded towards cranial cavity (1); present, outer periosteal bone of pars cochlearis expanded towards cranial cavity (2) (Geisler and Luo, 1996).

231. *Excavation of tegmen tympani at base of anterior process.*—Absent (0); present, fossa on dorsolateral side of tegmen tympani (1).

232. *Dorsal edge of tegmen tympani dorsolateral to internal acoustic meatus and anterior process* (ordered).—Present and high, dorsoventral height > 114% the width of pars cochlearis (0); present, height between 58% and 34% of promontorial

width (1); low, height between 23% and 11% (2); forms a low ridge or is absent, height < 4% of the width of pars cochlearis (3) (derived from Fordyce, 1994).

233. *Dorsal edge of tegmen tympani lateral to endolymphatic foramen* (ordered). —Present and very high, dorsoventral height > 112% of the width of pars cochlearis (0); high, height between 95% and 50% the promontorial width (1); low, height between 12% and 4% (2); faint ridge (3); absent (4).

234. *Fundus of internal acoustic meatus.*—Funnel-like, smaller at the blind end and wider near the rim (0); tubular (1) (Luo and Marsh, 1996).

235. *Lateral wall of internal acoustic meatus.*—Low, does not protrude noticeably from suprameatal fossa and surrounding bone (0); high, a wedge-shaped area of elevated bone occurs between dorsal edge of tegmen tympani

and internal acoustic meatus, extending the latter ventrally and increasing its depth (1).

236. *Foramen singulare* (ordered).—In common recess with the tractus spiralis foraminosus, transverse septum separating the foramen singulare from endocranial aperture of facial nerve is well developed (0); in common recess with tractus spiralis foraminosus, transverse septum separating it from facial nerve foramen is low, and endocranial aperture of facial nerve canal within internal acoustic meatus (1); separated by partitions of equal height from tractus spiralis foraminosus and endocranial aperture of facial nerve canal (2); in common recess with endocranial aperture of facial nerve canal (3) (modified from Luo and Marsh, 1996; Geisler and Luo, 1996).

237. *Endocranial aperture of facial nerve canal* (ordered).—Anterior to tractus spiralis foraminosus (0); slightly anterior, posterior edge of aperture of facial nerve canal is

lateral to center of tractus spiralis foraminosus (1); lateral to tractus spiralis foraminosus (2).

238. *Morphology of endocranial opening of facial nerve canal*.—Continuous with an anterior fissure (0); oval-shaped (1); circular (2) (Luo and Marsh, 1996).

239. *Articular rim* (ordered).—Absent (0); present but small, forms a ridge anterolateral to articulation surface of the posterior process of the petrosal and separated from it by a sulcus; the ridge fits into a corresponding cavity posterolateral and slightly dorsal to spiny process of squamosal (1); present, long, oriented posterodorsally, and posterior end intersects dorsal margin of petrosal; in lateral view has sigmoidal shape (2); present with sigmoidal shape and laterally elongate with hook-like process (3) (modified from Muizon, 1987).

240. *Contact of petrosal, not including anterior process, with skull* (ordered).—Distal end of posterior process of petrosal, lateral surface of posterior process of the petrosal, and entire dorsal edge of tegmen tympani (or homologous bone) contact squamosal and possibly parietal (0); same as state —0‖ except dorsal edge contacts from posterior end of posterior process of petrosal to region just lateral to endolymphatic foramen (1); only dorsal and lateral sides of posterior process articulate with squamosal (2); petrosal articulates with squamosal along hiatus epitympanicus and adjacent regions on the posterior process (3); petrosal only articulates with skull via ligaments (4).

241. *Articulation surfaces on posterior processes of ectotympanic and petrosal* (ordered).—Surfaces smooth (0); bear complimentary longitudinal grooves and ridges (1); fused in adults (2) (Kasuya, 1973; Geisler and Luo, 1996).

242. *Ventral surface of posterior process of petrosal, along a straight path perpendicular to its long axis* (ordered).—Concave (0); flat (1); convex (2).

243. *Bullar facet on posterior process of petrosal*.—Restricted to ventral surface (0); extends dorsally onto posteromedial face of posterior process (1) (Fordyce, 1994).

244. *Facial nerve sulcus*.—Long sulcus on posterior process of petrosal or the compound petrosal/tympanic posterior process of most mysticetes (0); short, no sulcus posterior to stylomastoid notch (1) (Luo and Marsh, 1996; Geisler and Luo, 1996).

245. *Length of posterior process of petrosal* (ordered).—Absent or very short, length < 47% the length of pars cochlearis (0); short, length between 88% and 119% of the promontorial length (1); slightly longer than pars cochlearis, length between 131% and 153% (2); long, length between 191% and 404% (3); very long, length > 613% of the length of pars cochlearis (4) (modified from the following: Kasuya, 1973 ; Barnes, 1990; Luo and Marsh, 1996). The length of the pars cochlearis is measured as discussed in character 194. The length of the posterior process is measured along its long axis which is usually directed posterolaterally.

246. *Orientation of posterior process of petrosal* (ordered).—Forms an angle < 130° with the long axis of tegmen tympani (0); forms an angle between 135° and 165° (1); directed nearly posteriorly, forms an 180° with tegmen tympani (2) (Kasuya, 1973; Geisler and Luo, 1996).

247. *Dorsal edge of posterior process, petrosal in lateral or medial view*.—Straight or convex ventrally (0); concave ventrally, helps to form the neck of posterior process of petrosal (1) (modified from Geisler and Luo, 1996).

248. *Posterior process of petrosal*.—Robust (0); horizontal plate and very thin for most of its length (1) (Luo and Marsh, 1996).

249. *Mastoid exposure of posterior process of petrosal on the outside of skull*.—Exposed externally (0); not exposed, enclosed by the exoccipital and squamosal (1) (Luo and Marsh, 1996; Geisler and Luo, 1996).

Ectotympanic

250. *Anterior spine, or conical anterior tip, of ectotympanic bulla* (ordered).—Absent (0); present but small (1); present and long (2) (Kasuya, 1973; Muizon, 1987, 1994).

251. *Shape of ectotympanic bulla.*—Narrow and long, width of bulla at sigmoid process is < 64% the length of bulla along its long axis (0); wide, width of bulla > 65% of its long axis (1) (Kasuya, 1973). Following Kasuya (1973) this is determined by comparing the width of the bulla at the sigmoid process to the length of the bulla, measured from anterior end to posterior edge of involucrum.

252. *Posterior end of ventromedial keel.*—Forms a smooth curve around posterior part of involucrum (0); protrudes and points medially (1).

253. *Accessory ossicle.*—Absent (0); present (1) (Luo and Marsh, 1996; Luo, 1998).

254. *Accessory ossicle.*—Small and oblong (0); large and subspherical (1) (Fordyce, 1994; Luo and Marsh, 1996). Cannot be scored for taxa that lack an accessory ossicle.

255. *Accessory ossicle or homologous region on lip of bulla.*—Fused to anterior process of petrosal (0); not fused (1) (Barnes, 1990; Fordyce, 1994; Luo and Marsh, 1996).

256. *Lateral furrow of ectotympanic bulla.*—Present (0); absent (1) (Kasuya, 1973; Messenger and McGuire, 1998).

257. *Lateral furrow.*—Broad sulcus (0); narrow crease (1). Cannot be scored for taxa that lack a lateral furrow.

258. *Sigmoid process.*—Forms a straight transverse plate that is directed perpendicular to long axis of bulla (0); forms a curved plate; proximal part is directed posterolaterally while the distal end curves to point laterally (1) (Kasuya, 1973).

259. *Ventral margin of sigmoid process.*—Present (0); absent; in its place the lateral margin of sigmoid process smoothly turns into a sulcus on lateral side of bulla (1).

260. *Dorsal edge of sigmoid process.*—Contacts sigmoid fossa of squamosal (0); distal end expanded anteriorly to articulate with lateral tuberosity of petrosal only (1); does not articulate with squamosal or petrosal (2) (modified from Luo and Marsh, 1996). This character is related to character eight of Muizon (1988a).

261. *Elliptical foramen of ectotympanic bulla.*—Present, connection between ectotympanic bulla and its posterior process is split into two pedicles (0); absent (1) (Kasuya, 1973).

262. *Anterior edge of posterior process of ectotympanic bulla*.—Contacts postmeatic process of squamosal (0); contact absence (1) (Kasuya, 1973).

263. *Posterior process of tympanic.*—Contains sporadic areas of laminated bone at posterodorsal end (0); almost entire process is laminated bone (1) (Kasuya, 1973).

264. *Thickness of posterior process of ectotympanic.*—Thick in region ventral to articulating surface with petrosal (0); forms a thin lamina (1).

265. *Distal end of posterior process of ectotympanic* (ordered).—Thinner or approximately the same thickness as more proximal portions (0); distal end thicker but not hypertrophied (1); hypertrophied in size, forms large nodular mass (2) (Flower, 1872; Kasuya, 1973).

266. *Median furrow of ectotympanic bulla* (ordered).—Absent (0); forms notch on posterior edge of bulla between medial and lateral prominences (1); forms continuous anteroposterior groove on ventral surface of bulla (2) (Kasuya, 1973).

267. *Median furrow.*—On posterior side of bulla, it is divided by a transverse ridge originating from the involucrum (0); transverse ridge is absent (1).

268. *Profile of ectotympanic bulla in lateral view.*—Ventral edge convex or flat (0); concave because of posteroventral expansion of lateral prominence (1).

269. *Medial prominence of involucrum.*—Posterior edge approximately in line with posterior edge of lateral prominence (0); posterior edge distinctly anterior to posterior edge of lateral prominence (1) (Kasuya, 1973; Muizon, 1987). Degree of posterior extension is determined relative to the long axis of the bulla, not the orientation of the bulla in the skull. This alleviates problems associated with the reorientation of the bulla in the skull.

270. *Involucrum.*—In medial view, dorsal and ventral borders converge anteriorly (0); excavated anterior to base of posterior process so that dorsal and ventral sides are parallel (1) (Fordyce, 1994).

271. *Involucrum.*—Bears prominent transverse groove on dorsal surface that divides involucrum into a thicker posterior part and thinner anterior part (0); groove absent (1).

272. *Ridge on inside of bulla*.—Present, transverse ridge extends laterally from involucrum and partially divides cavum tympani into anterior and posterior portions (0); absent (1).

273. *Ventromedial keel of the ectotympanic bulla*.—Present along entire length (0); terminates approximately at level of lateral furrow (1); poorly defined along entire length (2) (Kasuya, 1973).

274. *Shape of ventromedial keel, bulla in dorsomedial view*.—Nearly straight (0); bowed medially (1).

275. *Region on dorsomedial side of ventromedial keel*.—Flat or convex (0); gently concave (1).

Vertebral

276. *Length of prelumbar vertebral column* (ordered).—Very short, length of cervical plus thoracic portions of vertebral column from 77% to 55% condylobasal length of skull (0); short, length of cervical plus thoracic portions of vertebral column from 100 to 83% skull length (1); long, from 123% to 114% skull length (2); very long, > 135% skull length (3) (derived from Miller, 1923).

277. *Atlas* (ordered).—Ventral process larger than dorsal process (0); both processes are subequal (1); dorsal process larger (2) (modified from Muizon, 1987,1988a).

278. *Atlas and axis vertebrae.*—Unfused (0); fused together (1).

279. *Cervical vertebrae posterior to atlas* (ordered).—All are separate (0); only 2nd and 3rd are fused together (1); 2nd through 4th are fused together (2); 2nd through 5th are fused (3); 2nd through 6th are fused (4); 2nd through 7th are fused (5) (modified from Miller, 1923). Fusion of the cervical vertebrae is related to extreme shortening of the neck.

280. *Number of thoracic vertebrae* (ordered).—18 to 17 (0); 16 to 15 (1); 14 (2); 13 (3); 12 (4); 11 (5); 10 or less (6).

281. *Number of thoracic vertebrae with capitular articulations* (ordered).—11 (0); 10 (1); 9 (2); 8 (3); 7 (4); 6 (5); 4 to 5 (6); 3 or less (7) (Sanders and Barnes, 2002).

282. *Capitular articulation facets of the posterior vertebrae.*—Facets gradually shift downward on sequential vertebrae to fuse with the tubercular facets (0); facets abruptly shift from a position on the neural arch to a pedestal that

originates from the centrum on the subsequent vertebra (1) (Flower, 1869; Miller, 1923). Coding modified based on observations in Heyning (1989a).

