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Revalidation of Tursiops gephyreus Lahille, 1908 (Cetartyodactila: Delphinidae) from the Southwestern Atlantic Ocean

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Running head: Revalidation of *Tursiops gephyreus*

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ABSTRACT

Historically, the taxonomic status of the bottlenose dolphins, *Tursiops*, has been confusing. Over 20 nominal species have been described in, or transferred to, the genus, but most them have been synonymized as type species *T. truncatus.* Here we review the taxonomic status of *Tursiops gephyreus* Lahille, 1908, from the Southwestern Atlantic Ocean (SWA), a taxon long considered as either synonym or subspecies of *T. truncatus*. We examined a total of 280 bottlenose dolphin skulls, including the lectotype of *T. gephyreus*. We examined all specimens for morphological (14 characters) and morphometrical (29 measurements) differences. A set of univariate and multivariate analysis was conducted to observe the possible differences between groups. Based on morphological, both metric and non-metric analyzes of skulls as well as the vertebrae number of *Tursiops* specimens from SWA, we recognized two distinct morphological forms of bottlenose dolphins in the region, consistent with treatment of two species under the "diagnosable version of the "Phylogenetic Species Concept". Six qualitative characters were reliable for the identification of both species in the SWA, but the shape of the nasal process of the right premaxilla alone is sufficient to separate the species. Furthermore, the total number of vertebrae is higher in *T. truncatus* (62–64) than *T. gephyreus* (57–59). Based on these results we propose the revalidation of *T. gephyreus*.

Since *T. gephyreus* was recognized as inhabiting the estuaries and the surf zone alongside the Rio Grande do Sul in Brazil, Uruguay and Argentina coasts, the conservation efforts must take into account that this region presents similar threats to the species.

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INTRODUCCTION

Bottlenose dolphins, *Tursiops* Gervais, 1855, are widely distributed throughout tropical and temperate waters of all oceans, occurring in the coast and ocean, both over the continental shelf and in open ocean as well (Perrin et al. 2009). In the Southwestern Atlantic Ocean (SWA), these dolphins range from northern Brazil to Argentina's Chubut Province, 01°S–46°S (Siciliano et al. 2006), with a few records south to Tierra del Fuego (Goodall et al. 2008; Goodall et al. 2011).

The taxonomy of bottlenose dolphins has been and continues to be subject of debate. Over the past two and half centuries, more than 20 nominal species have been originally described in or transferred to *Tursiops* from various regions, but most of them have been subsequently synonymized to the single cosmopolitan species *T. truncatus* (Hershkovitz 1966; Ross 1977; Rice 1988). Bernard Germain Lacépède described in 1804 a bottlenose dolphin from the North Atlantic as *Delphinus nesarnack*. However, this name has not been used as valid in the literature. Seventeen years later, in 1821, George Montagu described a bottlenose dolphin from River Dart in Devonshire, UK, naming it as *Delphinus truncatus*. Afterwards, many authors described others species under the genus *Delphinus*: *Delphinus compressicauda* Lesson, 1828 (type locality: South Atlantic Ocean, 4° S, 26° W), *Delphinus aduncus* Ehrenberg, 1833 (type locality: Indian Ocean, Red Sea), *Delphinus hamatus* Wiegmann, 1841 (type locality: Indian Ocean, Red Sea), *Delphinus abusalam* Rüppell, 1842 (type locality: Indian Ocean, Red Sea).

In 1843, Gray transferred *D. truncatus* to *Tursio*; however, since this genus was a junior synonym of *Physeter* Linnaeus, 1758, the name *Tursiops* was coined in 1855 by Paul Gervais (Hershkovitz 1966; Rice 1988; Wells and Scott 2009). The species described in addition to the type species were: *Delphinus metis* Gray, 1846 (type locality: Indian Ocean, Red Sea), *Delphinus eurynome* Gray, 1846 (type locality: unknown), *Delphinus obtusus* Schlegel, 1862 (type locality: North Atlantic Ocean), *Tursiops catalania* Gray, 1862 (type locality: South Pacific Ocean, Australia), *Delphinus erebenus* Cope, 1865 (type locality: North Atlantic Ocean, Red Bank, USA), *Delphinus gadamu* Owen, 1866 (type locality: Indian Ocean, Vizagapatam), *Delphinus cymodoce* Burmeister, 1867 (type locality: unknown), *Tursiops gilli* Dall, 1873 (type locality: North Pacific Ocean, California, USA), *Delphinus caerulescens* Gigliori, 1874 (type locality: North Pacific Ocean, Japan), *Delphinus parvimanus* Lütken, 1887 (type locality: Adriatic Sea), *Steno perniger* Blanford, 1891 (type locality: Indian Ocean, Gulf of Bengal), *Tursiops fergusoni* Lyddeker, 1903 (type locality: Indian Ocean, Trivandrun, India), *Tursiops gephyreus* Lahille, 1908 (type locality: South Atlantic Ocean, La Plata river, Argentina), *Tursiops dawsoni* Lyddeker, 1909 (type locality: Indian Ocean, Trivandrun, India), *Tursiops nuuanu* Andrews, 1911 (type locality: North Pacific Ocean, 12° S, 120° W) and *Tursiops maugeanus* (type locality: Indian Oceana, Tasmania, Australia) (Hershkovitz 1996; Rice 1998; Jefferson et al. 2008; Wells and Scott 2009).

