PATTERNS OF SKULL VARIATION OF *BRACHYDELPHIS* (CETACEA, ODONTOCETI) FROM THE NEOGENE OF THE SOUTHEASTERN PACIFIC

CAROLINA SIMON GUTSTEIN,* MARIO A. COZZUOL, ALEXANDER O. VARGAS, MARIO E. SUÁREZ, CESAR L. SCHULTZ, AND DAVID RUBILAR-ROGERS

Laboratorio de Ecofisiología, Departamento de Ecología, Facultad de Ciencias, Universidad de Chile, Las Palmeras 3425, Ñuñoa, Santiago, Chile (CSG)
Museo Paleontológico de Caldera, Avenida Wheelright 1, Caldera, Region de Atacama, Chile (CSG, MES)
Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Avenida Antônio Carlos, 6627, Sala B2-246, Pampulha, 31270-910, Belo Horizonte, Minas Gerais, Brasil (MAC)
Departamento de Biología, Facultad de Ciencias, Universidad de Chile, Las Palmeras 3425, Ñuñoa, Santiago, Chile (AOV)
Departamento de Paleontologia e Estratigrafia, Instituto Geociências, Universidade Federal do Rio Grande do Sul, Avenida Bento Gonçalves, 9500, 91540-000, Porto Alegre, Rio Grande do Sul, Brasil (CLS)
Area Paleontología, Museo Nacional de Historia Natural, Santiago, Chile (DR-R)

Brachydelphis mazeasi Muizon, 1988a, from the Pisco Formation (middle Miocene, Peru), is an odontocete originally known from 2 incomplete skulls and a few associated postcranial elements, assigned to the family Pontoporiidae, and to the subfamily Brachydelphininae (= Brachydelphinae) created to include this genus. The holotype is considered here as a juvenile because it has no alveolar septa and presents wide-open cranial sutures. Consequently, some of the diagnostic features actually correspond to juvenile features and are not taxonomically significant. Here we offer a more comprehensive view of the morphology and variation of this taxon with new specimens from both Pisco and Bahía Inglesa formations (late Miocene, Chile). A revision of the original description of the genus, compared to other taxa of the Inioidea clade is provided. Additionally, a comparison by morphometric analysis (geometric and traditional) to *Pontoporia blainvillei* (living Pontoporiidae) is given. The shape variation of fetal, young, and adult specimens of *P. blainvillei* was compared to specimens of juvenile and adult *B. mazeasi* to evaluate ontogenetic, individual, and interspecific variation.

Key words: Bahía Inglesa Formation, *Brachydelphis mazeasi*, Inioidea, morphology, Neogene, Odontoceti, Pisco Formation, Platanistoidea, Pontoporiidae, variation

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The classification and phylogenetic relationships of the clade Platanistoidea (sensu Simpson 1945) of ''river dolphins'' have been confusing. The group includes 3 riverine species: *Platanista gangetica* (susu) from India, *Lipotes vexillifer* (Yangtze river dolphin or baiji) from China, and *Inia geoffrensis* (Amazon river dolphin or boto) from South America. The 4th species is *Pontoporia blainvillei* (franciscana or toninha) from coastal and estuarine waters of eastern South America. They have been grouped together by external morphological traits such as a long and narrow rostrum, a triangular dorsal fin, broad and visibly fingered flippers, and a flexible neck (Brownell 1989).

Despite these similarities, many morphological analyses emphasized the substantial differences among the 4 species (Kasuya 1973; Zhou 1982), and an alternative classification in 4 monotypic families (Rice 1998). The molecular phylogenetic study of Cassens et al. (2000) has interpreted these taxa as relict species whose adaptation to riverine habitats provided the conditions for their survival until nowadays. Nevertheless, Geisler and Sanders (2003:37), in their morphological phylogenetic analysis, have reaffirmed the validity of the Platanistoidea clade, but in a different configuration, which includes *Brachydelphis*, Iniidae, Pontoporiidae, Lipotidae, Platanistidae, and the genus *Eurhinodelphis*. The latter comes from North Atlantic Miocene beds and it is usually placed with other genera to make up the family Eurhinodelphinidae (see Abel