283. *Lateral edge of transverse processes of lumbar vertebrae*.—Oriented anteroposteriorly (0); angled anteromedially 45° or more, relative to a parasagittal plane (1) (Muizon, 1988a).

284. *Transverse processes of lumbar vertebrae*.—Oriented ventrolaterally (0); oriented laterally and horizontally (1) (Sanders and Barnes, 2002).

285. *Lumbar vertebrae*.—Transverse processes narrow distally or are approximately the same anteroposterior width as their bases (0); transverse processes bear greatly expanded distal ends (1) (Muizon, 1988a).

286. *Centrum of anterior lumbar vertebrae* (ordered).—Short, length < 63% the width (0); long, length between 79% and 136% the width (1); very long, length > 147% the width (2) (Muizon, 1988a; Barnes, 1990). The width is measured across the anterior face of the centrum.

287. *Number of lumbar vertebrae* (ordered).—3 or less (0); 4 (1); 6 (2); 7 to 8 (3); 9 to 10 (4); 11 to 12 (5); 13 to 16 (6); 16 to 19 (7). Geisler and Sanders

(2003) had 8 states for this character but no taxon had their state 0. This state is combined here with their state 1 yielding a total of 8 distinct character states.

288. *Number of caudal vertebrae* (ordered).—13 to 15 (0); 16 to 19 (1); 20 to 23 (2); 24 to 27 (3); 27 to 30 (4); 30 to 33 (5); 34 to 60 (6).

Forelimb and Pectoral Girdle

289. *Ventrolateral processes on manubrium of sternum.*—Absent (0); present but small, occurs ventral to articulation surface for first costal cartilage or rib (1) (Muizon, 1988).

290. *Sternum.*—Comprised of several bones (0); comprised of one bone (1) (Yablokov, 1964).

291. *Sternum.*—Several ribs attach to sternum (0); one rib attaches to sternum (1) (Messenger and McGuire, 1998).

292. *Coracoid process of scapula.*—Present (0); absent or barely distinguishable from edge of glenoid fossa (1) (Muizon, 1987, 1994).

293. *Supraspinous fossa of scapula.*—Present (0); absent or nearly absent, acromion process on anterior edge of scapula (1) (Muizon, 1987, 1994).

294. *Prominent deltoid crest on anterior edge of humerus*.—Present, forms greatest anteroposterior diameter along shaft (0); forms a knob-like tuberosity (1); tuberosity and crest absent (2) (Sanders and Barnes, 2002).

295. *Delto-pectoral tuberosity or farthest anterior point of crest* (ordered).—Closer to proximal head of humerus (0); approximately centered, proximodistally, on shaft (1); closer to distal end of humerus (2) (Muizon, 1988a).

296. *Radial and ulnar facets of humerus*.—Forms one articulation surface that is semicircular in lateral view (0); two distinct facets that in lateral view form an obtuse angle (1) (Barnes, 1990).

297. *Humerus* (ordered).—Longer than radius and ulna (0); approximately the same length as radius and ulna (1); shorter than radius and ulna (2) (Sanders and Barnes, 2002).

298. *Olecranon process* (ordered).—Present as a distinct process (0); present as slightly raised proximal posterior edge (1); absent (2) (Barnes, 1990; Messenger and McGuire, 1998).

299. *Manus*.—Pentadactyl (0); tetradactyl (1) (Yablokov, 1964).

Other

300. *Esophageal forestomach*.—Present, epithelium is either completely devoid of glands or may contain a small patch (0); absent, first chamber of stomach has glandular epithelium (1) (derived from Mead, 1989a; Rice and Wolman, 1990).

301. *External throat grooves* (ordered).—Absent (0); one pair, one on each side of midline (1); one to five pairs of grooves (2); more than five pairs (3).

302. *Throat grooves*.—Converge anteriorly (0); parallel (1) (Flower, 1872).

303. *Sexual dimorphism* (ordered).—Males 45% larger than females (0); males 14% to 30% larger than females (1); females and males approximately the same size (2); females 5% to 10% larger than males (3); females 20% to 30% larger than males (4) (modified from Yablokov, 1964). Size is based on maximum anteroposterior length of the entire body. Although state 1 or 2 is probably the primitive state for Cetacea, the assignment of states used here simplifies the inclusion of the between state homology assumptions (i.e. ordering the states) in the phylogenetic analyses.

304. *Dorsal Fin* (ordered).—Absent (0); dorsal hump (1); present (2) (Messenger and McGuire, 1998).

Characters Added in Geisler et al. (2012)

305. Dorsal margin of mesethmoid.—Below level of adjacent premaxilla (0); flush with or nearly flush with premaxilla (1); distinctly above level of adjacent premaxilla (2).

306. Straight line distance between posterior-most point of right premaxilla along opening of bony external nares and the right nasal.—Right premaxilla and nasal contact each other or are separated by a narrow gap that is < 15% of the maximum width of the external bony nares (0); intermediate separation, distance is between 30 and 50% of maximum nares width (1); wide, distance is > 60% of maximum nares width (2).

307. Orientation of the medial portion maxilla that is situated on either side of the vertex.—Faces mainly laterally (0); faces mainly dorsolaterally (1); faces mainly dorsally (2).

308. Deep wedge of supraoccipital between frontals on vertex.—Absent (0); present (1).

309. Lateral margin of posterolateral sulcus.—Low (0); high and as a result posterolateral sulcus is deeply entrenched (1).

310. Deep sagittal sulcus on middle of occiput.—Absent (0); present (1).

311. Longest side of nasal faces.—Dorsally (0); mainly anterodorsal (1); mainly anteriorly (2).

New character added in the present study

312. Shape of frontals in vertex: flat to slightly convex (0); inflated and expanded dorsally and laterally forming a knob-like process (1)

II. Review of Geisler et al. (2012) morphologic sub-matrix:

The revision of the character coding resulted in several differences scored differently here than in Geisler et al. (2011, 2012; Table S1).

Table S1 - List of modified characters and coding from the original matrix of Geisler and Sanders (2003) and Geisler et al. (2011, 2012).

	20	41	46	72	74	78	79	128	86	89	90
Pliopontos			0->2								
Pontistes			2								
Pontoporia								1->0			
Brachydelphis		?->0						1->0			

Meherrinia									
Inia				4,5 ->5					
Ischyrorhynchus	0->1		1->2	4,5 ->5	1->0	0,2 ->?	?->1	0->1	?->1
Lipotes									
Zarachis		0							
Platanista				4,5 ->5					

continued

	57	107	108	114	115	125	169	170	174	184
Pliopontos		?->0		2->1						0
Pontistes										0
Pontoporia	2									0
Brachydelphis	0->3	?->0						polimorphic ->?	?->1	0
Meherrinia								polimorphic ->?		0
Inia				2->1	?->0	1->0		2->3		0
Ischyrorhynchus			?	2->1	?->0					0
Lipotes							3->2	3->2		0
Zarachis				1->2			?->1	polimorphic ->?		2
Platanista		?->0	5	2						2

II. 1 **Redefinition of characters:**

We modified the definition of character 184 (adding all new codes) and exclude form the analysis characters 185, 186 and 187 of Geisler et al. (2012, Geisler and Sanders 2003), because we interpret as an unnecessary separation of one character and miss interpretation of some important basicranial anatomic features and its homologies.

In the skull, one of the most conspicuous and diagnostic feature in the otic region of the Platanistoidea is the subcircular fossa (de Muizon, 1987, 1988, 1991) or more primitive structures present in presumed more primitive species (Fordyce, 1994). As it was originally defined, the subcircular fossa is a depression of variable deepness in the ventral side of the squamosal, dorso-medial respect to the spinous process of the squamosal (de Muizon, 1987, 1991). Under this terms, any depression on the generally appropriate place may be considered homologous to those in other Platanistoidea.

Fordyce (1994) attempted to establish more precise criteria for the homologies of the structures of this region as well as for the features in the tympanoperiotic bones. Describing *Waipatia maerewhenua* he recognized on the squamosal a periotic fossa dorsally to the periotic and lateral to the parietal. It is divided into two portions by a supratubercular ridge. In the anterior portion of this fossa a foramen, the foramen spinosum, opens. He suggested that the anterior portion of the fossa and the enlarged foramen spinosum are homologous to the subcircular fossa described by de Muizon (1987, 1988, 1991).

However, this region of the skull in the odontocetes is extensively affected by the pterygoid and other middle ear sinuses (Fraser and Purves, 1960), and depressions similar to the periotic fossa and/or subcircular fossa may appear in several unrelated species, which introduce confusion on the homology criteria. It was observed (M.A.C. personal observation) a pseudo-periotic fossa in the paratype of *Kentriodon pernix* Kellogg (USNM 10670, Paleobiology Department), in several specimens of the off-shore form of *Tursiops truncatus* deposited at the collection of recent cetaceans in the National Museum of Natural History (Washington, D.C.), (USNM 570020, 571204, 57156, and

571181 among others), in some specimens of *Inia geoffrensis* (i.e. EEM Ig 9301) of different age from newborn to full adult, but not in other specimens of the same age range, and in one specimen of *Lagenorhynchus obscurus* (CNP-LMM LO8) (Fig.xx). Particularly in this last individual, the morphology is remarkably similar to that described by Fordyce (1994) for *Waipatia*; it is divided in an anterior and posterior portions by a ridge, but it differs from those of Platanistoidea because have no associated foramina.

Taking into account the above observations, seems possible to restrict the homology to the simultaneous presence of the fossae and the associated foramina. However, we failed to recognize any associated foramina to the small subcircular fossa in *Platanista gangetica* (USNM, collection of recent cetacea, 23456). It is possible to interpret that in *Platanista* the extensive invasion of the basicranium by the sinuses (mainly the peribulary and pterygoid sinuses) modified the region, determining the secondary reduccion of the fossa and loose of the related foramina, but the issue is not clear.

In *Squalodon calvertensis* (Kellogg, 1923, and personal observation on USNM, Paleobiology Collection, 328343) a similar fossa exists. It is located relatively anteriorly respect to the fossa in *Notocetus*, *Pomatodelphis*, *Zarhachis*, and *Platanista*, approximately in the region of the anterior portion of the periotic fossa in *Waipatia* and the specimen described here. It is associated to a foramen opening in the fossa and ending in the foramen oval. This is similar to that was described in *Waipatia* (Fordyce, 1994:158).

In *Phoberodon arctirostris* Cabrera 1926 (Cozzuol, in press-b) any indication of periotic fossa is absent, but the foramina, particularly the foramen spinosum, are present, and the region is very similar to that of *Waipatia*.

As it was stated above, Fordyce (1994) preliminary considered that the anterior portion of the periotic fossa of *Waipatia* and the enlargement of the foramen spinosum are homologous to the subcircular fossa. However, it must be reminded that the subcircular fossa was originally described in *Notocetus vanbenedeni* (see de Muizon, 1987) and a detailed redescription of the pertinent region in this species may help to shed light on these problems.

In the several individuals of this species we examined, the fossa have some variation in size and deepness, but it is always located very posteriorly in the squamosal, separated from the exoccipital by a thin lamina of bone (Figs. xx). It extends deeply in the squamosal dorsally and laterally to the spinous process and the only foramen opening in its interior runs dorsally, partially into the exoccipital-squamosal suture. The large articular rim of the periotic (sensu de Muizon, 1987) enter into the ventro-medial portion of the subcircular fossa. This description agrees with that of the posterior portion of the periotic fossa in *Waipatia* and in the specimen described here (see above) except for the absence in the periotic of the last two of a prominent articular rim.

Anteriorly to the subcircular fossa in *N. vanbenedeni* is a shallow depression, medial to the inner margin of the tympanosquamosal recess, and separated from the subcircular fossa by an elevated ridge. Posteromedially to this depression, close to the elevated ridge, is a foramen. About fourteen millimeters forward, on the alisphenoid-squamosal suture, there is another foramen, and even other one is located medially to the shallow anterior depression, onto the squamosal-parietal suture. We conclude that the depression is the anterior portion of the periotic fossa, the foramen close to the ridge is the foramen spinosum, the foramen on the alisphenoid-squamosal suture is the foramen 1, and that onto the squamosal-parietal foramen the foramen 2 described in *Waipatia* (sensu Fordyce, 1994, fig8b), but the foramen apparently homologous to the spinous foramen runs into the brain cavity, not into the foramen oval. Consequently the subcircular fossa of *Notocetus* should be homologous to the posterior portion of the periotic fossa of *Waipatia* (sensu Fordyce, 1994) and the specimen here described, not of the anterior part as it was proposed (Fordyce, 1994). In the specimens of *Pomatodelphis* and *Zarhachis* we examined (M.A.C. personal observation), the subcircular fossa is located in the same position than in *Notocetus.* Like in this last genus, the apparently homologous of the foramen spinosum runs into the brain cavity. In the platanistoid specimen here described the same condition of *Notocetus*, *Zarhachis*, and *Pomatodelphis* was observed.