Rice (1984) demonstrated that the name *Tursiops truncatus* (Montagu, 1821) has been in universal use for the North Atlantic bottlenose dolphins for over 160 years, and then asked the International Commission on Zoological Nomenclature (ICNZ) to use its plenary powers to suppress the name *Delphinus nesarnack* Lacépède, 1804. This was accepted in Opinion 1413 of the ICZN (1986).

It is worthy of note that most of the species of bottlenose dolphins have been described based on a small number, or even a single incomplete (e.g. a lower jaw only) specimen, and subtle differences in coloration and cranial morphology. Therefore, some of the morphological characters may represent individual and/or ontogenetic variations (Rice 1998; Wells and Scott, 2009).

Recent studies, both morphological and molecular, have provided evidence that the genus includes at least two other species: *T. aduncus* (Ehrenberg, 1833) in the coastal waters of the Indo-Pacific (Wang et al. 2000a; Wang et al. 2000b) and *T. australis* Charlton-Robb et al. 2011, in inshore waters of Victoria southeastern Australia (Charlton-Robb et al. 2011). However, this last species was contested by the Committee on Taxonomy of the Society for Marine Mammalogy (Committee on Taxonomy 2015) based on the limited number of specimens representing this taxon, minor mean morphometric differences, and low support in molecular analyses.

Only two species of bottlenose dolphins have been so far described from the Southwestern Atlantic. René Primevère Lesson, briefly characterized *D. compressicauda* as having "teeth small, conical, hooked; head colored; belly whitish; pectoral short; upper jaw longest; nose short; base of the tail compressed on each side" (see Gray 1850). In contrast, Lahille (1908: 364) described in detail *T. gephyreus* based on two complete skeletons, a male and a female. According to him, *T. gephyreus* differs from *T. truncatus* by having a longer rostrum; pterygoids separated from each other (*vs*. joined to each other in *T. truncatus*); premaxilla apex acute (*vs*. rounded); lower number of vertebrae; four similarly-sized maxillary foramina (*vs*. irregularly distributed, varying in size, and usually in number of three); teeth thicker; and lower jaws longer than upper jaws. However, Hershkovitz (1966) recognized *T. gephyreus* as a junior synonym of *Tursiops truncatus aduncus* without explicit justification. More recently, Barreto (2000) proposed (p. 46), based on skull measurements and mitochondrial DNA sequences, that bottlenose dolphins occurring from about 27° S to 35° S in Southwestern Atlantic Ocean should be treated at the subspecific level as *Tursiops truncatus gephyreus*. However, he did not deeply explained it or established any biogeographic relation for the species.

In this context, we present further morphological evidence for raising *T. gephyreus* Lahille, 1908 to its original species rank. We adopted here the diagnosable version of the "Phylogenetic Species Concept". This concept has been proposed by several authors as "the smallest detected samples of self-perpetuating organisms that have sets of characters" (Nelson and Platnick 1981); "the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" (Cracraft 1983); and "the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)" (Nixon and Wheeler 1990).

MATERIALS AND METHODS

Specimens examined.— We examined 280 bottlenose dolphin skulls (including the lectotype of *T. gephyreus* – MACN54.113) (see Varela et al. 2010), deposited in the following collections: Brazil: mammal collection of the Museu Paraense Emílio Goeldi (MPEG), under supervision of Grupo de Estudos de Mamíferos Marinhos da Amazônia (GEMAM), Belém, Pará; Associação de Pesquisa e Conservação de Ecossistemas Aquáticos (AQUASIS), Fortaleza, Ceará; Centro de Mamíferos Aquáticos, Instituto Chico Mendes de Conservação da Biodiversidade (CMA/ICMBIO), Ilha de Itamaracá, Pernambuco; Instituto Baleia Jubarte (IBJ), Salvador, Bahia; Instituto Mamíferos Aquáticos (IMA), Salvador, Bahia; marine mammal collection of the Instituto Oswaldo

Cruz (IOC/FIOCRUZ), under supervision of Grupo de Estudos de Mamíferos Marinhos da Região dos Lagos (GEMM-Lagos), Rio de Janeiro, Rio de Janeiro; mammal collection of the Museu Nacional/Universidade Federal do Rio de Janeiro (MNRJ), Rio de Janeiro, Rio de Janeiro; Laboratório de Mamíferos Aquáticos, Universidade Federal do Rio de Janeiro (MAQUA/UFRJ), Rio de Janeiro, Rio de Janeiro; Laboratório de Biologia da Conservação de Mamíferos Aquáticos (LABCMA/USP), São Paulo, São Paulo; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, São Paulo; Instituto de Pesquisas Cananéia (IPeC), Cananéia, São Paulo; Laboratório de Ecologia e Conservação, Universidade Federal do Paraná (LEC/UFPR), Pontal do Sul, Paraná; Museu de Ciências Naturais da Universidade Federal do Paraná (MCN/UFPR), Curitiba, Paraná; Universidade da Região de Joinville (UNIVILLE), Joinville, Santa Catarina; Museu Oceanográfico da Universidade do Vale do Itajaí (MOVI/UNIVALI), Itajaí, Santa Catarina; Laboratório de Mamíferos Aquáticos, Universidade Federal de Santa Catarina (LAMAQ/UFSC), Florianópolis, Santa Catarina; Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul (GEMARS), Torres, Rio Grande do Sul; Laboratório de Tartarugas e Mamíferos Marinhos, Universidade Federal do Rio Grande (LTTM/FURG), Rio Grande, Rio Grande do Sul. Uruguay: Private Collection Researcher Paula Laporta, Punta Del Diablo, Rocha; Museo Nacional de Historia Natural (MNHN), Montevideo, Montevideo; Facultad de Ciencias de La Universidad de La República (ZVC) Montevideo, Montevideo. Argentina: Fundación Marybio, Las Grutas, Rio Negro; Universidad Nacional del Mar del Plata (UNMDP), Mar del Plata, Buenos Aires; Parque Temático y Oceanário Mundo Marino, San Clemente Del Tuyu, Buenos Aires; Museu Nacional de História Natural "Bernardino Rivadavia" (MACN), Buenos Aires, Buenos Aires; and Laboratório de Mamíferos Marinos DEL Centro Nacional Patagônico (LAMAMA/CENPAT), Puerto Madryn, Chubut.