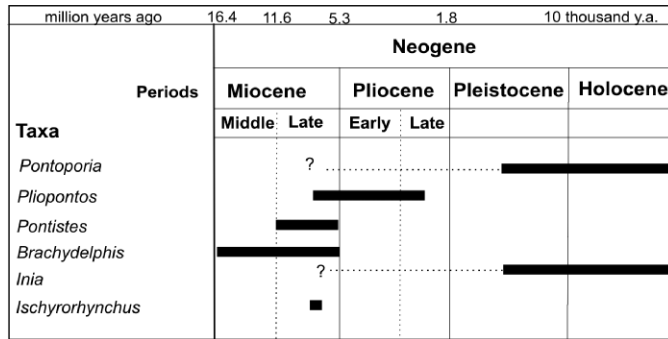* * Correspondent: sgcarolina@gmail.com

FIG. 1.—Stratigraphic ranges of Pontoporiidae and Iniidae in South America based on Cozzuol (1996), Fordyce and Muizon (2001), C. S. Gutstein and M. A. Cozzuol (in litt.), Nascimento et al. (in litt.), and Cione et al. (2000). The black bars correspond to confirmed records and dotted lines correspond to unconfirmed ones.

1901; Lambert 2005a, 2005b). The only fossil taxon allegedly belonging to Pontoporiidae in this analysis, *Brachydelphis* (sensu Muizon 1988a, 1988b), is found in a basal position from the "river dolphin" clade (Iniidae + Pontoporiidae + Lipotidae + Platanistidae).

On the other hand, the monophyly of Inioidea (Pontoporiidae + Iniidae) has been accepted by different authors (Arnason and Guldberg 1996; Geisler and Sanders 2003; Muizon 1988b; Yang and Zhou 1999). Sometimes Lipotidae (*Parapontoporia* + *Lipotes vexillifer* Miller, 1918) appears within Inioidea or as its sister group (Barnes 1985; Heyning 1989; Yang and Zhou 1999), or also as a sister group of the Inioidea + Delphinoidea clade, called Delphinida by Muizon (1988b) and corroborated by Messenger and McGuire (1998). Molecular studies confirm the polyphyly of "river dolphins" but also suggest the sister-group relationship of *L. vexillifer* (Lipotidae) with Inioidea + Delphinoidea (Cassens et al. 2000; Hamilton et al. 2001) or the monophyly of *L. vexillifer* and South American river dolphins group (*Inia* + *Pontoporia*— Nikaido et al. 2001).

The only living species of Pontoporiidae is *Pontoporia blainvillei* (Gervais and d'Orbigny, 1844), which is restricted to the southern South Atlantic Ocean from Espírito Santo (Brazil) to Península de Valdés (Argentina—Crespo et al. 1998; Siciliano 1994). However, the fossil record includes 3 formally described genera assigned to Pontoporiidae (*Pliopontos*, *Pontistes*, and *Brachydelphis*) from the Pacific and Atlantic oceans. The genus *Pontoporia* is reported with doubts in the late Miocene of Argentina (Cozzuol 1985) and the living species, *P. blainvillei*, in the Pleistocene in Argentina and southern Brazil (Cozzuol 1996; Ribeiro et al. 1998). The fossil record of Pontoporiidae ranges from the middle Miocene to Recent and is mostly restricted to South America (Fig. 1). However, North Atlantic fragmentary records have been assigned to the family more recently, such as: cf. *Pontoporia* from the Pliocene of Yorktown Formation (United States— Whitmore 1994), *Protophocaena minima* (Lambert and Post 2005), Pontoporiidae indet., and cf. *Pontistes* (Pyenson and Hoch 2007) from the Neogene of Europe. The oldest record is

B. mazeasi, from the middle Miocene, Pisco Formation (Peru— Muizon 1988a); followed by *Pontistes rectifrons* Burmeister, 1885, from the early late Miocene, Paraná Formation (Argentina—Cione et al. 2000); and *Pliopontos littoralis* Muizon, 1983, from the Pliocene levels of the Pisco Formation.

