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# Revalidation of *Tursiops gephyreus* Lahille, 1908 (Cetartiodactyla: Delphinidae) from the southwestern Atlantic Ocean

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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 under *T. truncatus*, the type species of the genus. 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 morphometric (29 measurements) differences. Univariate and multivariate analyses were conducted to test differences between groups. Based on qualitative and quantitative analyses of skulls as well as the vertebrae number of *Tursiops* specimens from SWA, we recognized 2 distinct morphological forms of bottlenose dolphins in the region, consistent with treatment of 2 species under the "diagnosable version of the Phylogenetic Species Concept." Six qualitative characters are 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 in *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.

Historicamente, o *status* taxonômico do golfinho-nariz-de-garrafa, gênero *Tursiops*, tem sido confuso. Mais de 20 espécies nominais foram descritas ou transferidas para o gênero; porém, a maioria delas foi sinonimizada a *T. truncatus*, que é a espécie tipo do gênero. No presente estudo, reavaliamos o *status* taxonômico de *Tursiops gephyreus* Lahille, 1908 no Oceano Atlântico Sul Ocidental (SWA), um táxon considerado por muito tempo como sinônimo de *T. truncatus*. Foram examinados 280 crânios de golfinhos-nariz-de-garrafa, incluindo o lectótipo de *T. gephyreus*. Análises uni e multivariadas foram realizadas para testar diferenças morfológicas (14 caracteres) e morfométricas (29 medidas) entre os grupos. Baseado nas análises qualitativas e quantitativas dos crânios, bem como no número de vértebras de espécimes de *Tursiops* do SWA, reconhecemos duas formas morfológicas distintas de golfinhos na região, consistente com o Conceito Filogenético de Espécies. Seis caracteres qualitativos são considerados confiáveis para a identificação das duas espécies no SWA, entretanto a forma do processo nasal do pré-maxilar direito é suficiente para diagnosticar as duas espécies. Além disso, o número total de vértebras é maior em *T. truncatus* (62–64) do que em *T. gephyreus* (57–59). Sendo assim, propomos a revalidação de *T. gephyreus*. Visto que *T. gephyreus* foi reconhecido como habitante dos estuários e da zona de arrebentação ao longo da costa do Rio Grande do Sul (Brasil), Uruguai e Argentina, os esforços de conservação devem levar em conta que estas regiões apresentam ameaças semelhantes à espécie.

Key words: bottlenose dolphin, geographic variation, skull morphology, taxonomy, *Tursiops truncatus*

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

The taxonomy of bottlenose dolphins has been the subject of debate. Over the past 200 years, more than 20 nominal species from various regions have been originally described in or transferred to *Tursiops*, but most of them have been subsequently synonymized under the single cosmopolitan species *T. truncatus* (see Hershkovitz 1966; Ross 1977; Rice 1998). Bernard Germain Lacépède described in 1804 a bottlenose dolphin from the North Atlantic as *Delphinus nesarnack*. However, this name was only followed by Hall (1981, *apud* Rice 1998). Seventeen years later, in 1821, George Montagu described a bottlenose dolphin from River Dart in Devonshire, United Kingdom, naming it *Delphinus truncatus*. Afterwards, many authors described other 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 Gervais (Hershkovitz 1966; Rice 1998; 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, United States), *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, United States), *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 Ocean, Tasmania, Australia—see Hershkovitz 1966; Rice 1998; Jefferson et al. 2008; Wells and Scott 2009).

Hershkovitz (1961, 1963) resurrected the senior synonym *T. nesarnack* (Lacépède, 1804) for this species, but was only followed by Hall (1981) as we mentioned above; subsequently, Hershkovitz (1966) reverted to *T. truncatus* as a "*nomem conservandum*." Later, 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 (ICZN) to use its plenary powers to suppress the name *Delphinus nesarnack* Lacépède, 1804. This request was accepted in Opinion 1413 of the ICZN (1986).