The specimens we examined were identified as either *T. truncatus* (*n* = 144) or *T. gephyreus* (*n* = 136), based on the qualitative characters described by Lahille (1908) and Barreto (2000), which included shape of the pterygoid recess and conformation of pterygoids. We divided specimens into three age groups according to Tavares et al. (2010): juvenile (bones unfused, bones move freely or they are disarticulated and the alveoli are opened), subadult (bones partially fused, some movement and semi-closed alveoli), and adult (fused bones, closed sutures and closed alveoli). Some specimens with partially fused nasal bones were considered adults because they had other skull sutures fused and closed alveoli. All the specimens used in this study were found stranded ashore or were incidentally captured by fishery gears and then collected, cleaned and deposited in scientific collections (Supporting Information S1); therefore, no permits were required. The study area includes Brazilian, Uruguayan, and Argentinean waters in the Southwestern Atlantic.

Sexual dimorphism.— Based on the low sexual dimorphism reported in the literature (Hersh et al. 1990; Tolley et al. 1995; Barreto 2000), sexes were pooled together for comparisons between *T. truncatus* and *T. gephyreus*.

Skull morphometrics.— In order to avoid ontogenetic effects, we measured only adults (n = 192) of both *T. truncatus* and *T. gephyreus* with digital 300mm, and 500 and 600mm analogical calipers. A total of 52 measurements were taken from each specimen based on previous studies (Perrin 1975; Wang et al. 2000b; Kemper 2004). However, due to a strong and positive correlation among some measurements, we reduced the number to 29 measurements (Supporting Information S2).

Alveoli and vertebral counts.— We counted only well-defined dental alveoli in left and right, upper and lower jaws of specimens whenever possible, in order to prevent over or underestimations. We counted the number of vertebrae of all available skeletons, totaling 22 specimens (*T. truncatus, n* = 13; *T. gephyreus, n* = 9). In specimens missing some vertebrae (*T. truncatus*, *n* = 2; *T. gephyreus*, *n* = 3), the total number was estimated following the method described in Perrin (1975, 1984).

Skull morphology.— We examined all specimens of each age group for qualitative, morphological differences in characters between *T. truncatus* and *T. gephyreus*. Fourteen morphological characters were analyzed. The anatomical nomenclature mainly followed Mead and Fordyce (2009) (Supporting Information S3).

Statistical analysis.— We checked the normality of all data of each group with Kolmogorov-Smirnov test. The differences in the means of the measurements between *T. truncatus* and *T. gephyreus* were tested with Student's t test or Mann-Whitney U-test (Vanzolini 1993). All tests were conducted in the software SigmaStat 3.5 (Systat Software Inc.).

In order to detect *a priori* groups of specimens we carried out a Principal Component Analysis (PCA) over the covariance matrix of the log-transformed measurements. A Cluster Analysis using 16 variables (without missing data) was performed to access the groups found in PCA. Both analyses were conducted with the software PAST (Hammer et al. 2001). Furthermore, we used Cohen's kappa coefficient to measure the reliability of agreement between the *a priori* identification specimens (based on the diagnosis proposed by Barreto [2000]), and the results of cluster analysis. Cohen's kappa coefficient ranges from -1 to 1, with values less than 0 indicating that the observed agreement is less agreement than would be expected by chance, 0 indicating that the observed agreement is as likely as an agreement by chance, and positive values indicating that the agreement is more likely than would be expected by chance (Vieira and Garrett 2005).

Afterwards, we conduct the Canonical Variates Analysis (CVA), to confirm patterns previously suggested by the PCA. In addition, a discriminant analysis was performed in order to generate classification functions that allow to distinguish statistically the *a priori* groups proposed by PCA. These classification functions were based on the five most different linear measurements among groups and reflect shape differences among the studied groups. This analysis was conducted in software SPSS18 (SPSS Inc. 2009).

RESULTS

Skull morphometrics.—

Multivariate analysis.— The first seven principal components explained more than 75% of the variance (Fig. 1). PC1 and PC2 respectively explained 39.2% and 16.3% of the total variance. The Cluster Analysis (n=139) identified two distinct groups.

Univariate analysis.— A total of 26 out of 29 measurements presented significant mean differences between *T. truncatus* and *T. gephyreus*; in 23 of these, differences were highly significant ($P \leq 0.001$). *Tursiops gephyreus* is, on average, larger than *T. truncatus* in 23 out of 29 measurements (Fig. 2: Supporting Information S4).