Brachydelphis mazeasi was described as a member of the Pontoporiidae with a short rostrum. This type species is based on 2 partial skulls, associated bullae, periotics, and a few postcranial remains. A 2nd record of sin-cranial remains (periotic) also was reported as belonging to *Brachydelphis* sp. nov. unnamed Muizon, 1988a. This taxon was referred to a new subfamily by Muizon (1988a) mainly because of its short rostrum. Muizon (1988b) considered this taxon as a basal member of the Pontoporiidae within the subfamily Brachydelphininae (sensu Fordyce and Muizon 2001 [= Brachydelphinae Muizon, 1988b]), differing from Pontoporiinae (sensu Muizon 1988b) by the absence of reversion in the condition of 2 characters: reappearance of the lateral lamina of the pterygoid and acquisition of symmetrical vertex.

Additional fossil skulls of *Brachydelphis* have been recovered from late Miocene beds. Here we evaluate the implications of this new material by conducting a morphometric study of skulls of *Brachydelphis* and comparing it to the extant species *Pontoporia blainvillei*. A revision of the original description of the genus, compared to other taxa of the Inioidea clade is provided. The reasons for the placement of this genus in the family Pontoporiidae, as well as the definition and polarity of the characters that are traditionally used in this group, are also discussed.

MATERIALS AND METHODS

Material examined.—The specimens are housed in the Sección Paleontología at the Museo Nacional de Historia Natural in Santiago, Chile (under the collection numbers SGO-PV 746–750, 757, 758b, 759, 966, 968, 972, and 1109); the Museo Paleontológico de Caldera at Caldera, Atacama Region, Chile (MPC 202, 377s, and 391s); and the Museo Nacional de la Universidad Mayor de San Marcos, Lima, Peru (MUSM 565, 590, 591, 593, and 884–887). Additionally, photos (in Muizon 1988b) of the holotype from the Museum National d'Histoire Naturell, Paris, France (MNHN PPI 121) and paratype (MNHN PPI 124) were included in both morphological and morphometric analyses.

Morphometrics.—Geometric morphometric analysis was performed with the landmarks (Fig. 2) plotted on complete skulls of *P. blainvillei* from the Laboratório de Mamíferos Aquáticos, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, Brasil (UFSC 1004, 1022, 1023, 1037–1039, 1058, 1059, 1066, 1070, 1091, 1092, 1121, 1214, 1217, 1221, 1262, 1284, 1288, 1290, 1310, and 1314); the holotype of *B. mazeasi*; and the more complete specimens (SGO-PV 746, 750, 1109, MPC 391s, 377s, MUSM 565, 887, and MNHN PPI 121). Because the holotype described by Muizon (1988a—MNHN PPI 121) and 2 other specimens (SGOPV 746 and 748) have some characteristics observed in juvenile *P. blainvillei* (explained below), 2

analyses were performed: 1 only with confirmed adults from both species, and the other including skulls of all available ontogenetic stages for *P. blainvillei* and all of the more complete skulls of *B. mazeasi*. As a criterion of ontogenetic ordination, we compared the growth curve of Ramos et al. (2000a) with the presence of a rostral groove and the presence or number or both of ossified alveoli, because these features were observed in nonmature specimens (approximately 3 years old, estimated using the growth curve) and also in some fossil specimens. Because the growth curve was described for the northern form of *P. blainvillei*, which is larger (Ramos et al. 2000a), and the present work deals with southern specimens, this discrepancy could generate error in considering a nonmature specimen as mature, but not the opposite.

The landmarks were digitized using TPSdig 2.04 (Rohlf 2005) on dorsal skull photos (Fig. 2A). The data matrix with geometrical coordinates was transferred to PAST 1.4 (Hammer 1998) and then transformed to Procrustes coordinates to eliminate size effects (Monteiro and Reis 1999) and rotate to the major axis. Principal component analysis shape (2-dimensional; principal component analysis for landmarks data) was run to visualize the distribution of the specimens, and a nonparametric multivariate analysis of variance (NPMA-NOVA) significance test was used because the samples were neither of equal size nor multivariate normally distributed. An exploratory cluster analysis also was run on PAST 1.4, and the nonparametric correlation (rho) was used as a measure of similarity, comparing the results of both single and paired linkage index to identify the more robust groups.