If the above interpretation is correct, then the fossa in *Squalodon* spp. is not homologous to the subcircular fossa in *Notocetus* and other members of the Squalodelphidae-Platanistidae clade, but probably to the anterior portion of the periotic fossa in *Waipatia* and the specimen described here.

IX. CONCLUSIONES POR CAPITULOS

IX. 1. Capitulo 1

En resumen la Región de Atacama posee 85% de los registros de Chile. Lo que en términos del registro sudamericano corresponde a 50% de las familias registradas hace 10 años, en la última revisión (Cozzuol 1996). Hasta el momento no hay registros, en la literatura, de cetáceos en el Neógeno marino de las formaciones Ranquil, Lincai y Mejillones, aún que probablemente se necesitan campañas de prospección y estudio de los materiales, ya que restos vertebrales han sido observados informalmente (exposición del museo de la Universidad de Antofagasta), provenientes de la Fm. Mejillones.

La fauna de cetáceos de la Fm. Bahia Inglesa es similar a la registrada en niveles miocenos de la Fm. Pisco (Suárez et al., 2005), e incluye un significativo componente de cetáceos fósiles, como: *P. littoralis* (Plioceno inferior, Fm. Pisco), *B. mazeasi* (Mioceno Medio, Fm. Pisco) y *P. rectifrons* (Mioceno Tardío, Fm. Ituzaingó, Argentina). Los registros chilenos amplían el rango cronoestratigráfico y paleobiogeográfico de las especies mencionadas, haciendo más compleja la historia evolutiva de la familia. Sin embargo, también deja en evidencia que los 'niveles de vertebrados' descritos para la Formación Pisco (Muizon y DeVries, 1985) no tienen su correspondencia en los estratos de la Formación Bahía Inglesa, que presenta re-trabajo pero no con niveles pliocenos. Tanto en el caso de los tiburones (*C. carcharias* y *C. hastalis*) ampliamente utilizados como indicador cronoestratigráfico, como en el caso de los taxa de odontocetos (ej. Pontoporiidae, Phocoenidae) utilizados en la Fm. Pisco (Muizon y Devries, 1985) parecen no ser exactos, ya que taxa propuestos como guías del Mioceno Tardío y Plioceno en la Fm. Pisco (sensu Muizon y Devries, 1985) se encuentran juntos en el "bonebed" (Mioceno Tardío; Achurra 2004, Suárez y Marquardt, 2003; Walsh y Suárez, 2005).

La Formación Bahia Inglesa cuenta con capas bien expuestas con tal aglomeración de restos que fueron llamadas "capa de huesos" (bonebeds) de edad Messiniano-Tortoniano (Mioceno Tardío). El estudio de la fauna de cetáceos, bien como la fauna y flora general, tiene potenciales como el de ampliar el entendimiento en los tiempos de formación de la corriente de Humboldt (e.g. Rubilar-Rogers et al., 2009) y por ende en la expansión hasta estas latitudes del desierto de Atacama. Como estas capas condensan la diversidad de estas edades con un registro diverso y abundante, su ensamble debería reflejar las modificaciones macro-climáticas como el establecimiento de la corriente de Humboldt y la expansión del desierto de Atacama.

Se destacan los nuevos registros que amplían el rango cronoestratigráfico de *Pliopontos littoralis*, que se consideraba un especie tipo del Plioceno y aquí aparece en capas del Mioceno Tardío. Además de la presencia de *Pontistes rectifrons*, como primer registro en el Océano Pacífico. Estos hallazgos refuerzan la importancia de la Formación Bahia Inglesa en el entendimiento de la biodiversidad del final del Neógeno y especialmente de la evolución y biogeográfica de los Inioidea, grupo hasta ahora enigmático y muy interesante dado su cambio morfológico y ambiental correlacionados (Gutstein et al. sometido).

IX.2. Capitulo 2

Nuestros resultados demuestran que la morfología externa del pars cochlearis esta relacionada con los tipos cocleares internos. Además, tanto la la forma del pars cochlearis como la forma del meato acústico reflejan las diferentes propiedades acústicas de los ambientes que sus respectivos taxa habitan, lo que nos permitió diferenciar los entornos fluviales y marinos (es decir, plenamente marinas o costeras/estuarinas).

Aunque trabajos anteriores habían demostrado que las dimensiones del pars cochlearis divide los odontocetos en morfotipos cocleares sensu Ketten (1992), en estudio se utilizó morfometría y análisis estadístico para discriminar entre las morfologías representativas y sus categorías ambientales. En consecuencia, sostenemos que en Delphinida y Platanistoidea, las ecomorfologias de los perióticos reflejan las propiedades acústicas de los ambientes de aguas abiertas y claras que exigen una menor precisión de ecolocalización que en los sistemas fluviales de agua turbia. Estos resultados también permiten esbozar la morfología del periótico como un posible indicador (proxi) para descifrar las preferencias ambientales de los odontocetos extintos. En cuanto a la perspectiva del tiempo (geológico), encontramos separaciones morfológicas entre los perióticos de odontocetos del Mioceno inferior, Mioceno medio y Mioceno tardío al Holoceno, un hallazgo previamente apoyado sólo por estudios cualitativos en la literatura (Muizon, 1987, 1988a; Cozzuol, 1996).

Estos tiempos de separación es consistente con la diversificación en odontocetos de manera locales (Hamilton, 2001) y, más recientemente, globales (Steeman et al., 2009). Estos estudios hacen hincapié en factores físicos (es decir, geológicos y oceanográficos, respectivamente) como contexto de la historia evolutiva de los cetáceos, especialmente congruente con el marco temporal de los proxies ecomorfológicas descritos en el presente estudio.

IX.3. Capitulo 3

Se generaron marcadores óseos para la presencia, forma y tamaño de las estructuras blandas relacionadas a la ecolocalización, que pueden servir como proxies para presencia y forma de estas estructuras en taxa fósiles.

Utilizando medidas óseas que describen dichas estructuras blandas, se determinó que el largo del melón fue relevante en la clasificación ambiental y de tiempo geológico, donde se encontró que el melón más largo y estrecho se correlaciona con los ambientes fluviales. Esto es interesante, ya que el largo del melón ha sido sugerido como una característica funcional relacionada al aumento de la habilidad de “filtrar” el sonido y así enfocar el haz de sonido producido (Cranford 1999). Una mayor capacidad de enfoque también es coherente con el complejo hábitat de vida de los delfines de río y su comportamiento. Además, el largo del melón ha sido considerado como un proxy relacionado al limite inferior de las frecuencias de sonido producidos (low-frequency cutoff, Mackenna et al. 2011) y que esta diferencia seria alométrica (independiente del tamaño de la cabeza).

Los sacos aéreos han mantenido una la distribución general en los grupos de Delphinida. Sin embargo, en Inioidea estos son complejos, subdivididos, de textura lisa y bien ajustados a los huesos del cráneo subyacente (esto último también se observa en Phocoena, Delphinoidea). En los Delphinidae (Delphinoidea) se observan sacos vestibulares espesos, pigmentados y arrugados. Esto es interesante, porque se ha propuesto que los sacos aéreos, que rodean el melón, podrían estar relacionados con un haz de ecolocalización más concentrado. La disposición de los espacios aéreos podría funcionar como un espejo cóncavo acústico (Pilleri y Gihr, 1979), teniendo en cuenta el límite tejido-aire que generaría la reflexión de la onda sonora.

IX. 4. Capitulo 4

Se describen dos nuevos taxa del Pacifico Sur y Atlántico Norte, en base a una morfología craneal única.

La configuración general de la morfología facial de los nuevos taxa pueden deberse a diferencias en el patrón y la distribución de la musculatura facial y órganos. En consecuencia, el telescopaje de los cráneos de odontocetos podría ser más complejo de lo que se pensaba anteriormente.

Los estudios sobre la fisiología y la correlación morfofuncional de las estructuras anatómicas relacionadas con la ecolocalización (ej: generación, enfoque y recepción del sonido) fueron aplicados para la reconstrucción de los sacos aéreos de las especies presentadas. Estas especies, además, fueron contextualizadas en un estudio filogenético siendo ubicado inequívocamente en Iniodea.

El registro fósil, muy extendido con los nuevos taxa presentados, parece revelar que había una mayor diversidad morfológica durante el Neógeno, además, de la mayor diversidad de especies en este periodo, en particular en el caso de la Inioidea.

X. Análisis de Hipótesis

Las diferencias morfológicas, relacionadas a la ecolocalización, entre las familias de Delphina son producto de la especialización de los taxa a su modo particular de vida.

Predicciones:

- Se podrán reconocer estructuras básicas homólogas comunes (homología de posición) que están relacionadas a la ecolocalización en todas las familias de Delphina y los taxa hermano a este grupo, tanto fósiles como vivientes.

Se cumple que: en los análisis morfológicos de las tomografías se observaron siempre las mismas estructuras a saber: el melón, los sacos aéreos (vestibulares, nasofrontales y premaxilares), el músculo del plug nasal y en la porción ventral los sinos aéreos del pterigoides (posterior, peribular, anterior y orbitarios) así como el ducto coclear.

- Se espera encontrar en términos generales una alta correlación entre las medidas y caracteres merísticos relacionados a la ecolocalización y el ambiente particular que habitan o habitaron.

Se cumple que: los análisis estadístico de las medidas sincraneales recuperaron grupos significativos en las variables ambiente y edad geológica separándolos en ambientes marinos, costero-estuarinos y fluviales, y en Mioceno temprano, Mioceno medio-Plioceno y Pleistoceno-

Holoceno.

- Se podrá evidenciar un patrón de aparición de caracteres morfológicos relacionados a la ecolocalización. Este patrón mostrará características básicas en común también presentes en los grupos externos, es decir, características conservadas asociadas a los requerimientos mínimos para ecolocalizar.

Se cumple, en el análisis preliminar (ver apéndice), que se observa una semejanza entre el patrón de aparición de las propiedades acústicas del haz de sonido emitido para ecolocalizar (Fig. 3) y la morfología del ducto coclear (M, I y II, Ketten 1992) (Fig. 5). Con un patrón poco claro aparecen la morfología del pars coclearis (Fig. 6) y de las estructuras blandas faciales como el melón (Fig. 4) y los sacos nasofrontales (Fig. 7). Estos últimos tuvieron poca resolución debido a los pocos taxa con este carácter codificado.

- Por otro lado, se observará una distribución consistente entre la aparición de las estructuras especializadas con el ambiente en el cual habitan o habitaron los taxa en cuestión, lo que no estará dado por la relación de ancestría-descendencia entre los mismos.

Esta predicción no se cumple, ya que las características asociadas a los ambientes fluviales en la actualidad (y en el análisis morfométrico Capítulos 2 y 3) ya se encontraban presentes en especies ancestrales,

más antiguas y marinas, como *Notocetus* (Platanistoidea) (ver apéndice I Figs. 5 y 6) y Physeteriidae, que presentan un ducto coclear semejante a lo de los delfines de río actuales (con menos vueltas), sugiriendo mas bien que esta característica es compartida por la mayor parte de loo odontocetos excepto los modernos Delphinidae que poseen el haz de ecolocalización bimodal y una cóclea con más vueltas, ademas de ser marinos en su mayoría. Por otra parte, la comparación de las invasiones a los sistemas fluviales (Apéndice I, Fig. 1) difiere del patrón de aparición de las propiedades acústicas (Apéndice I, Figs. 3 y 5).

- Para el caso particular de las especies, *Inia geoffrensis* (Inioidea: Iniidae) y *S. fluviatilis* (Delphinoidea: Delphinidae), de distinto origen filogenético y con diferentes tiempos de incursión al sistema fluvial amazónico, que cohabitan actualmente, se espera que presenten: i) especializaciones en distintos grados, relacionadas a este ambiente, respecto de sus ancestros marinos, *Pontoporia blainvillei* y *S. guianensis*, respectivamente; ii) cambios en la morfología del oído interno asociada a diferencias en frecuencias de emisión, ya que los ambientes marinos son abiertos permitiendo el uso de frecuencias preferenciales emitidas /recibidas "bajas" y presentando un haz de ecolocalización bimodal, mientras que los ambientes fluviales, más cerrados y con obstáculos, obligarían el uso de frecuencias "muy altas", de alta definición pero baja penetración, presentando un haz de ecolocalización de banda estrecha; iii) estructuras faciales y de aislamiento acústico especializadas morfológicamente distintas en los taxa de río y de mar; iv) las formas ancestrales fósiles (ej.: *Brachydelphis, Ischyrorhynchus*) a *Inia* presenten morfologías que estimen capacidades auditivas (ej.: forma de la cóclea) acorde al ambiente de depositación (marino y fluvial, respectivamente) de donde provienen dichos fósiles.