In the Kappa analysis 53 out of 57 specimens (93%) were classified as *T. truncatus*, whereas 72 out of 82 specimens (87%) were classified as *T. gephyreus*. Cohen's coefficient was 0.79 demonstrating "good" strength of agreement between *a priori* identification of specimens and the results of the Cluster analysis (Vieira and Garrett 2005).

The discriminant analysis resulted in a model with five measurements and 100% correct identification (Wilk's lambda = 0.068, n = 87). A specimen is assigned to the group for which the function result is higher. The functions are as follows:

1. *Tursiops gephyreus* = -549.687 + (2.106 Condylobasal length) + (0.455 Height of rostrum at mid length) + (0.767 Anterior width of the ascendant right process of premaxillary) + (-2.233 Length of left pterygoid) + (-0.29 Hindmost width of lateral lamellae of palatines).
2. *Tursiops truncatus* = -438.688 + (1.739 Condylobasal length) + (- 0.441 Height of rostrum at mid length) + (- 0.203 Anterior width of the ascendant right process of premaxillary) + (-0.599 Length of left pterygoid) + (-0.271 Hindmost width of lateral lamellae of palatines).

Skull morphology.— We identified six qualitative characters that, taken together, can be used to easily differentiate the two taxa. A description of these characters with some remarks on the states for each taxon is given below (Fig. 3: Supporting Information S5). A complete list, including the unsatisfactory characters (e.g. those that did not show marked differences between the two groups compared) is available in the "Supporting Information S6".

Character 5: Shape of the nasal process of the right premaxilla: falcate or subrectangular. The nasal process of the right premaxilla is falcate in outline in all specimens of *T. gephyreus*, whereas it is subrectangular in *T. truncatus*. These two conditions are present in all specimens, regardless age group.

Character 6: Superficial shape of the prenarial region: planar or concave. In almost all specimens of *T. truncatus* (93 out of 94), the nasal portion of the premaxilla anterior to nasal fossa is planar; whereas it is concave in 84 out of 85 specimens of *T. gephyreus*.

Character 9: Shape of the vertex of the skull (formed by frontals, nasals, and nuchal crest): square or rectangular. In most adult and subadult (95%), and in all juvenile specimens of *T. truncatus,* the vertex is square-shaped. In specimens of *T. gephyreus*, whereas, the vertex is rectangular-shaped irrespective of the age group.

Character 11: Conformation of premaxillaries: joined to, or fused with, each other along their medial sides. In adult specimens of *T. gephyreus* (58%), the left and right premaxillaries are fused with each other in part of their rostral portion. In all but a single adult specimen of *T. truncatus*, the premaxillaries are not joined to each other by a suture.

Character 12: Shape of the antorbital notch: "U"- or "W"-shaped. In juvenile (100%) and adult (87%) specimens of *T. truncatus*, the interorbital notch has a "U" shape, whereas the notch is "W"-shaped in most (98%) adults of *T. gephyreus*.

Character 14: Conformation of the nasal process of the premaxilla and the right nasal: separated or joined from each other. In 69% of adults specimens of *T. truncatus* the posterior portion of the premaxilla joins the external surface of the right nasal bone. Whereas, in all specimens of *T. gephyreus* the premaxilla is distinctly separated from the right nasal bone.

If considered together, characters 6, 9, 11, 12 and 14 allow a correct and precise differentiation between *T. truncatus* and *T. gephyreus*. More importantly, the conformation of the nasal process of the premaxilla and the right nasal bone (character 14) can be used alone to identify *T. truncatus*, whereas Shape of the nasal process of the right premaxilla (character 5) is diagnostic for both *T. truncatus* and *T. gephyreus* in the SWA.

Dental alveoli and vertebrae counts.— The mean number of dental alveoli does not differ between *T. truncatus* and *T. gephyreus*. Nevertheless, specimens of *T. truncatus* always had more than 25 alveoli per teeth row (Supporting Information S7). The number of vertebrae ranged from 62 to 64 and from 57 to 59 in the *T. truncatus* and *T. gephyreus*, respectively. However, a single specimen of *T. truncatus* (AQUASIS 02C1311/031) exhibited 68 vertebrae.

DISCUSSION

Based on the Phylogenetic Species Concept (PSC) (Nixon and Wheeler 1990), our findings support the recognition of two lineages of bottlenose dolphins in the Southwestern Atlantic. Thus, here we revalidate and raise *T. gephyreus* Lahille, 1908 to the species level. We suggest “Lahille’s Bottlenose Dolphin” as the English common name for the species.

Barreto (2000) treated this taxon as a subspecies, *T. truncatus gephyreus*. However, under PSC, a species is delimited by fixed, diagnostic characters. Therefore, there is no arbitrary distinction between species or subspecies in a polytypic species (Cracraft 1983). The alleged argument that subspecies is conceptually equivalent to the “phylogenetic species” (*e.g.* Remsen 2005) is not backed by any evidence at all. In fact, all subspecies concepts proposed so far (*e.g.* Mayr and Ashlock 1991) are not even similar to the diagnosable version of PSC.