It is worthy to note that most species of bottlenose dolphins have been described based on a small number of, or even single incomplete (e.g., a lower jaw only) specimens, 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 morphological and molecular studies have provided evidence that the genus includes at least 2 other species: *T. aduncus* (Ehrenberg, 1833) in the coastal waters of the Indo-Pacific (Wang et al. 2000a, 2000b); and *T. australis* Charlton-Robb et al. 2011, in inshore waters of Victoria southeastern Australia (Charlton-Robb et al. 2011). However, until recently the validity of this last species was contested by the Committee on Taxonomy of the Society for Marine Mammalogy and only in 2016 was it recognized as a valid species (Committee on Taxonomy 2016).

Only 2 species of bottlenose dolphins have been so far described from the southwestern Atlantic. Lesson (in Gray 1850:109) 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." In contrast, Lahille (1908:364) described in detail *T. gephyreus* based on 2 complete skeletons of a male and a female. According to him, *T. gephyreus* differs from *T. truncatus* by the longer rostrum; pterygoids separated from each other (versus joined to each other in *T. truncatus*); premaxilla apex acute (versus rounded); lower number of vertebrae; 4 similarly sized maxillary foramina (versus irregularly distributed, varying in size, and usually 3 in number); 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, based on skull measurements and mitochondrial DNA sequences, Barreto (2000:46) proposed that bottlenose dolphins occurring from about 27°S to 35°S in the southwestern Atlantic should be treated at the subspecific level as *Tursiops truncatus gephyreus*. However, he neither provided convincing evidence nor established any biogeographic relationship for the species.

In this context, we present further morphological evidence for raising *T. gephyreus* Lahille, 1908 to its original species level. 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 (MN), 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 of 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.

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 classified specimens into 3 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 gear and then collected, cleaned, and deposited in scientific collections (Supplementary Data SD1); 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 (very few external and skull measurements present sexual dimorphism—Hersh et al. 1990; Tolley et al. 1995; Barreto 2000), sexes were pooled for comparisons between *T. truncatus* and *T. gephyreus*.

*Skull morphometrics.*—In order to avoid ontogenetic effects, we measured only adults of *T. truncatus* ($n$ = 81) and *T. gephyreus* ($n$ = 111) with a 300-mm digital caliper, and 500- and 600-mm analogical calipers. Fifty-two measurements were taken from each specimen based on Perrin (1975), Wang et al. (2000b), and Kemper (2004). However, due to a strong and positive correlation among some measurements, we reduced the number used in analyses to 29 measurements (Supplementary Data SD2).

*Alveoli and vertebral counts.*—Whenever possible, we counted only well-defined dental alveoli in left and right, upper and lower jaws of specimens 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; Supplementary Data SD3).

*Statistical analysis.*—We checked the normality of all data of each group with Kolmogorov–Smirnov tests. The differences in the means of the measurements between *T. truncatus* and *T. gephyreus* were tested with Student's $t$-tests or Mann–Whitney $U$-tests (Vanzolini 1993). All tests were conducted in SigmaStat 3.5 (Systat Software Inc. 2007, San Jose, California).

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 of specimens (based on the diagnosis proposed by Lahille [1908] and 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 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 conducted a canonical variate analysis to confirm patterns previously suggested by the PCA. In addition, a discriminant analysis was performed in order to generate classification functions that allowed us to distinguish statistically the a priori groups proposed by PCA. These classification functions were based on the 5 most different linear measurements among groups and reflected shape differences among the studied groups. These analyses were conducted in SPSS18 (SPSS Inc. 2009).

## Results

*Skull morphometrics.*—Multivariate analysis: The first 7 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) retrieved 2 distinct groups, representing *Tursiops truncatus* and *T. gephyreus*, with the primary type of *T. gephyreus* within the dispersion cloud of *T. gephyreus*. 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*