Se cumple que: como lo esperado en i) se observaron mayores diferencias, referentes a la ecolocalización, entre *Pontoporia* e *Inia* que las halladas entre *S. guianensis* y *S. fluviatilis*. Sin embargo, aunque *S. fluviatilis* se separa de *S. guianensis*, en el análisis morfométrico (CVA) (capítulos 2 y 3), no presenta características morfo-funcionales distintas de *S. guianensis;* ii) no se cumple la predicción ya que, *S. fluviatilis*, presenta ducto coclear tipo II, mientras *S. guianensis* presenta tipo I presentando el patrón inverso a lo observado en los demás grupos con transición mar-río. En iii), se cumple parcialmente la predicción ya que presenta diferenciación en el análisis morfométrico estadístico de las medidas de los perióticos pero no caracteres morfológicos fácilmente distinguibles. En iv), se cumple la predicción ya que tanto las comparaciones morfométricas como las morfológicas entre *Ischyrorynchus* (fluvial) y *Brachydelphis* (marino y costero) son consistentes con sus ambientes de depositación.

Por lo tanto, *Inia* presenta mas que una historia de especialización al sistema fluvial amazónica, una historia de retención de características de estados ancestrales la que aparece ocurrir con los delfines de río del Ganges (*Platanista*) y del Yang tse (*Lipotes*), mientras que *Sotalia*, siendo ambas especies derivadas e insertas en un grupo marino, en general, con un tipo de ecolocalización bimodal.

XI. CONCLUSIONES GENERALES

- Se encontró una correlación morfológica consistente con el ambiente al que pertenecen los distintos taxa de Delphina y Platanistoidea, por otro lado, también se aprecio que las propiedades acústicas del haz de ecolocalización y la morfología asociada a estas poseen una historia evolutiva distinta al patrón de invasión a los sistemas fluviales.
- Se determinó la correspondencia ósea de las "estructuras blandas" faciales y óticas relacionadas a la ecolocalización en todos los taxa analizados, creando estimadores de estas estructuras.
- Se pudo inferir la forma de dichas estructuras en especímenes fósiles o con características de anatomía blanda y/o acústicas desconocidas. Los resultados indican que la morfología funcional del cráneo (capitulo 3) y perióticos (capitulo 2) se relacionan con la preferencia de ambiente o paleoambientes. Además, también se recuperó una diferencia morfológica entre las diferentes épocas geológicas, entre el Mioceno inferior, Mioceno medio al Plioceno y el Pleistoceno hasta la actualidad.
- Se obtuvo un árbol filogenético, basado en matrices ya publicadas (Geisler *et al.* 2012) incorporando y revisando codificaciones para los taxa fósil sudamericanos, en donde fue posible establecer las relaciones filogenéticas de los Delphina.
- Los resultados del análisis filogenético apoyan la idea ya conocida (Nikaido *et al.* 2001) de invasiones independientes a los ambientes fluviales (Apéndice I, Fig. 1). Con la excepción de *Lipotes,* que no posee grupos hermanos fósiles conocidos en el Neógeno, todos los taxa de río tienen a grupos hermanos o cercanos

costeros/estuarinos (Apéndice I, Fig. 1 y 2).

. El los linajes: Inioidea (delfines de río sudamericanos) y Delphinoidea (delfines marinos costeros y oceánicos) se observan diferencias en le evolución de la ecolocalización. Ya que poseen diferentes contextos filogeneticos y diferentes caracteres ancestrales en el momento de la invasión al ambiente fluvial. Por ejemplo, en el caso de los inioides (*Inia, Ischyrorhynchus* y los ancestros marinos) el haz de ecolocalización es de banda estrecha; mientras que en los delfinoides (*S. fluviatilis* y los Delphinoidea excepto Phocoenidae, costero) el haz de ecolocalización es bimodal. De esta manera, *Inia* presenta más que una historia de especialización al sistema fluvial amazónica, una historia de retención de características de estados ancestrales la que aparece ocurrir con los delfines de río del Ganges (*Platanista*) y del Yang tse (*Lipotes*), mientras que *Sotalia*, siendo ambas especies derivadas e insertas en un grupo marino, en general, con un tipo de ecolocalización bimodal.

XII. APENDICE I

XII. I Asignación de caracteres, relacionados a la ecolocalización, partir de la evolución morfológica craneal en odontocetos

Con el objeto de contextualizar filogeneticamente los caracteres o proxies desarrollados en los capitulos 2 y 3, de acuerdo a la hipótesis filogenética obtenida en el capitulo 4, fueron definidos y mapeados 6 caracteres detectables (Tabla S2). Estos fueron definidos a partir del análisis discriminante obtenido a partir de varias características morfométricas en los delfines marinos y fluviales de ambos continentes, Asia y America del Sur, con un énfasis en taxa que hasta el presente trabajo eran poco revisados en la literatura. Las características se definieron de acuerdo a las estructuras descritas por las mediciones significativamente relevantes (análisis discriminante CVA), tanto para el cráneo (capitulo 3) como para los perióticos (capitulo 2).

Aspectos de la morfología craneal que resultaron estar relacionada con la forma general del melón (alargada /esférica) fue determinada basándose en las mediciones de la superficies de inserción de las conexiones tendinosas del melón (proxy de la extensión melón anteroposterior) y el ancho de la muesca antorbital (proxy del ancho máximo del melón) (como descrito en el capitulo 3), tabla n 1.

Utilizando, para estos efectos, el cladograma generado anteriormente (capitulo 4), siendo el más completo muestreo taxonómico para el taxón lnioidea. Se procedió a mapear los caracteres de la Tabla 5.1 en el árbol mas parsimonioso encontrado (capitulo 4). Se calcularon los nodos ancestrales utilizando el criterio de parsimonia en Mesquite 2.75 (Maddinson y Maddinson, 2011). Posteriormente se utilizó el mismo programa Mesquite 2.75 para aplicación del Jacknife.

Tabla 1- Caracteres relacionados a la morfología craneal definidos como proxies para el tipo de ecolocalización y ambiente que fueron mapeados en la hipótesis filogenética resultante:

N	Descripción de los caracteres mapeados
1	Preferencia de hábitat/dato paleoambiental: marino-oceánico (0), costero/estuarino (1) ó fluvial (2)
2	Propiedades acústicas del haz de sonido de ecolocalización: baja-frecuencia <50kHz, banda estrecha (1), bimodal (2)
3	Forma del melón: melón alongado/cilíndrico, relación entre el ancho y la longitud del melón o sus proxies >30% (0), melón redondeado a subesféricos, ancho y longitud del melón o sus proxies (1), en forma de caja con una porción anterior plana (2)
4	Tipo de ducto cochlear: tipo M (0), tipo I (0), tipo II (1) (sensu Ketten 1992)
5	Forma del *pars cochlearis*: aproximadamente esférica a equidimensional(0) ó delgado y plano (1)
6	Sacos nasofrontales: amplios,, en forma de media luna extendidos a lo largo del borde de las fosas nasales en sentido anteroposterior (0), region nasal restringida (1)

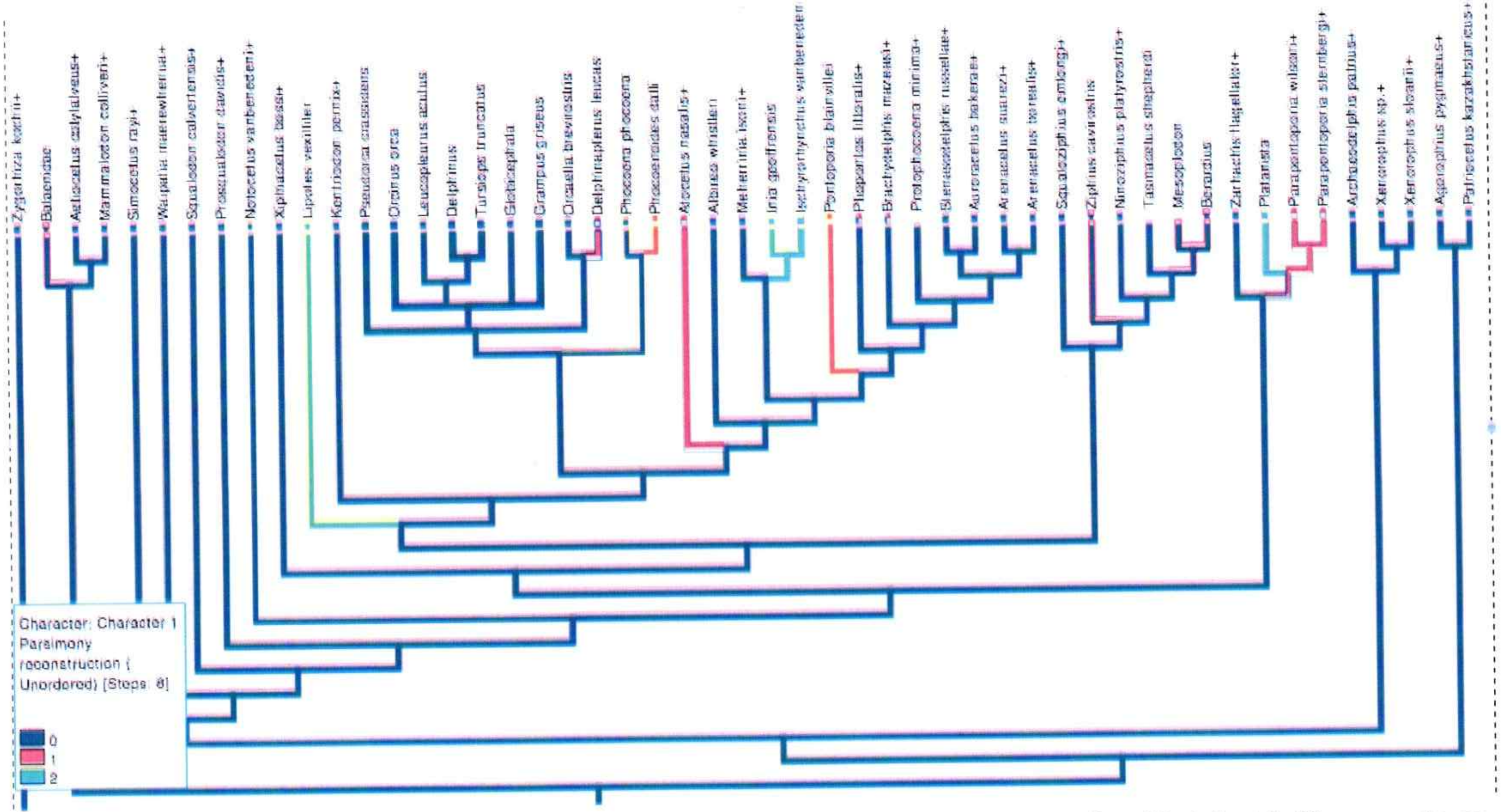


Figura 1 - Preferencia de hábitat/dato paleoambiental: marino-oceánico (0), costero/estuarino (1) ó fluvial (2), mapeado en cladograma resultante de analisis de parsimonia con implied-weight.