For identification of rostrum type (short or long), a traditional morphometric study was done, with centimeter-to-centimeter width measures from the base (given by a line between the antorbital notches) to the anterior extremity. These measures were plotted in a log-scale chart to maximize curve tendencies of width decreasing across the rostrum. These measurements were taken using TPSdig 2.04 (Rohlf 2005) to minimize error, because some specimens could only be measured from photographs (e.g., holotype) and only relative values were used for rostrum morphometry. The deformed specimens were not measured. Other descriptive traditional measurements (Fig. 2B) taken with calipers (precision 0.05 mm) followed Muizon (1988a) with smaller modifications. Mean and *SD* values are given.

Localities, geology, age, and correlation.—The fossil materials come from Neogene marine sediments belonging to the Pisco Formation (middle Miocene–early Pliocene interval—DeVries and Schrader 1997) in Peru and the Bahía Inglesa Formation (late Miocene–late Pliocene interval—Achurra 2004) in Chile. Both formations were shaped by marine transgressive–regressive systems (Achurra 2004; Muizon and DeVries 1985) and present large Neogene marine vertebrate assemblages, including fish, birds, crocodyliformes, pinnipeds, and cetaceans (Muizon 1981, 1983, 1984, 1988a; Sallaberry et al. 2007; M. E. Suárez and C. Marquardt, in litt.; Stucchi and Urbina 2004; Walsh and Hume 2001; Walsh and Naish 2002; Walsh and Suárez 2005).

The Bahía Inglesa Formation corresponds to a coquina intercalated with sandstones and roofed by phosphatic beds
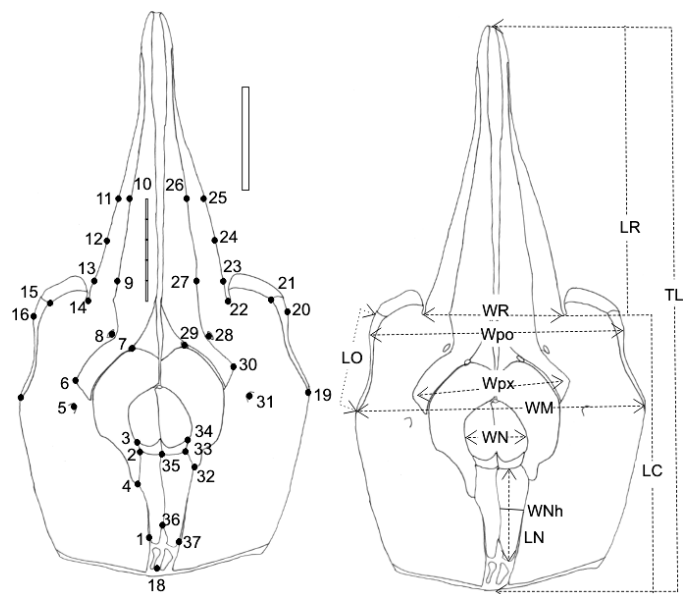

FIG. 2.—Schematic drawing of skull of *Brachydelphis mazeasi* with the measurements and landmarks used. A) Landmarks are marked with black circles. B) Measurements according to Muizon (1988a) are given by letters as follows: TL = total length of skull, LC = length of cranium from antorbital notch to nuchal crest (modified from Muizon [1988a]), LR = length of rostrum, WR = width of rostrum at the base, WPo = width between preorbital processes, WPx = maximum width of premaxillae, WN = maximum width of nasal fossa, LN = length of right nasal, WNh = width of right nasal in half length, WM = width of maxillaries in postorbital process level, LO = length of orbit from postorbital process apex to lacrimal–frontal suture at lateral border of skull (modified from Muizon [1988a]), LZ = length of zygomatic process of squamosal, SH = height of supraoccipital, WB = bicondyle width, and WFm = foramen magnum width. Black bar = 50 mm.