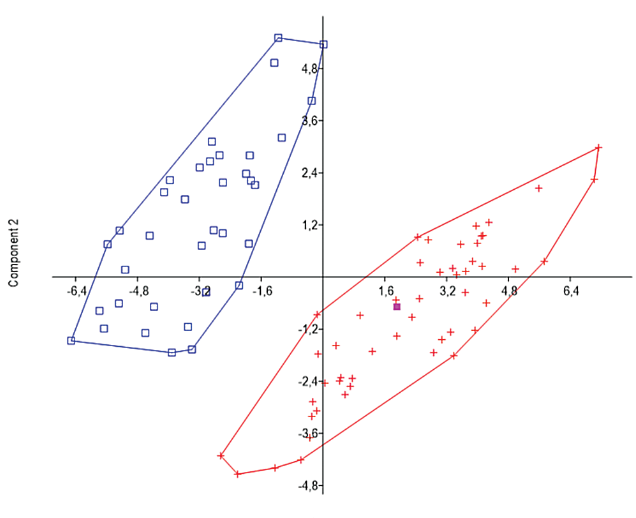


**Fig. 1.**—Results of the principal component analysis (PCA) for 29 measurements of *Tursiops truncatus* (square) and *T. gephyreus* (cross). The lectotype of *T. gephyreus* (MACN 54.113) is shown with a filled square.

*gephyreus* is, on average, larger than *T. truncatus* in 23 out of 29 measurements (Fig. 2; Supplementary Data SD4). 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 5 measurements and 100% correct identification (Wilks' 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 6 qualitative characters that, taken together, can be used to easily distinguish the 2 taxa. A description of these characters with some remarks on the states for each taxon is given below (Fig. 3; Supplementary Data SD5). A complete list, including characters that did not show marked differences between the 2 groups compared (non-useful), is available in the Supplementary Data SD6.

*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 2 conditions are present in all specimens, regardless of 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 the 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 adults and subadults (95%), and in all juveniles of *T. truncatus*, the vertex is square-shaped. In *T. gephyreus*, the vertex is rectangular-shaped irrespective of age group.

*Character 11:* Conformation of premaxillaries: joined to, or fused with, each other along their medial sides. In adults 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 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 juveniles (100%) and adults (87%) 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 of *T. truncatus*, the posterior portion of the premaxilla joins the external surface of the right nasal bone,

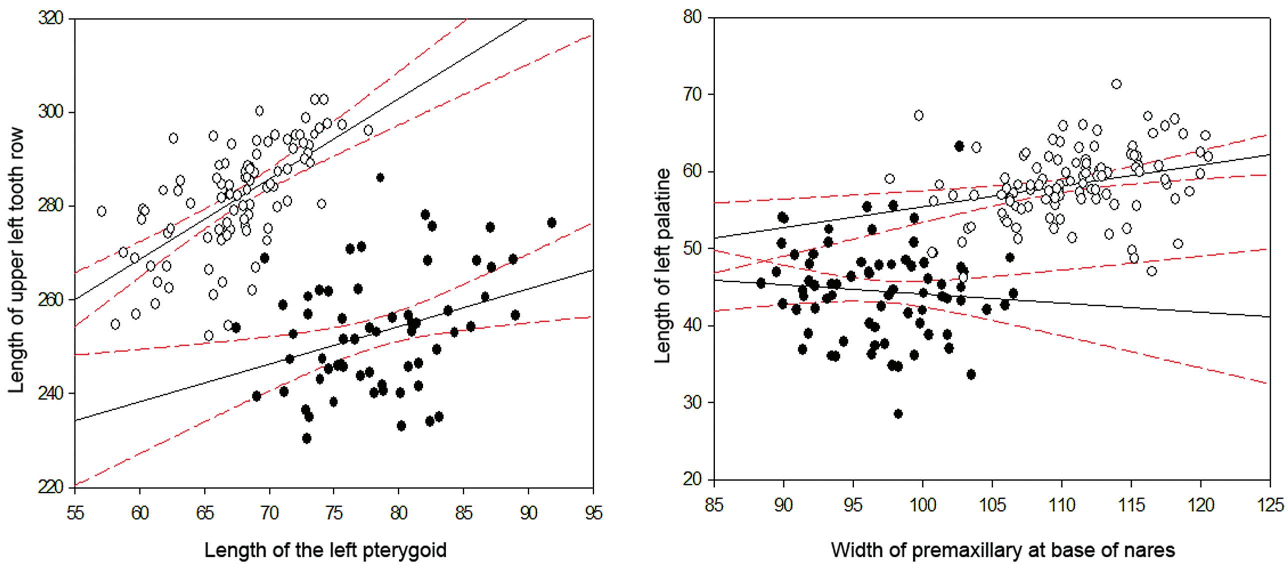


**Fig. 2.**—Scatter plot for skull measurements of adult *Tursiops truncatus* (black circles) and *T. gephyreus* (open circles). Dotted line = 95% *CI*.