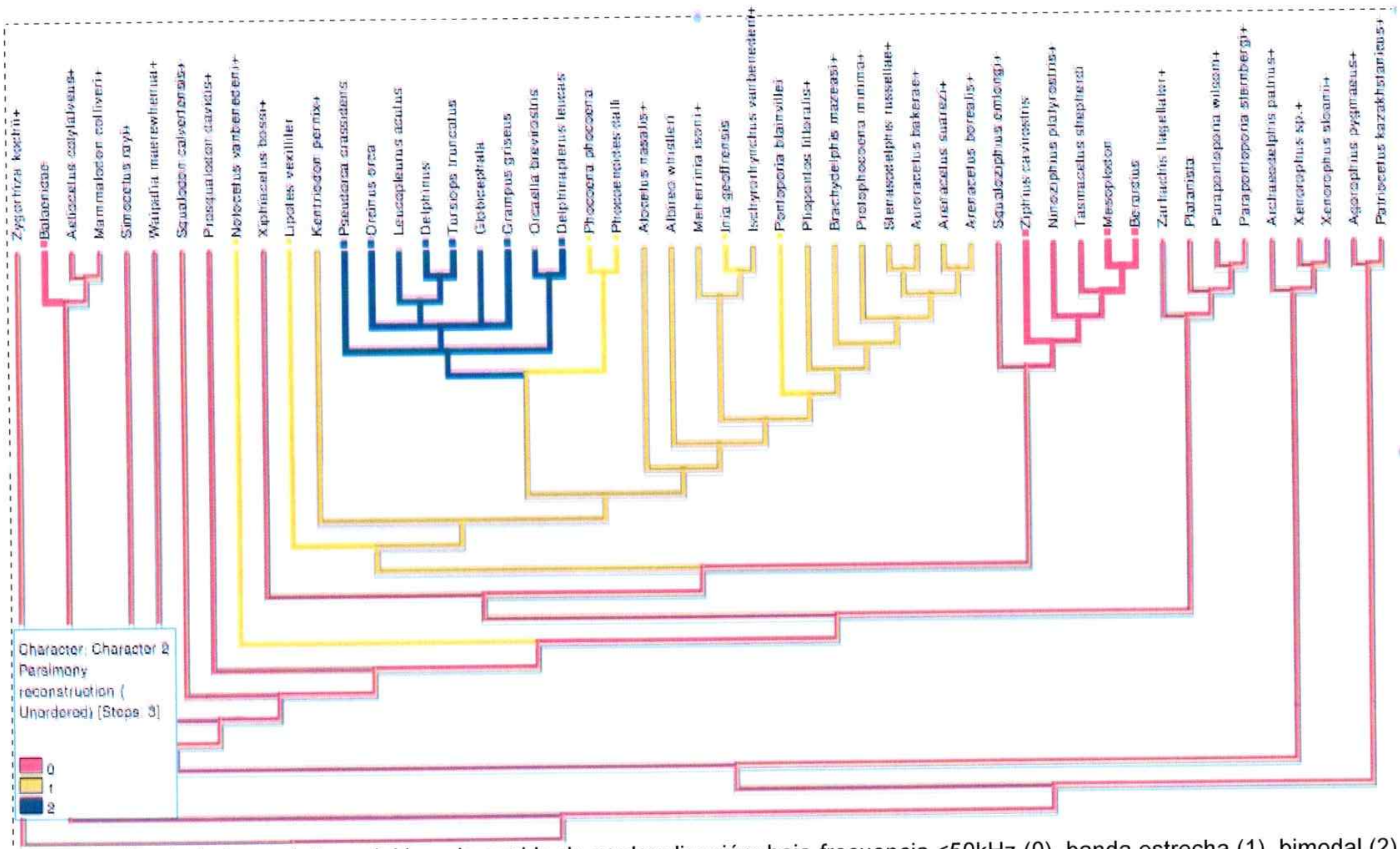


Figura 2 - Propiedades acústicas del haz de sonido de ecolocalización: baja-frecuencia <50kHz (0), banda estrecha (1), bimodal (2).

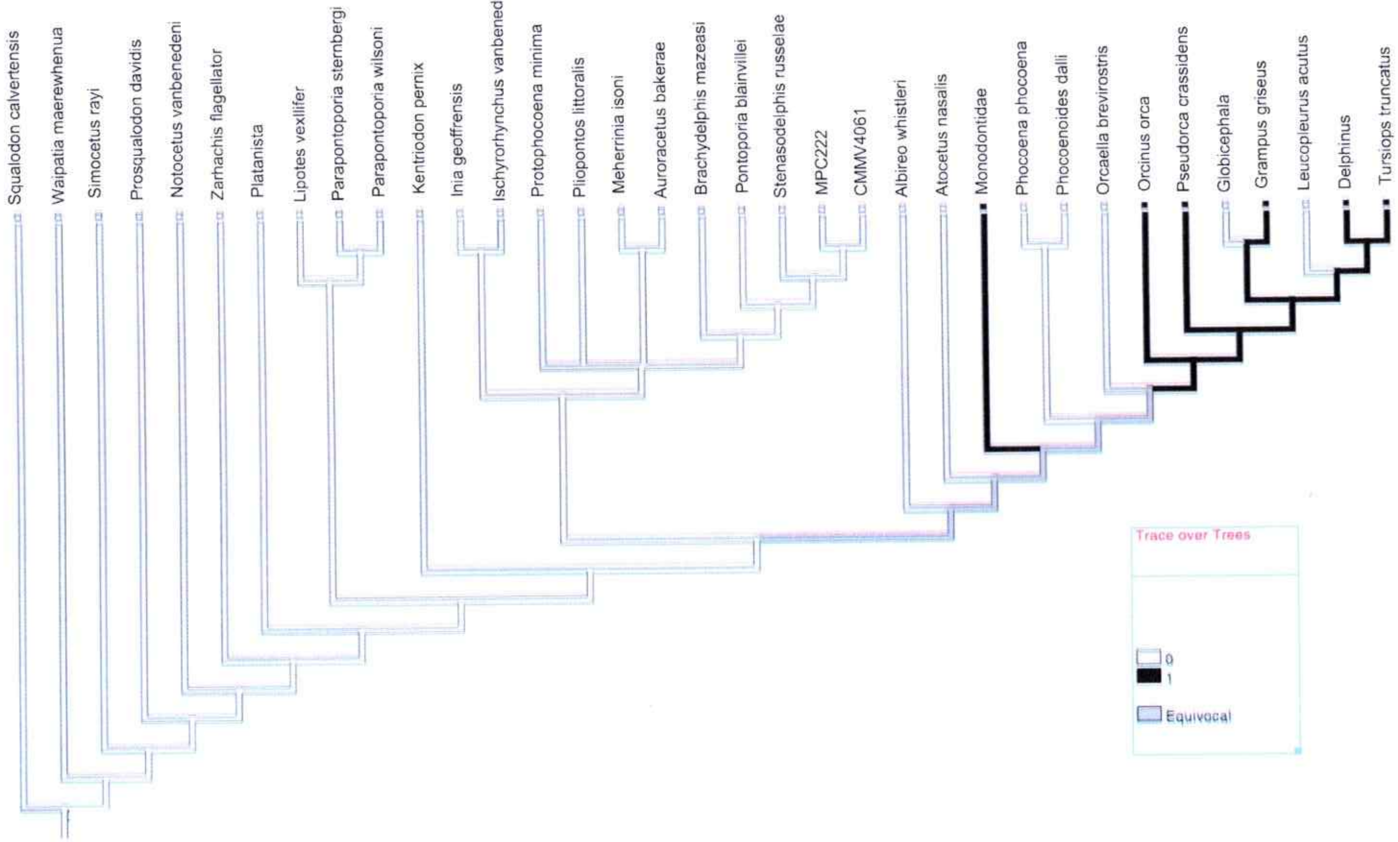


Figura 3 - Propiedades acústicas del haz de sonido de ecolocalización: banda estrecha (~100 kHz) (0), bimodal (60-100 kHz) (1).

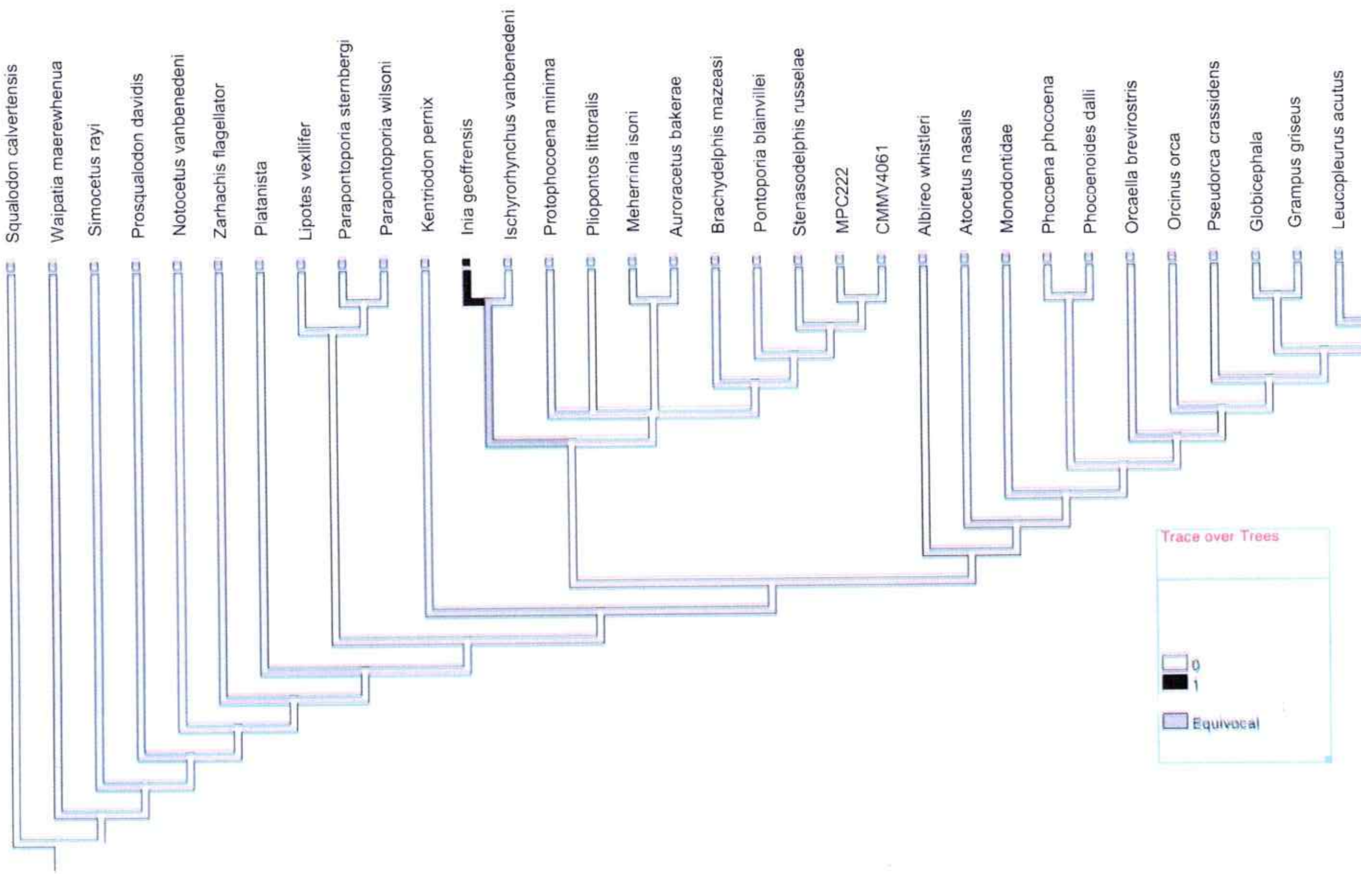


Figura 4 - Forma del melón: melón alongado/cilíndrico, relación entre el ancho y la longitud del melón o sus proxies >30% (0), melón redondeado a subesféricos, ancho y longitud del melón o sus proxies (1).