In the Southwestern Atlantic, *T. gephyreus* can be consistently diagnosed from its congener by a combination of qualitative, meristic, and morphometric characters. Six qualitative anatomical characters had proven reliable for separating both taxa, one of which (named as “shape of the nasal process of the right premaxilla”) is sufficient to identify one species from another: it is falcate in outline in *T. gephyreus* and subrectangular in *T. truncatus* (Fig. 4). The other qualitative characters are: 1) Superficial shape of the prenarial region planar in *T. truncatus* (*vs.* concave in *T. gephyreus*); 2) Shape of the vertex the skull square in *T. truncatus* (*vs.* rectangular in *T. gephyreus*); 3) Conformation of premaxillaries no fused in *T. truncatus* (*vs.* fused in *T. gephyreus*); 4) Antorbital notch U-shaped in *T. truncatus* (*vs.* W-shaped in *T. gephyreus*); 5) Nasal process of the premaxilla often in contact to the right nasal in *T. truncatus* (*vs.* never in contact in *T. gephyreus*). Furthermore, the total number of vertebrae differs between the two species: 57–59 in *T. gephyreus vs*. 62–64 in *T. truncatus*. This character in particular was highlighted in the original description of Lahille (1908: 364), who considered it as a diagnostic for the species. *Tursiops gephyreus* is, on average, larger than *T. truncatus* of Southwestern Atlantic, although measurement overlapping does occur. However, the results of the uni- and multivariate statistical analyses of skull measurements clearly led to the conclusion that specimens can be separated into two recognizable groups.

In comparison with *T. aduncus*, the other species accept for the genus, *T. gephyreus* is larger in external and in skeletal dimensions. It has less and larger teeth, a thicker and longer rostrum, and a much bigger brain case. *Tursiops aduncus* also has dark spots on the belly (Ross and Cockcroft 1990, Wang et al. 2000a). There is just one record of bottlenose dolphin with spots on the belly in SWA (Ott et al. *in press*). *Tursiops aduncus* e *T. gephyreus* differ from *T. truncatus* in having the pterygoids slightly separated from each other (Fig. 5).

Based on the identification of the stranded specimens analyzed in the present study, it seems that the two species have different stranding patterns in SWA (Fig. 6). The northernmost record of *T. truncatus* specimen examined in this study was in the state of Pará on the northern Brazilian coast. The southernmost record was in Buenos Aires Province, Argentina. In this region, bottlenose dolphins are found both inshore and offshore and around oceanic islands such as St. Peter and St. Paul’s rocks and Atol das Rocas (Moreno et al. 2009; Baracho et al. 2007). It is worthy to note that, 142 (98,61%) out of 144 specimens were collected in Brazil north of Tavares in Rio Grande do Sul, with single specimen each from Uruguay and Argentina. A stranded bottlenose dolphin found in Tierra del Fuego in Argentina (Goodall et al. 2011) was not examined in this study.

Conversely, *T. gephyreus* seems to have a more restricted stranding pattern, associated with coastal waters and inhabiting estuarine area. The northernmost record of specimens of *T. gephyreus was* Atami Beach in the state of Paraná and the southernmost record was Union Beach, Rawson, on the central coast of Argentina. In this region, rivers, estuaries and coastal lagoons are transition from tropical to temperate habitats. Moreover, the costal environments of south Brazil and Uruguay have unique geomorphologic and hydrologic characteristics. The coastal waters are highly turbid due to river discharge (e.g. La Plata River and Patos Lagoon) and wind resuspension. Furthermore, local temperature varies from 13 to 19.5°C in the winter and from 21 to 30°C in the summer, and salinity varies from 8 to 35 ppm in some lagoons (Ramos and Vieira 2001).

In this same region, small communities of bottlenose dolphins have been recorded in estuaries of south Brazil, namely Mampituba, Tramandaí, and Chuí estuaries and Laguna and Patos Lagoon systems (Simões-Lopes et al. 1998; Fruet et al. 2011; Daura-Jorge et al. 2013; Costa et al. 2015). We identified three specimens from these populations as *T. gephyreus*: one from Mampituba River (GEMARS 0333), another from Tramandaí River (GEMARS 1259), and the last from Chuí River (TTBC 220310) on the Brazilian–Uruguayan border (Tabajara 1992; Costa et al. 2015). These individuals were photo-identified and re-sighted several times, which suggests some degree of site fidelity (Giacomo and Ott *in press*).

It is important to mention that are records of two of these three dolphins populations cited above being a cooperative fishing with local fishermen in Mampituba and Tramandaí estuaries. This interaction has been occurring for decades in this estuaries and in Laguna and the fishers claim that it guarantees a good fishing yields to both dolphins and humans (see Pryor 1990; Simões-Lopes et al. 1998; Zappes et al. 2010).

The genetic structure of bottlenose dolphins communities appears to support the morphological results and the putative distribution limits in the present study, since they show that the species is highly dependent on the type of habitat occupied (Möller et al. 2007). Protected coastal habitats, such as embayment, lagoons and estuaries are usually inhabited by genetically differentiated small groups with a high degree of site fidelity, local adaptation to different ecological conditions and differential resource use strategies (Costa et al. 2015). In this sense, the presence of *T. gephyreus* seems to be currently associated to the estuaries in Southern Brazilian coast, but the historical process involved in the speciation process remains unknown. In contrast, open coastal waters are usually inhabited by larger communities, presenting lower genetic differentiation and higher genetic diversity than those restricted in distribution (Natoli et al. 2004; Fruet et al. 2011). However, none of these studies compared their genetics results with morphology.