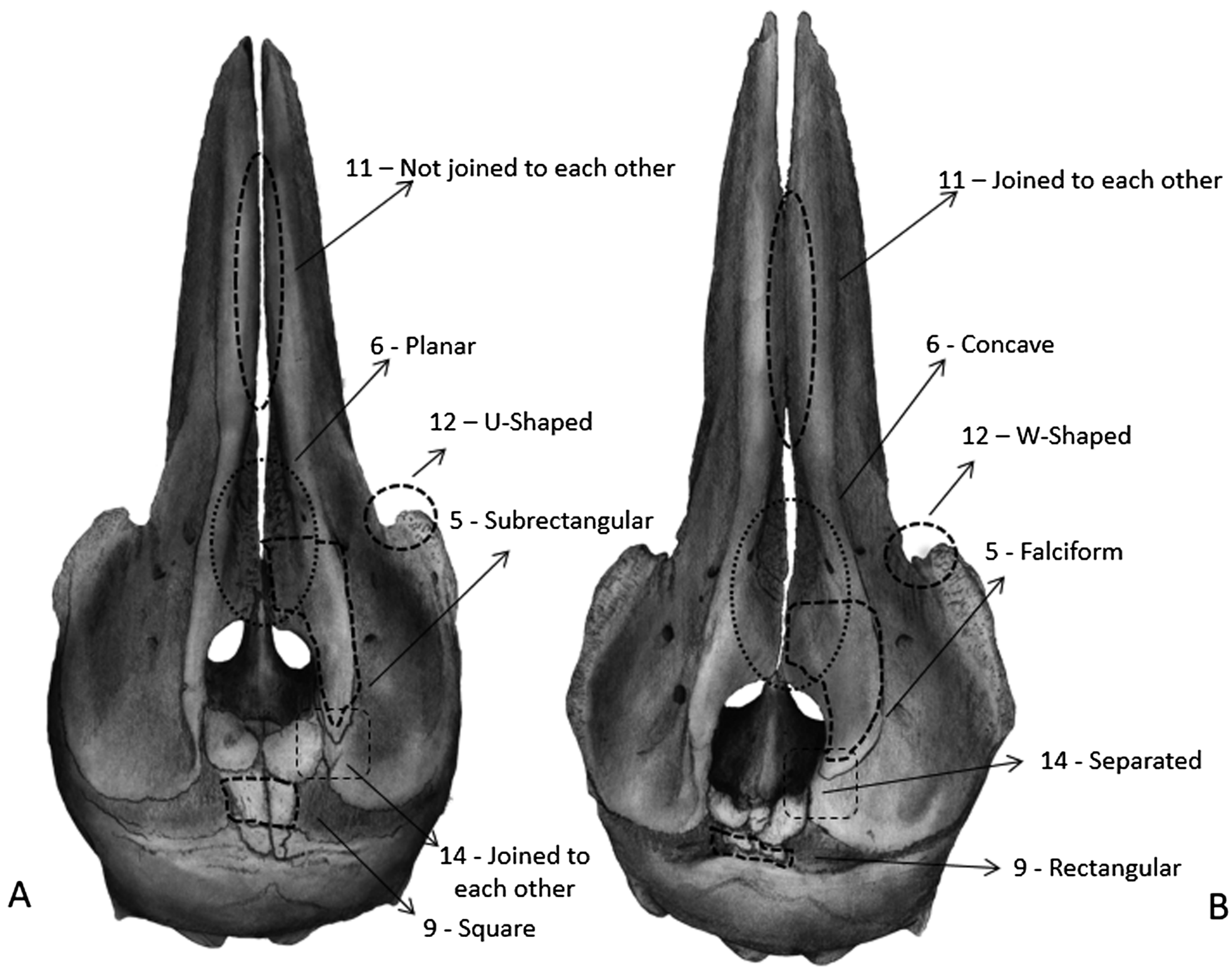


**Fig. 3.**—Skull illustrations of A) *Tursiops truncatus* (GEMARS 1495) and B) *T. gephyreus* (GEMARS 0333) in dorsal view, with 6 diagnostic characters (see details in "Results" section).