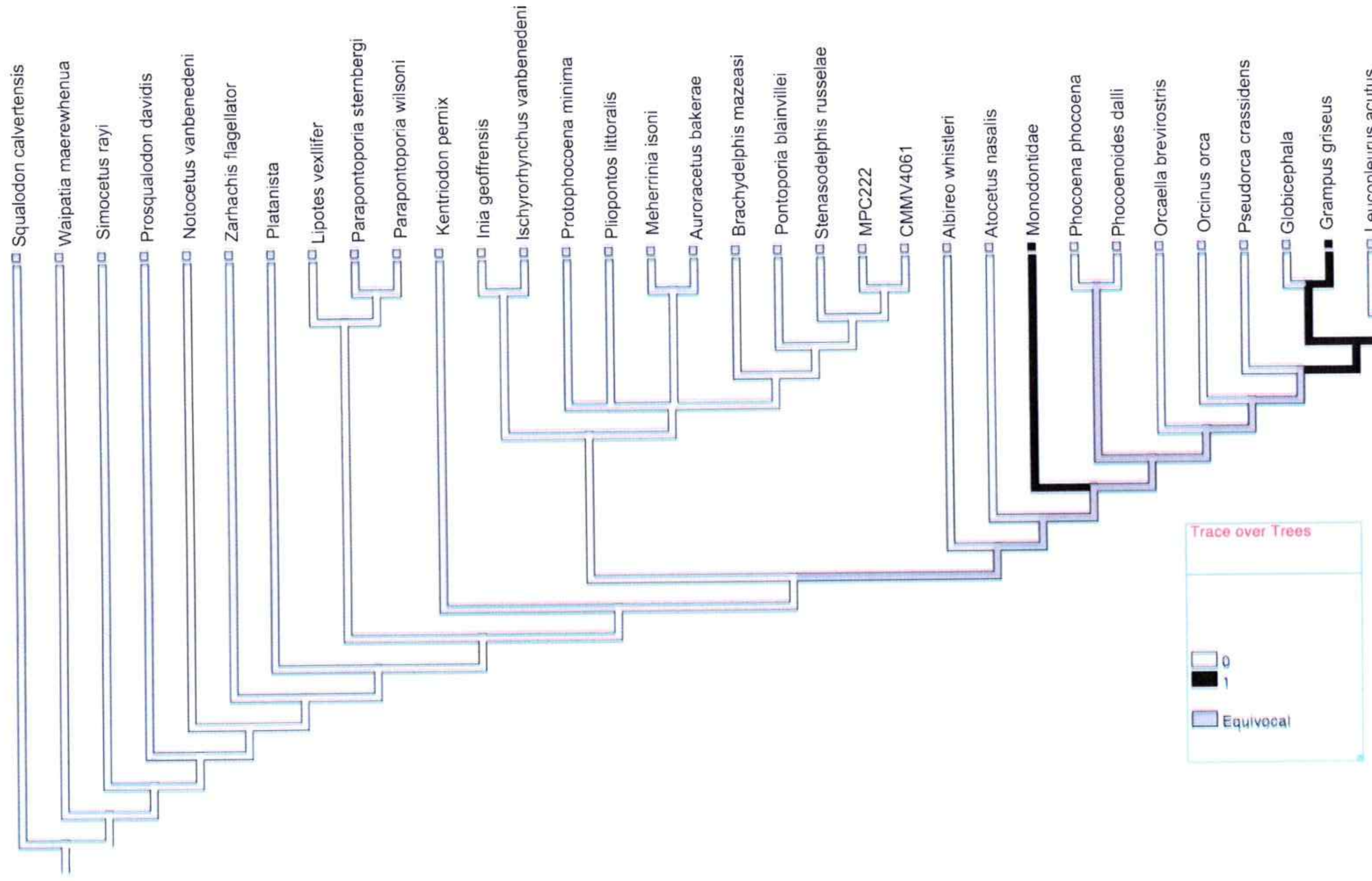


Figure 5 - Tipo de ducto coclear: tipo I (0), tipo II (1) (sensu Ketten 1992).

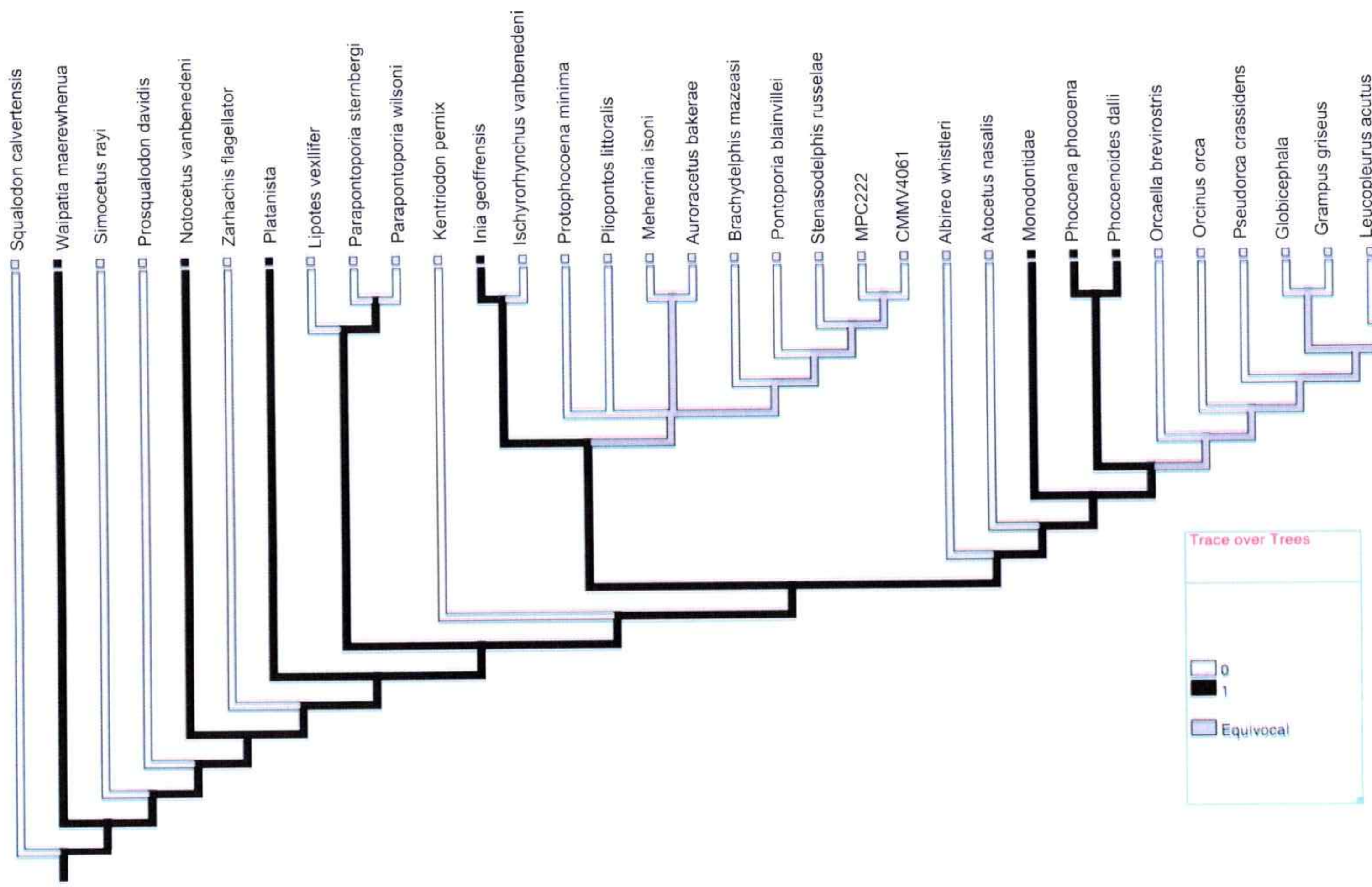


Figura 6 - Forma del pars cochlearis: aproximadamente esférica a equidimensional (0) o delgado y plano (1)

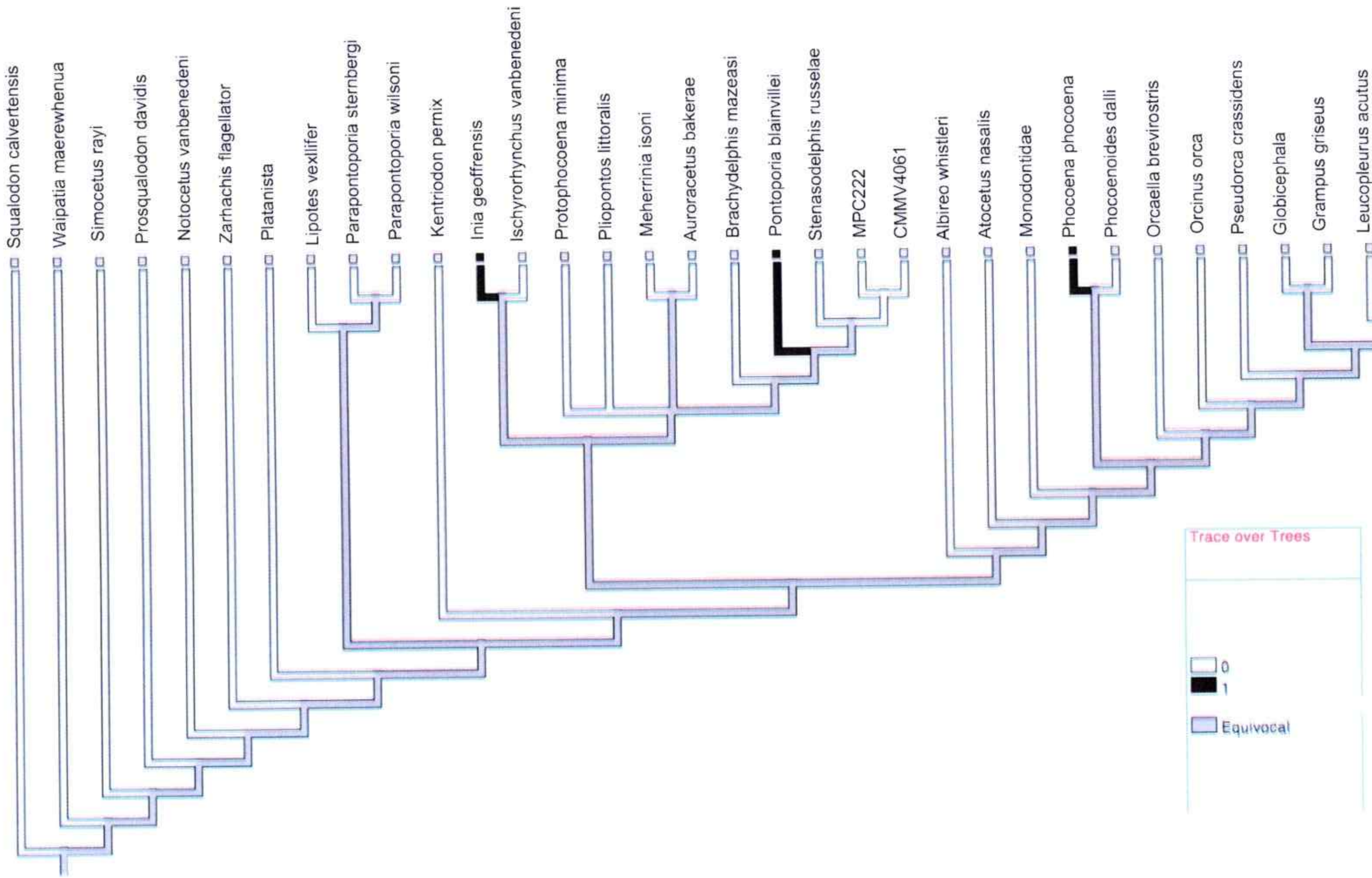


Figure 7 - Sacos nasofrontales: amplios, en forma de media luna extendidos a lo largo del borde de las fosas nasales en

sentido anteroposterior (0), región nasal restringida (1).

XII.2 Integrando información morfológica y hipótesis filogenéticas

Los resultados apoyan la idea ya conocida de tres invasiones a los ambientes fluviales (carácter 1, fig. 1). Con la excepción de *Lipotes* que no posee grupos hermanos fósiles conocidos en el Neógeno, todos los taxa de río tienen a grupos hermanos o cercanos con habito costero o estuarino (ver Fig. 5.1).

Además, el haz de ecolocalización de banda estrecha (carácter 2, fig. 3) se recuperó como un rasgo primitivo, lo cual fue confirmado también por el mapeo de caracteres y la reconstrucción de los nodos ancestrales del tipo de conducto cochlear (carácter 4, fig. 5). Los otros caracteres no fueron concluyentes, probablemente debido a la escasez de datos, habiendo muchos taxa sin grabaciones o otro dato acústico y la dificultad de estimar parámetros acústicos en taxa fósiles.

En la Fig. 5 se observa que el tipo I de ecolocalización, el cual ha sido comúnmente interpretado como un rasgo especializado, asi como los cambios morfológicos observados en los delfines de río. En luz del presente analisis se pudo estimar que este carácter habría estado presente desde la separación de Delphinoidea y Inioidea, con *Lipotes.* Por lo tanto, estaría presente en Delphinida (a excepción de algunos Delphinoidea) y *Notocetus* (carácter 2 y 4) y las invasiones de los hábitats fluviales serian derivados posteriormente al aparecimiento del ducto coclear tipo I, de manera convergente en tres (cuatro con *Sotalia fluviatilis*) contextos filogenéticos, geológicos y temporales diferentes (carácter 1) por convergencias, en tres posiciones filogenéticas distintas, contextos geológicos y temporales (carácter 1). El clado formado después de la separación de Phocoenidae (*Phocoena phocoena* + *Phocoenoides dalli*) del resto de Delphinoidea es consistente en el trazado de los caracteres comunes 1, 2 y 4, siendo cada uno de ellos también relacionados con el medio ambiente, las propiedades acústicas de ecolocalización de haz y el oído interno la morfología (tipo de conducto coclear).