(Marquardt 1999), called bone bed (Walsh and Hume 2001), corresponding to P- and D-phosphates of late Miocene age (Achurra 2004). Following the model of Garrison (1992) for Neogene bone-bed genesis, D-phosphate is mostly reworked and occurs preferentially above unconformities. The analysis of local versus global variation of the sea level of the Caldera Basin (Achurra 2004) and strontium (Sr) isotopes dating series give a 6.8 million years ago (mya) antiquity (Messinian stage, late Miocene) to layers above the bone bed (unit 5). This Sr series dating differs from the K-Ar dating of 7.6 ± 1.3 mya (Messinian–Tortonian stage—Marquardt 1999), which was interpreted to correspond to a reworked ash layer (Achurra 2004), but both give a late Miocene age for the bone bed. These age hypotheses are corroborated by biostratigraphic data from mollusks (N. Guzmán et al., in litt.) and vertebrate association studies (Walsh and Hume 2001; Walsh and Naish 2002; Walsh and Suárez 2005). The transgressive-regressive cycles result from global eustatic levels, with some local variation (Achurra 2004). Thus, the phosphatic rocks of the Bahía Inglesa Formation seem to be synchronic with the phosphatic hardground at the top of the Cerro la Bruja locality (Pisco Formation—DeVries 1998; DeVries and Schrader 1997).
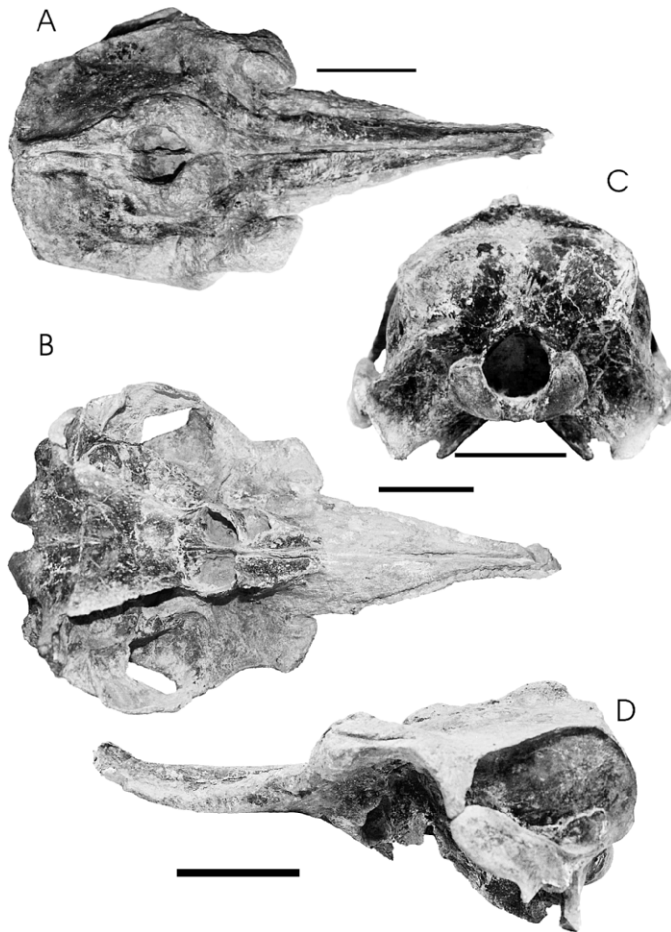
Fig. 3.—Specimen MUSM 565, the most complete specimen (old individual) of *Brachydelphis mazeasi*, in A) dorsal, B) ventral, C) occipital, and D) lateral view. Black bar = 50 mm.