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 distinction 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 southwestern Atlantic.

*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* often had more than 25 alveoli per teeth row (Supplementary Data SD7). The number of vertebrae ranged from 62 to 64 and from 57 to 59 in *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 2 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 a subspecies is conceptually equivalent to the "phylogenetic species" (e.g., Remsen 2005) is not backed by any evidence. 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 distinguished from its congener by a combination of qualitative, meristic, and morphometric characters. Six qualitative cranial characters proved reliable for separating both taxa, 1 of which (named as "shape of the nasal process of the right premaxilla") is sufficient to distinguish 1 species from another: it is falcate in outline in *T. gephyreus* and subrectangular in *T. truncatus* (Fig. 4). In addition, differences in the total number of vertebrae distinguished the 2 taxa, which was highlighted in the original description of Lahille (1908:364), who considered it as diagnostic for the species. *Tursiops gephyreus* is larger than *T. truncatus* in the southwestern Atlantic, on average, although some overlap occurs. Results of the univariate and multivariate statistical analyses for skull measurements clearly led to the conclusion that specimens can be identified into the 2 recognized species.

In comparison with *T. aduncus*, the other species accepted for the genus, *T. gephyreus* is larger in external and in skeletal dimensions. It has fewer and larger teeth, a thicker and longer rostrum, and a much bigger braincase. *Tursiops aduncus* also has dark spots on the belly (Ross and Cockcroft 1990; Wang et al. 2000a). There are a few records of bottlenose dolphins with small brown spots on the belly in the southwestern Atlantic (S. Siciliano, FIOCRUZ, Rio de Janeiro, Rio de Janeiro, Brazil, pers. comm.). *Tursiops aduncus* and *T. gephyreus* differ from *T. truncatus* by having the pterygoids slightly separated from each other (Fig. 5).

Based on identification of the stranded specimens analyzed in the present study, it seems that the 2 species have different stranding patterns in the southwestern Atlantic (Fig. 6). The northernmost record for *T. truncatus* examined here 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 Saint Paul's

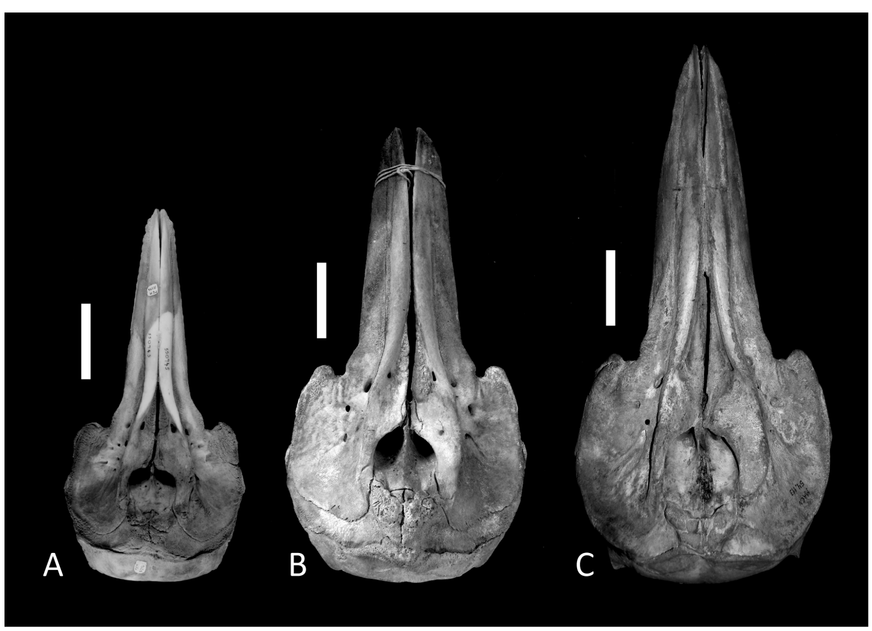


**Fig. 4.**—Dorsal view of adult bottlenose dolphin skulls: A) *Tursiops aduncus* (NMNH 550945), B) *Tursiops truncatus* (UFSC 1287), and C) *Tursiops gephyreus* Lectotype (MACN 54.113). Scale bars = 10 cm.