Esta secuencia de transformación de caracteres es parcialmente coherente con el escenario propuesto para la evolución convergente de los delfines de río (Nikaido et al., 2005). La hipótesis propuesta por estos últimos autores, sobre la base de la filogenia molecular, dice que la convergencia observada sería el resultado de la supervivencia diferencial de los linajes antiguos en los ambientes fluviales. En cierto modo, los resultados obtenidos en esta tesis indican que la morfología funcional del cráneo y perióticos (Capitulo 2) se relacionan con la preferencia de hábitat o los datos paleoambientales disponibles. Además, también se recuperó una diferencia morfológica entre las diferentes épocas geológicas: Mioceno inferior, Mioceno medio al Plioceno y el Pleistoceno hasta la actualidad.

En el caso de *Sotalia*, por ejemplo, la diferenciación morfológica funcionalmente relacionada a la ecolocalización es tenue y se dio entre el Plioceno y el Pleistoceno (Cozzuol, 2010; Cunha *et al.*, 2011). *S. fluviatilis* no presenta las modificaciones esperadas para una ecolocalización de banda estrecha como se observo en los demás defines de río. Ademas, a partir de esta informaciones (filogenética y morfológica), se podría sugerir que *S. fluviatilis* presentaría un tipo de haz de sonido bimodal, ya que hasta el momento no se cuenta con esta información.

De esta manera, aunque se encontró correlación morfológica consistente con el ambiente al que pertenecen los distintos taxa de Delphina y Platanistoidea, también se apreció que la propiedades acústicas del haz de ecolocalización y la morfología asociada a estas poseen una historia evolutiva (bimodal aparece dentro de Delphinoidea) distinta al patrón de invasión a los sistemas fluviales (cuatro veces aisladas).

XIII Referencias Bibliográficas

Au, W.W.L. 1993. The sonar of dolphins. Springer-Verlag, New York.

Au, W. W. L., L. N. Andersen, A. R. Rasmussen, H. L. Roitblat, P. E. Nachtigall. 1995. Neural network modeling of a dolphin's sonar discrimination capabilities. The Journal of the Acoustical Society of America 98:43.

Au, W.W.L., Benoit-Bird, K.J. 2003. Automatic gain control in the echolocation system of dolphins. Nature 423: 861-863.

Au, W.W.L., Herzing, D.L. 2003. Echolocation signals of wild Atlantic spotted dolphin (Stenella frontalis). Journal of Acoustic Society of America 113(1): 598-604.

Au, W. W. L. 2004. Echolocation signals of wild dolphins. Acoustical Physics 50:454-462.

Banguera-Hinestroza, E., Cárdenas, H., Ruiz-García, M., Marmontel, M., Gaitán, E., Vázquez, R., García-Vallejo, F. 2002. Molecular Identification of Evolutionarily Significant Units in the Amazon River Dolphin Inia sp. (Cetacea: Iniidae). The Journal of Heredity 93(5): 312-322.

Brandt, J. F. 1873. Untersuchungen uber die fossilen und subfossilen Cetaceen Europa's. – Memóires de l'Académie Impériale des Sciences de St.-Petersbourg, 7e serie 22 (1): 1–361, 34 pls.

Burmeister, G. 1885. Examen crítico de los mamíferos y reptiles fósiles denominados por D. Augusto Bravard y mencionados en su obra precedente. Anales del Museo Nacional de Buenos Aires 97-174 + 2 plates.

Cassens, I., Vicario, S., Waddell, V.G., Balchowsky, H., Van Belle, D., Ding, W., Fan, C., Lal Mohan, R.S., Simões-Lopes, P.C., Bastida, R., Meyer, A., Stanhope, M.J., Milinkovitch, M.C., 2000. Independent adaptation to riverine habitats allowed survival of ancient cetacean lineages. Proc. Natl. Acad. Sci. USA 97: 11343–11347.

Clarke, M.R. 2003. Production and control of sound by the small sperm whales, *Kogia breviceps* and *K. sima* and their implications for other Cetacea. Journal of the Marine Biological Association of the United Kingdom 83: 241-263

Cozzuol, M.A.1985. The Odontoceti of the Mesopotamiense of the Parana River ravines. Systematic review. in G. Pilleri (ed.) Investigations on Cetacea 39-52.

Cozzuol, M.A. 1989. Una nueva especie de Saurodelphis Burmeister, 1891 (Cetacea: Iniidae) del "Mesopotamiense" (Mioceno Tardío-Plioceno Temprano) de la provincia de Entre Ríos, Argentina. Ameghiniana 25: 39-45.

Cozzuol, M.A. 1993. Mamíferos acuáticos del Mioceno medio y tardío de Argentina. Sistemática, evolución y biogeografía. Tesis doctoral, Universidad Nacional de La Plata, Facultad de Ciencias Naturales y Museo de La Plata, inédita.

Cozzuol, M.A. 1996. The records of the aquatic mammals in Southern South America. Münchner Geowissen Abhandlungen 30: 321-342.

Cunha, H. A., Moraes, L.C., Medeiros, B.V., Lailson-Brito, J., da Silva, V.M.F., Solé-Cava, A.M., Schrago, C.G. 2011. Phylogenetic Status and Timescale for the Diversification of Steno and Sotalia Dolphins. PLoS ONE 6:e28297.

Cranford T.W., Amundin M., Norris K.S. 1996. Functional morphology and homology in the odontocete nasal complex: Implication for sound generation. Journal of Morphology 228: 223-285.

Cranford T.W. Krysl, P., Hildebrand, J.A. 2008. Acoustic pathways revealed: simulate sound transmission and reception in Cuvier's beaked whale (*Ziphius cavirostris*). Bioinspiration and Biomimmetics 3: 1-10.

Crisci, J.V., López, M.F.A. 1983. Introducción a la teoría y práctica de la Taxonomía Numérica. Secretaria General de la OEA, Programa Regional de Desarrollo Cientifico y Tecnológico, Washington, Serie de Biología, Monografía nº 26, 132pp.

Cunha, H.A., da Silva, V.M.F., Lailson-Brito Jr, J., Santos, M.C.O., Flores, P.A.C., Martin, A.R., Azevedo, A.F., Fragoso, A.B.L., Zanelatto, R.C., Solé-Cava, A.M. 2005. Riverine and marine ecotypes of *Sotalia* dolphins are different species. Marine Biology, 148(2): 449-457.

Farris, J. S. 1989. The retention index and rescaled consistency index. Cladistics 5:417-419.

Farris, J.S. 2008. Parsimony and explanatory power. Cladistics 24: 825–847.

Fordyce, R.E. 1994. *Waipatia maerewhenua*, new genus and species (Waipatiidae, New Family), an archaic Late Oligocene dolphin (Cetacea: Odontoceti: Platanistoidea) from New Zealand. En A. Berta and T. Deméré (eds), Contributions in Marine Mammal Paleontology honoring Frank C. Whitmore, Jr. Proceedings of the San Diego Society of Natural History 29 pp. 147-176.

Fordyce, R.E. 2002. *Simocetus rayi* (Odontoceti: Simocetidae, New Family): A bizarre new archaic Oligocene dolphin from the eastern North Pacific. En Emry, R.J. (ed) Cenozoic Mammals of land and sea: tributes to the career of Clayton E. Ray. Smithsonian Institution Press, Washington DC. Pp. 185-222

Fraser, F.C., Purves, T.E. 1960. Hearing in Cetaceans. Evolution of the Accessory air sacs and the structure and function of the outer and middle ear in recent cetaceans. Bulletin of the British Museum (Natural History) Zoology Vol 7 no 1, 140 p. London.

Gatesy J. (1997) More DNA support for a Cetacea/Hippopotamidae clade: the blood-clotting protein gene Y-Fibrinogen. Molecular Biology and Evolution 14(5): 537-543.

Gatesy J., Milinkovitch, M., Waddell, V., Stanhope, M. 1999. Stability of cladistic relationships between Cetacea and higher-level artiodactyl taxa. Systematic Biology 48(1): 6-20.

Geisler, J. H., Godfrey, S.J., Lambert, O. 2012. A New Genus and Species of Late Miocene Inioid (Cetacea , Odontoceti) from the Meherrin River, North Carolina, U.S.A. Journal of Vertebrate Paleontology 32:198-211.

Geisler, J. H., McGowen, M.R., Yang, G., Gatesy, J. 2011. A supermatrix analysis of genomic, morphological, and paleontological data from crown Cetacea. BMC Evolutionary Biology 11:112.

Geisler, J.H., Sanders, A.E. 2003. Morphological evidence for the phylogeny of Cetacea. Journal of Mammalian Evolution 10: 23–129.

Geisler, J.H., Uhen, M.D. 2003. Morphological Support for a close relantioship between Hippos and Whales. Journal of Vertebrate Paleontology 23(4): 991-996.

Giraud-Sauveur D. 1969. Recherches biophysiques sur les osselets des Cetaces. Mammalia 33: 285-340.

Gingerich, P. D., y D. E. Russell. 1981. Pakicetus inachus, a new archaeocete (Mammalia, Cetacea) from the early-middle Eocene Kuldana Formation of Kohat (Pakistan). Contributions from the Museum of Paleontology, University of Michigan, 25:235-246.

Gingerich, P.D., Wells, N.A., Russell, D.E., Shah, S.M.I. 1983. Origin of whales in epicontinental remmant seas: new evidences from the early Eocene of Pakistan. Science 220: 403-406.

Gingerich, P.D. 2001. Origin of whales form early Artiodactyls: hands and feet of Eocen Protocetid from Pakistan. Science 293: 2239-2242.

Gingerich, P.D., Russel, D.E. 1981. *Pakicetus inachus*, a new Archaeocete (Mammalia, Cetacea) from the early-middle Eocene Kuldana Formation of Kohat (Pakistan). Contributions of th e Museum of Paleontology, University of Michigan 24: 190-203.

Godfrey, S.J., Barnes, L. G. 2008. A new genus and species of Late Miocene pontoporiid dolphin (Cetacea: Odontoceti) from the St. Marys Formation in Maryland. Journal of Vertebrate Paleontology 28(2): 520-528.

Goloboff, P.A., Farris, J.S., Källersjö, M., Oxelman, B., Ramírez, M., Szumik, C.A. 2003. Improvements to resampling measures of group support. Cladistics 19: 324-332.

Goloboff, P.A., Farris. J.S., Nixon, K.C. 2008. TNT, a free program for phylogenetic analysis. Cladistics 24: 774-786.

Gutstein, C.S, Canals, M., Cozzuol, M. 2010. *Presencia de melón en Brachydelphis mazeasi (Platanistoidea) del mioceno de la Formación Pisco, Peru. Libro de resúmenes: XIII Reunión de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur, Montevideo, Uruguay.*

Gutstein, C.S., Cozzuol, M.A. 2002. La presencia de Kentriodon sp. en el Oligoceno tardio Mioceno temprano de la Patagonia. I Congreso Latinoamericano de Paleontología de Vertebrados, Santiago. Chile, p. 35-36.

Gutstein, C.S., Cozzuol, M.A. 2004. Filogenia preliminar da família Kentriodontidae (Odontoceti, Cetacea). XX Jornadas Argentinas de Paleontología de Vertebrados, La Plata, Argentina. p. 33.

Gutstein, C.S., Cozzuol, M. 2006. The Pontoporiids (Cetacea, Odontoceti) from Bahía Inglesa Formation (Middle Miocene-Pliocene). Biological Research, 39(Suplemento B): R-97.

Gutstein, C.S., Cozzuol, M.A., Suárez, M. 2006. The cetaceans from Bahía Inglesa Formation (Atacama, Chile): Taphonomic approach and paleogeographical implications. Journal of Vertebrate Paleontology 26(3): 71A.

Gutstein, C.S., Cozzuol, M.A., Vargas, A.O., Suárez, M., Schultz, C.L., Rubilar-Rogers, D. 2009. Skull variation of Brachydelphis (Cetacea, Odontoceti, Pontoporiidae) from South-Easthern Pacific Neogene. Journal of Mammalogy *90 (2): 215-230*

Hamilton, H., Caballero, S., Collins, A., Brownell, R. L. Jr. 2001. Evolution of river dolphins. Proc. R. Soc. London B. 268: 549-556.

Harper, C.J., McLellan, W.A., Rommel, S.A., Gay, D.M., Dillaman, R.M., Pabst, D.A. 2008. Morphology of the melon and its tendinous connections to the facial muscles in bottlenose dolphins (*Tursiops truncatus*). Journal of Morphology 269:820–839.

Hemilä, S., Nummela, S. y Reuter, T. 1999. A model of the odontocete middle ear. Hearing Research, 133: 82-97.