The presence of two species of bottlenose dolphins in the Southwestern Atlantic is remarkable relevant from a conservationist viewpoint. Both species face threats from by-catch in fisheries, pollutants, loss and habitat degradation, and disturbance from human activities (Daura-Jorge 2013; Fruet et al. 2014). This is particularly serious for *T. gephyreus*, which has a more restricted pattern of occurrence. The list of the endangered fauna of Rio Grande do Sul has been recently updated (in 20014) according to IUCN (2001) criteria. Two subpopulations of bottlenose dolphins have been designated for the purpose of conservation in the state: (a) an oceanic population inhabiting waters beyond the continental shelf (herein considered as *T. truncatus*) and (b) a costal/estuarine population, referred herein to *T. gephyreus*. The costal/estuarine population is classified as "Vulnerable" due to high anthropogenic pressure and declining habitat quality.

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Figure Legends:

Fig. 1.—Results of the Principal Components Analysis (PCA) of 29 measurements of *Tursiops truncatus* (square) and *T. gephyreus* (cross). The lectotype of *T. gephyreus* (MACN 54.113) is shown with circle around it.

Fig. 2.—Scatter plot of measurements of adults skulls of *Tursiops truncatus* (black circles) and *T. gephyreus* (hollow circles). Dotted line = 95% confidence interval.

Fig. 3.—Skull illustrations of *Tursiops truncatus* (GEMARS 1495) (A) and *T. gephyreus* (GEMARS 0333) (B) in dorsal view, with five diagnostic characters (see details in results section).

Fig. 4. – Dorsal view of adult bottlenose dolphin skulls. a) *Tursiops aduncus* (NMNH 550945), b) *Tursiops truncatus* (UFSC 1287) and c) *Tursiops gephyreus* Lectotype (MACN 54.113). Scale 10cm.

Fig. 5. – Ventral view of adult bottlenose dolphins skulls: a) *Tursiops aduncus* (NMNH 550945), b) *Tursiops truncatus* (UFSC 1287) and c) *Tursiops gephyreus* Lectotype (MACN 54.113). Scale 10cm.

Fig. 6.—Sampling locations in the Southwestern Atlantic Ocean (SWA) of bottlenose dolphins analyzed in this study. A) Circles with dot: *Tursiops truncatus;* Algodoal and Chapadmalal are the limits of the *T. truncatus* based on verified records. B) Hollow circles: *Tursiops gephyreus*. Atami Beach and Union Beach are the limits of the *T. gephyreus* based on verified records.

Supporting Information

Supporting Information S1.—List of bottlenose dolphin specimens examined and sampling information.

Supporting Information S2.—Syncranial measurements and meristics analyses for bottlenose dolphin, *Tursiops* specimens in this study. *= Measurements modified from literature. [c] = Variables used in the Cluster analysis.

Supporting Information S3.—Morphological characters analyzed and the observed states in each specimen of bottlenose dolphin, *Tursiops* spp.

Supporting Information S4.—Descriptive statistic of cranial measurements taken from adult specimens of *Tursiops gephyreus* and *Tursiops truncatus*.

Supporting Information S5.—Frequency of occurrence of morphological characters of juvenile, subadult and adult of specimens of *Tursiops truncatus* and *Tursiops gephyreus.*

Supporting Information S6.—Unsatisfactory cranial morphology characters.

Supporting Information S7.—Descriptive statistics of dental alveoli counting performed on adult specimens of *Tursiops truncatus* and *Tursiops gephyreus.*

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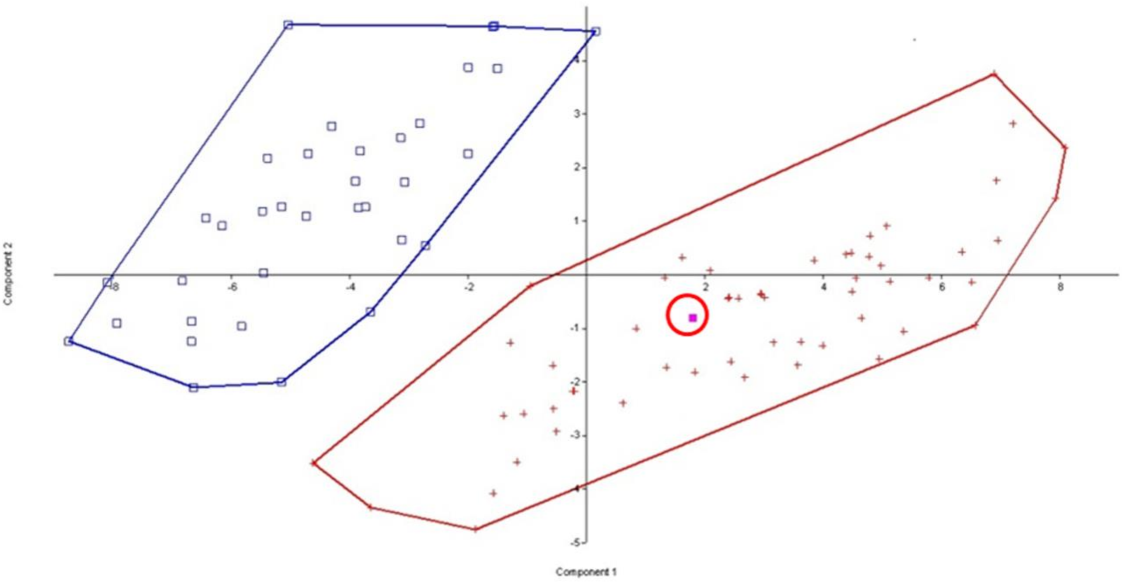