Rocks and Atol das Rocas (Baracho et al. 2007; Moreno et al. 2009). It is worthy to note that 142 out of 144 (98.6%) specimens were collected in Brazil north of Tavares in Rio Grande do Sul, with single specimens from Uruguay and Argentina. The stranded bottlenose dolphins found in Tierra del Fuego in Argentina (Goodall et al. 2011) were not examined in this study.

Conversely, the distribution of strandings of *T. gephyreus* has a more restricted pattern, usually close (or in adjacent waters) to coastal estuaries and lagoons in southern Brazil, Uruguay, and northern Argentina. The northernmost record for *T. gephyreus* analyzed here is in Atami Beach, state of Paraná, and the southernmost record is in Union Beach, Rawson, central coast of Argentina. In this region, rivers, estuaries, and coastal lagoons are transitions from tropical to temperate habitats. Moreover, the costal environments of southern Brazil and Uruguay have unique geomorphologic and hydrologic characteristics. The coastal waters are highly turbid due to river discharge

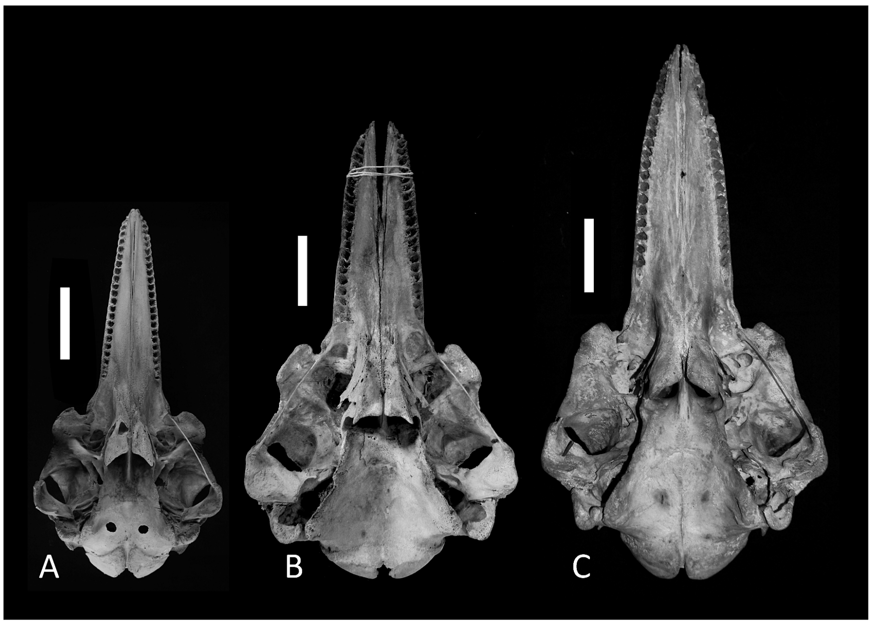


**Fig. 5.**—Ventral view of adult bottlenose dolphins skulls: A) *Tursiops aduncus* (NMNH 550945), B) *Tursiops truncatus* (UFSC 1287), and C) *Tursiops gephyreus* Lectotype (MACN 54.113). Scale bars = 10 cm.