Heyning, J.E. 1989. Comparative facial anatomy of beaked whales (Ziphiidae) and a systematic revision among the families of extant Odontoceti. Contributions in Science Natural History Museum of Los Angeles County 405: 1-64.

Ichishima, H.; Barnes, L.G.; Fordyce, R.E.; Kimura, M., Bohaska, D.J. 1994. A review of Kentriodontine dolphin (Cetacea: Kentriodontidae): systematics and biogeography. The Island Arc 3(4): 486-492.

Jacobs, D.W., Hall, J.D. 1972. Auditory Thresholds of a Fresh Water Dolphin, *Inia geoffrensis* Blainville. Journal of the Acoustic Society of America 51(2): 530-533.

Kasuya, T. 1973. Systematic consideration of recent toothed whales based on the morphology of tympano-periotic bone. Scientific Reports of the Whales Research Institute 25: 1-103.

Kellogg, R., 1928: The history of whales – their adaptation to life in the water. Quarterly Review of Biology 3: 174–208.

Kellogg, W. N., Kohler, R. 1952. Reactions of the porpoise to ultrasonic frequencies. Science 116: 250-252.

Kellogg, W. N., Kohler, R., Morris, H. N. 1953. Porpoise sounds as sonar signals. Science 117: 239-243.

Ketten, D. R. 1992: The marine mammal ear: specializations for aquatic audition and echolocation. En Webster, D., Fay, R., Popper, A.N. (eds). The Evolutionary Biology of Hearing New York: Springer-Verlag, pp. 717–754.

Ketten, D. R. 1992. THE CETACEAN EAR: FORM, FREQUENCY, AND EVOLUTION; pp. 53-75 in J. Thomas (ed.), Marine Mammal Sensory Systems. Plenum Press, New York.

Kinkel, M.D., Thewissen, J.G.M., Oelschläger, H.A. 2001. Rotation of middle ear ossicles during cetacean development. Journal of morphology 249: 126-131.

Lambert, O. 2005. Phylogenetic affinities of the long-snouted dolphin *Eurhinodelphis* (Cetacea, Odontoceti) from the Miocene of Antwerp. Palaeontology 48(3): 653-679.

Lambert, O., Post, K., 2005. First European pontoporiid dolphins (Mammalia: Cetacea, Odontoceti), from the Miocene of Belgium and The Netherlands. Deinsea 11: 7-20.

Latrubesse, E.M., da Silva, S.A.F., Cozzuol, M.A., Absy, M.L. 2007. Late Miocene continental sedimentation in southwestern Amazonia and its regional significance: Biotic and geological evidence. Journal of South American Earth Sciences 23: 61-80.

Maddison, W.P., Maddison, D.R. 2011. Mesquite: A modular system for evolutionary analysis. Version 2.75. http://mesquiteproject.org

Maddison, W.P., Maddison, D.R. 2007. Mesquite: a modular system for evolutionary analysis. Version 2.01. Http://mesquiteproject.org.

Nikaido, M., Nishihara, H., Hukumoto, Y., Okada, N. 2003. Ancient SINEs from

African endemic mammals. Molecular Biology and Evolution 20: 522-7.

Madsen, P. T., Kerr, I., Payne, R. 2004. Echolocation clicks of two free-ranging delphinids with different food preferences: False killer whales *Pseudorca crassidens* and Risso's dolphin *Grampus griseus.* Journal of Experimental Biology 207: 1811-1823.

Manly, B.F.J. 2004. Multivariate statistics methods: a primer. 3ª ed. Chapman & Hall/CRC press, Washington, 214pp.

Marino, L. 1998. A comparison of encephalization between odontocete cetaceans and anthropoid primates. Brain Behavioral Evolution 51: 230-238.

Marino, L. Rilling, J.K., Linc, S.K., Ridgwayd, S.H. 2000. Relative volume of the cerebellum in dolphins and comparison with anthropoid primates. Brain Behavioral Evolution 56: 204-211.

Marino, L. Connor, R.C., Fordyce, R.E., Herman, L.M., Hof, P.R., Lefebvre, L., Lusseau, D., McCowan, B., Nimchinsky, E.A., Pack, A.A., Rendell, L., Reidenberg, J.S., Reiss, D., Uhen, M.D., Van der Gucht, E., Whitehead, H. 2007. Cetaceans have complex brains for complex cognition. PLoS Biology 5(5, essay 139): 966-972.

Martínez-Cáceres, M., Muizon, C. 2011. A new basilosaurid (Cetacea, Pelagiceti) from the Late Eocene to Early Oligocene Otuma Formation of Peru. Comptes Rendus Palevol 10:517-526.

McCormick, J. G., Wever, E.G., Palin, J., Ridgway, S.H. 1970: Sound conduction in the dolphin ear. Journal of the Acoustic Society of America 48: 1418-1428.

McKinney, M.L., McNamara, K.J. 1991. Heterochrony: the evolution of ontogeny. New York, Plenum Press Ed. 437p.

Messenger, S.L., McGuire, J.A. 1998. Morphology, molecules, and the phylogenetics of cetaceans. Systematic Biology 47: 90-124.

Mitchell E.D. 1989. A new cetecean from the Late Eocene La Meseta Formation, Seymour Island, Antarctic Peninsula. Canadian Journal of Fisheries and Aquatic Sciences 46: 2219-2235.

Milinkovitch, M. C., Ortí, G., Meyer, A. 1993. Revised phylogeny of whales suggested by mitochondrial ribosomal DNA sequence. Nature 361: 346-348.

Milinkovitch, M. C., Meyer, A., Ortí, G. 1994. Phylogeny of all major groups of cetaceans based on DNA sequences from three mitochondrial genes. Molecular Biology and Evolution 11: 939-948.

Muizon, C. de.1983. *Pliopontos littoralis* un nouveau Platanistidae Cetacea du Pliocéne de la côte péruvienne. Comptes Rendus de l'Académie de Sciences de Paris. Sér. II. 296: 1203-1206.

Muizon, C. de.1988a. Vertebrés fossiles de la Formation Pisco (Pérou) III: Les Odontocètes (Cetacea: Mammalia) du Miocène. Recherche sur les Civilizations, Institut Français d'Études Andines, Memoire 78:1- 244.

Muizon, C. de.1988b. Les relations phylogenétiques des Delphinida (Cetacea; Mammalia). Annales de Paléontologie (Vert.-Invert.) 74(4):159-227.

Muizon, C. de. 1993. Walrus-like feeding adaptation in a new cetacean from the Pliocene of Peru. Nature 365: 745-748.

Nikaido, M., Matsuno, F., Hamilton, H., Brownel, R. L. Jr, Cao, Y., Ding, W., Zuoyan, Z., Shedlock, A. M., Fordyce, R. E., Hasegawa, M., Okada, N. 2001. Retroposon analysis of major cetacean lineages: The monophyly of toothed whales and the paraphyly of river dolphins. Proceedings of the National Academy of Sciences 98(13): 7384-7389.

Norris, K. S., Prescott, J. H., Asa-Dorian, P. V., Perkins, P. 1961. An Experimental Demonstration of Echolocation Behavior in the Porpoise Tursiops truncatus (Montagu), Biol. Bull. 120, 163-176.

Nummela, S., Reuter, T. Hemilä, S., Holmberg, P., Paukku, P. 1999a. The anatomy of the killer whale middle ear (Orcinus orca). Hearing Research, 133, 61–70.

Nummela, S., Wägar, T. Hemilä, S., Reuter, T. 1999b. Scaling of the cetacean middle ear. Hearing Research, 133: 71-81.

Nummela, S., Thewissen, J.G.M., Bajpai, S., Hussain, S.T., Kumar, K. 2004. Eocene evolution of whale hearing. Nature 430: 776-778.

Nummela, S., Hussain, S.T., Thewissen, J.G.M. 2006. Cranial anatomy of Pakicetidae (Cetacea, Mammalia). Journal of Vertebrate Paleontology 26:746-759.

Nummela, S., Thewissen, J.G.M., Bajpai, S., Hussain, S.T., Kumar, K. 2007. Sound Transmission in Archaic and Modern Whales: Anatomical Adaptations for Underwater Hearing. The Anatomical Record 290: 716-733.

O'Leary, M. A., Geisler, J. H. 1999. The position of Cetacea within Mammalia: phylogenetic analysis of morphological data from extinct and extant taxa. Systematic Biology 48(3): 455-490.

O'Leary, M.A., Gatesy, J. y Novacek, M.J. 2003. Are the dental data really at odds with the molecular data? Morphological evidence for whale phylogeny (re)reexamined. Systematic Biology 52(6):853-64.

Perrin, W.F., Yablokov, A.V., Cass, V.L. 1982. Preliminary report on the use of non-metrical skull characters to discriminate populations of pelagic dolphins. National Marine Fisheries Service/ Southwest Fisheries Center. 1-32.

Pilleri, G. 1990. Adaptation to water and the evolution of echolocation in the Cetacea. Ethology, Ecology and Evolution 2: 135-163.

Pyenson, N. D., Hoch, E. 2007. Tortonian pontoporiid odontocetes from the Eastern North Sea. Journal of Vertebrate Paleontology 27(3): 757-762.

Ribeiro, A.M., Drehmer, C.J., Buchmann, F.S.C., Simões-Lopes, P.C. 1998. Pleistocene skull remains of Pontoporia blainvillei (Cetacea, Pontoporiidae) from the coastal plain of Rio Grande do Sul State, Brazil, and the relationships of pontoporids. Revista da Universidade de Guarulhos 3(6): 71-77.

Rice, D. W. 1998. Marine Mammals of the World: Systematics and Distribution. Special publication 4. The Society for Marine Mammals, Lawrence, KS.

Schevill, W. E., Lawrence, B. 1956. Food-finding by a captive porpoise (*Tursiops truncatus*). Breviora, Mus. Comprative Zoology 53: 1-15.

Spoor, F., Bajpai, S., Hussain, S., Kumar, T.K., Thewissen, J.G.M. 2002. Vestibular evidence for the evolution of aquatic behaviour in early cetaceans. Nature 417: 163-166.

Sassu, R., Cozzi, B. 2006. The External and Middle Ear of the Striped Dolphin Stenella coeruleoalba (Meyen 1833). Anatomia, Histologia, Embryologia 36(3):197-201.

Thewissen, J.G.M., Hussain, S.T. (1993). Origin of underwater hearing in whales. Nature 361: 444-445.

Thewissen, J.G.M., Madar, S.I., Hussain, S.T. 1998. Whales ankles and evolutionary relationships. Nature 395: 452.

Thewissen, J.G.M., Madar, S.I. 1999. Ankle morphology of the earliest cetaceans and its implications for the phylogenetic relations among Ungulates. Systematic Biology 48(1): 21-30.

Thewissen, J.G.M., Williams, E.M., Roe, L.J., Hussain, S.T. 2001. Skeletons of terrestrial cetaceans and the relationship of whales and artiodactyls. Nature 413: 277-281.

Thewissen, J.G.M., Cooper, L.N., Clementz, M.T., Bajpai, S., Tiwari, B.N. 2007. Whales originated from aquatic artiodactyls in the Eocene epoch of India. Nature 450: 1190-1195.

Uhen, M.D. 2004. Form, function, and anatomy of *Dorudon atrox* (Mammalia, Cetacea): an archaeocete from the middle to late Eocene of Egypt. University Michigan Papers Paleontol. no. 34.

Watkins, W. A. 1980. Click sounds from animals at sea. In Animal Sonar Systems (ed. R. G. Busnel and J. F. Fish), pp. 291-298. New York: Plenum

Press.

Wever, E.G. ,McCormick, J. G., Palin, J., Ridgway, S.H. 1971. Cochlea of the dolphin, Tursiops truncatus: the basilar membrane. Proceedings of the National Academy of sciences of Unite States of America 68(11): 2708-2711.

West-Eberhard, M.J. 1989. Phenotypic plasticity and the origins of diversity. Annual Review of Ecology and Systematics 20: 249-278.

Whitmore, F.C. 1994. Neogene climatic changes and the emergence of the modern whale fauna of the North Atlantic Ocean. En Berta, A., Deméré, T. (eds). Contributions in Marine Mammal Paleontology honoring Frank C. Whitmore, Jr. Proceedings of the San Diego Society of Natural History Pp. 221-227.

ZAR, J.H. 1996. Biostatistical analysis. Prentice Hall, Upper Saddle River, New Jersey. USA. 662 pp.

Zhou, K. 1982. Classification and phylogeny of the Superfamily Platanistoidea, with notes on evidence of the monophyly of the Cetacea. Scientific Report Whales Research Institute 34: 93-108.