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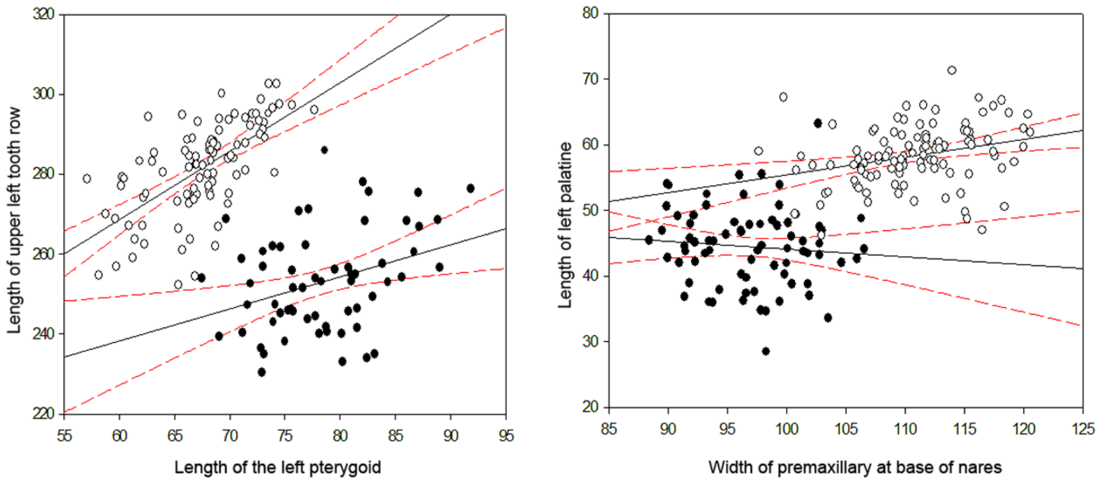
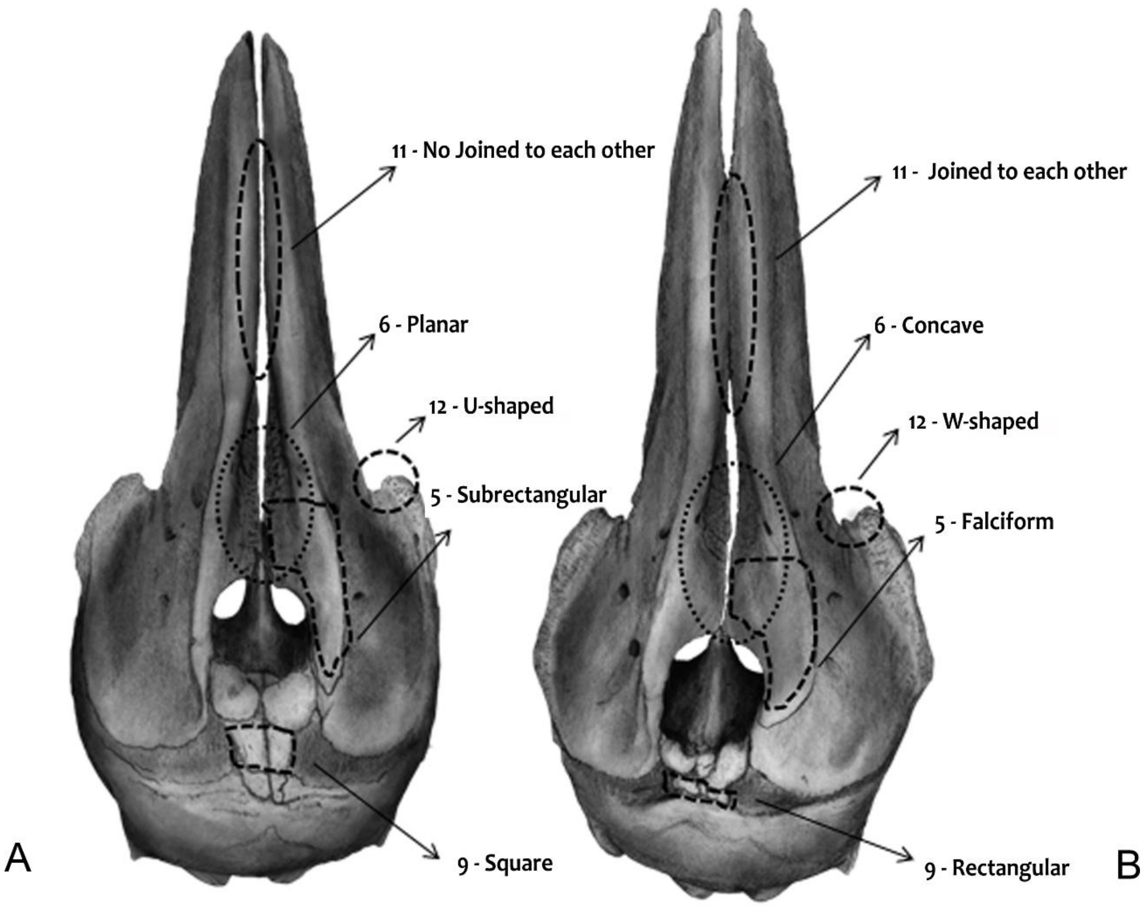


Figure 2. Scatter plot of measurements of adults skulls of *Tursiops truncatus* (black circles) and *T. gephyreus* (hollow circles). Dotted line = 95% confidence interval.