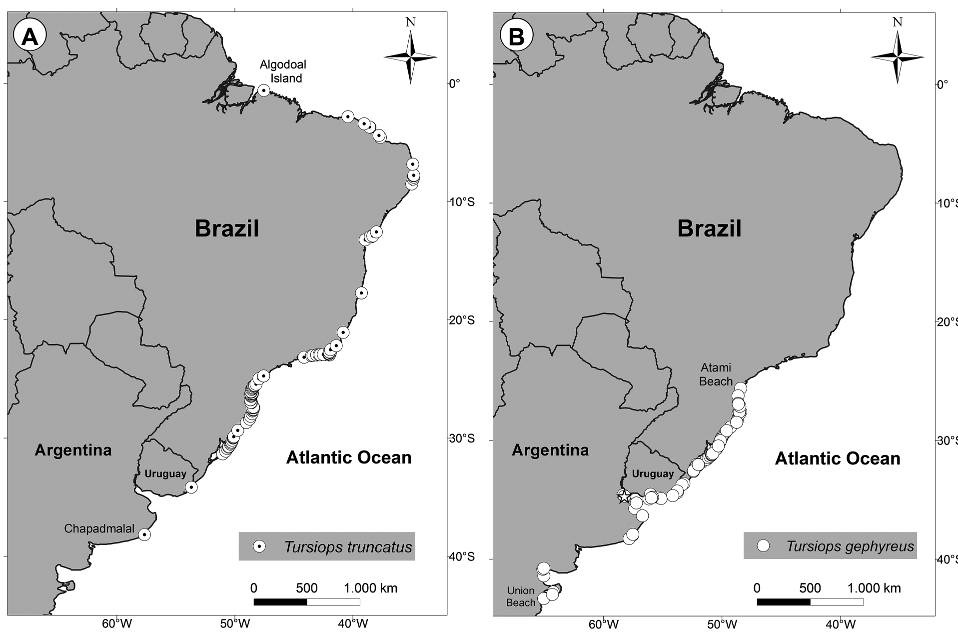


**Fig. 6.**—Sampling localities in the southwestern Atlantic Ocean (SWA) of bottlenose dolphins analyzed in this study: A) circles with dot: *Tursiops truncatus*, with Algodoal and Chapadmalal as the limits based on verified records; B) open circles: *Tursiops gephyreus*, with Atami Beach and Union Beach as the limits of the *T. gephyreus* based on verified records. Star: Lectotype of *T. gephyreus* (MACN 54.113).

(e.g., La Plata River and Patos Lagoon) and wind resuspension. Furthermore, local temperature varies from 13°C to 19.5°C in the winter and from 21°C 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 southern 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 3 specimens from these populations as *T. gephyreus*: 1 from Mampituba River (GEMARS 0333), another from Tramandaí River (GEMARS 1259), and the last from Chuí River (TTBC 220310) on the Brazil–Uruguay boundary. Individuals from Tramandaí River were photo-identified and resighted several times in this estuary, suggesting some degree of site fidelity (Simões-Lopes et al. 1998; Giacomo and Ott, in press).

There also are records of dolphins from Mampituba and Tramandaí estuaries fishing cooperatively with local fishermen. This interaction has been occurring for decades in these estuaries and in Laguna, and the fishers claim that it guarantees 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 dolphin 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 embayments, 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 with the estuaries along the 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 contrasted genetic and morphological differentiation.

The presence of 2 species of bottlenose dolphins in the southwestern Atlantic is relevant from a conservation viewpoint. Both species face threats from bycatch in fisheries, pollutants, habitat loss or degradation, and disturbance from human activities (Daura-Jorge et al. 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 2014) according to IUCN (2001) criteria. Two subpopulations of bottlenose dolphins have been designated for the purpose of conservation in the state: an oceanic population inhabiting waters beyond the continental shelf (herein considered *T. truncatus*) and a coastal-estuarine population, referred herein to *T. gephyreus*. Following IUCN criteria, the coastal-estuarine population is classified as "vulnerable" due to high anthropogenic pressure and declining habitat quality.

## Supplementary Data

**Supplementary Data SD1.**—List of bottlenose dolphin specimens examined and sampling information.

**Supplementary Data SD2.**—Syncranial measurements and meristic analyses for bottlenose dolphin (*Tursiops*) specimens in this study. *Measurements modified from literature. [c]Variables used in the Cluster analysis.

**Supplementary Data SD3.**—Morphological characters analyzed and the observed states in each specimen of bottlenose dolphin (*Tursiops* spp.).

**Supplementary Data SD4.**—Descriptive statistic of cranial measurements taken from adults of *Tursiops gephyreus* and *Tursiops truncatus*.

**Supplementary Data SD5.**—Frequency of occurrence of morphological characters of juveniles, subadults, and adults of *Tursiops truncatus* and *Tursiops gephyreus*.

**Supplementary Data SD6.**—Non-useful morphological skull characters.

**Supplementary Data SD7.**—Descriptive statistics of dental alveoli counting performed on adults of *Tursiops truncatus* and *Tursiops gephyreus.*

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