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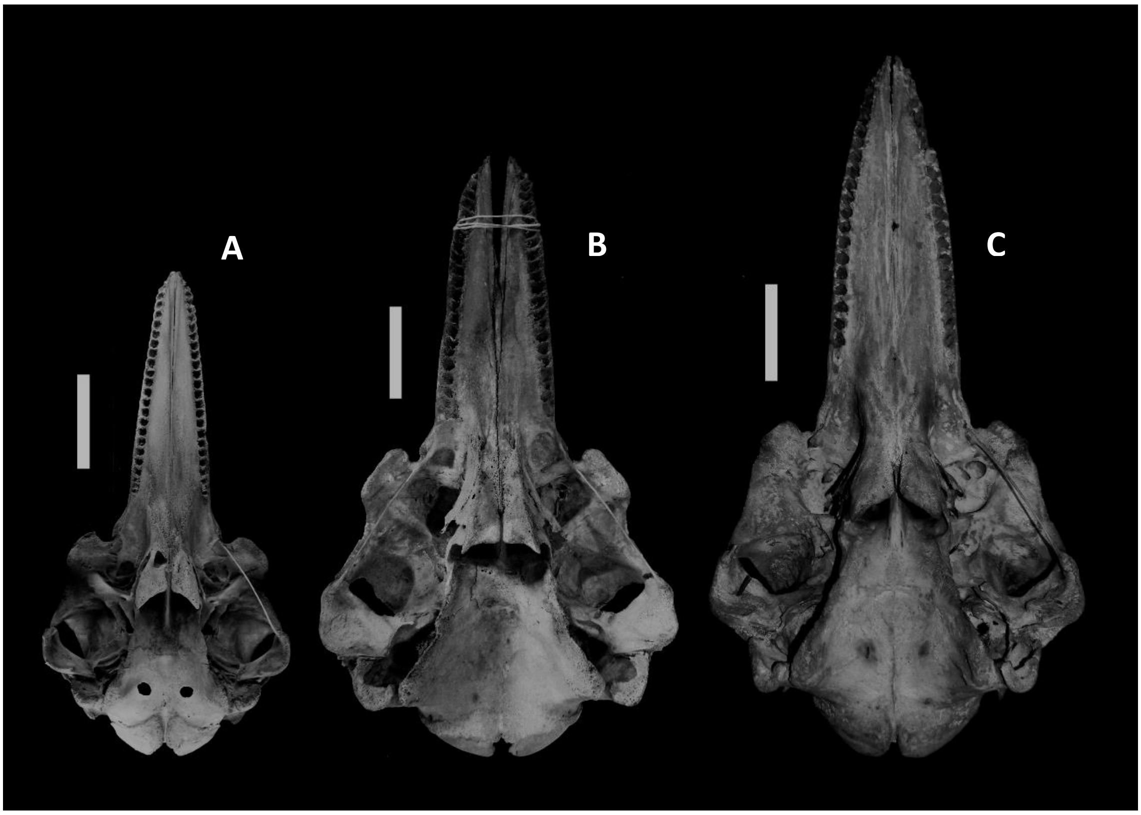

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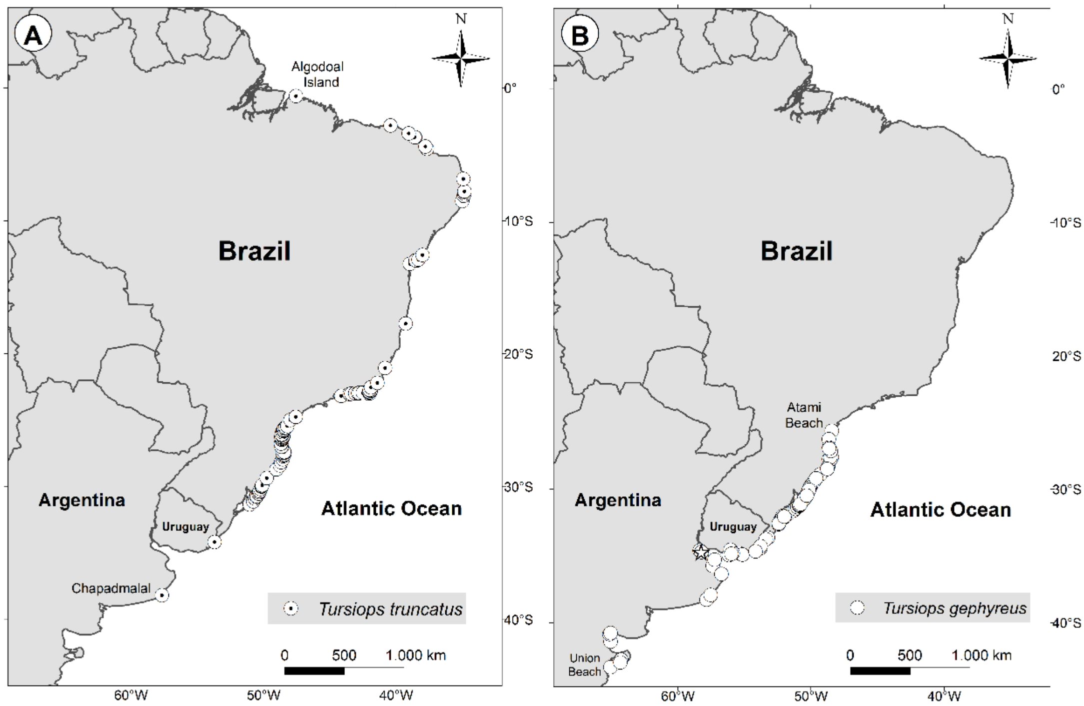

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