RESULTS

Order Cetacea Brisson, 1762

Suborder Odontoceti Flower, 1864

Superfamily Platanistoidea Simpson, 1945
(sensu Geisler and Sanders 2003)

Genus *Brachydelphis* Muizon, 1988

Brachydelphis mazeasi Muizon, 1988

Referred materials, localities, and age (Figs. 3–6).—The Peruvian specimens are from middle–late Miocene beds of the Pisco Formation (DeVries and Schrader 1997; Muizon 1988b; Muizon and DeVries 1985) and the Chilean specimens are from late Miocene beds of the Bahía Inglesa Formation (Messinian–Tortonian stage—Achurra 2004; Marquardt 1999). The materials are dorsal portions of skulls (SGO-PV 746, 748, 750, and MPC 377s) and ventral portions (SGOPV 749, 966, and MPC 202) from the Mina Fosforita locality (Caldera, Chile). Three partial skulls are from the Corre Viento locality (Ica, Peru—in addition to the holotype and paratype): MUSM 593, 885, and MUSM 886, with mandibles. There are 2 virtually complete skulls: MUSM 565 (from Cerro Colorado

locality, Ica), with almost complete mandibles; and MUSM 887 (Corre Viento locality), a complete skull with articulated mandibles (still in the matrix).

Revised diagnosis for the cranial characters.—Referred to stem-Platanistoidea (sensu Geisler and Sanders 2003) by presenting: thick maxilla overlying the anterolateral corner of the frontal, maxillary crest, long zygomatic process of the squamosal, and basioccipital crests form a highly acute angle. Unique characters of the genus and species (from the original diagnosis—Muizon 1988a): it differs from *Pliopontos*, *Pontistes*, and *Pontoporia* by presenting posterior process of premaxilla contacting nasal on vertex, vertex slightly asymmetric, and deep antorbital notch with large lacrimal; it differs from *Pliopontos* and *Pontistes* by the thick antorbital process with high maxillary crests and paroccipital process excavated by the fossa for the posterior pterygoid sinus.

New unique characters are: it differs from *Pontoporia*, *Pontistes*, *Pliopontos*, *Inia*, and *Lipotes* by the short triangular upwardly curved rostrum; by presenting a medial groove on the palate that shows the premaxilla, anteriorly; the convex maxilla at the level of the antorbital notch; and the upwardly curved mandibles, with small (less than one-half of mandible length) and not fused symphysis. It differs from *Pliopontos*, *Pontistes*, *Inia*, and *Lipotes* by the prominent premaxilla between the premaxillary foramina in the nasal passage. It differs from *Pontoporia* and *Inia* by presenting a visible palatine lateral lamina–maxillary suture, including old specimens. It differs from *Pontoporia* by subequal cranium length and width; from *Inia* by the pterygoid hamular process that is complete; and from *Pliopontos* by the high occipital shield and temporal fossa. Finally, *B. mazeasi* differs from *Pontoporia* and is similar to *Inia* in having a triangular-shaped postorbital process.

Measurements (Fig. 2).—Definitions of abbreviations are given in Fig. 2 caption. Measurements are in millimeters. TL, 220.5 (46.21, $n = 5$); LC, 108.57 (21.2, $n = 5$); LR, 116.17 (27.01, $n = 6$); WR, 57.52 (9.57, $n = 12$); WPo, 99.06 (10.66, $n = 11$); WPx, 55.44 (9.63, $n = 8$); WN, 26.19 (2.99, $n = 9$); LN, 30.28 (5.94, $n = 6$); WNh, 7.77 (1.71, $n = 6$); WM, 109.09 (21.46, $n = 10$); LO, 48.63 (5.6, $n = 10$); LZ, 51.03 (6.54, $n = 2$); SH, 86.33 (14.6, $n = 2$); WB, 56.77 (6.75, $n = 2$); WFm, 26.8 (4.94, $n = 2$).

General description.—The preservation varies from well-preserved partial or complete skulls to deteriorated partial skulls. Some specimens (MUSM 593, 885, 886, and SGO-PV 966) seem to be deformed by diagenesis, but the main characters can be observed. The rostrum is here confirmed to be upwardly curved because it appears in all specimens, particularly in the well-preserved MUSM 887 (Fig. 6), being less accentuated in the ones deformed by dorsoventral compression. The same is true for the cranial asymmetry, but with significant variation.

Cranium.—The cranium (sensu Fordyce 1994) has subequal width and length and is telescoped, presenting anteroposterior compression (sensu Barnes 1985). The premaxilla reaches a posterior position over the supraorbital process of the maxilla, contacting the nasal in most cases. The vertex is slightly asymmetric and curved to the right, which differs from that observed
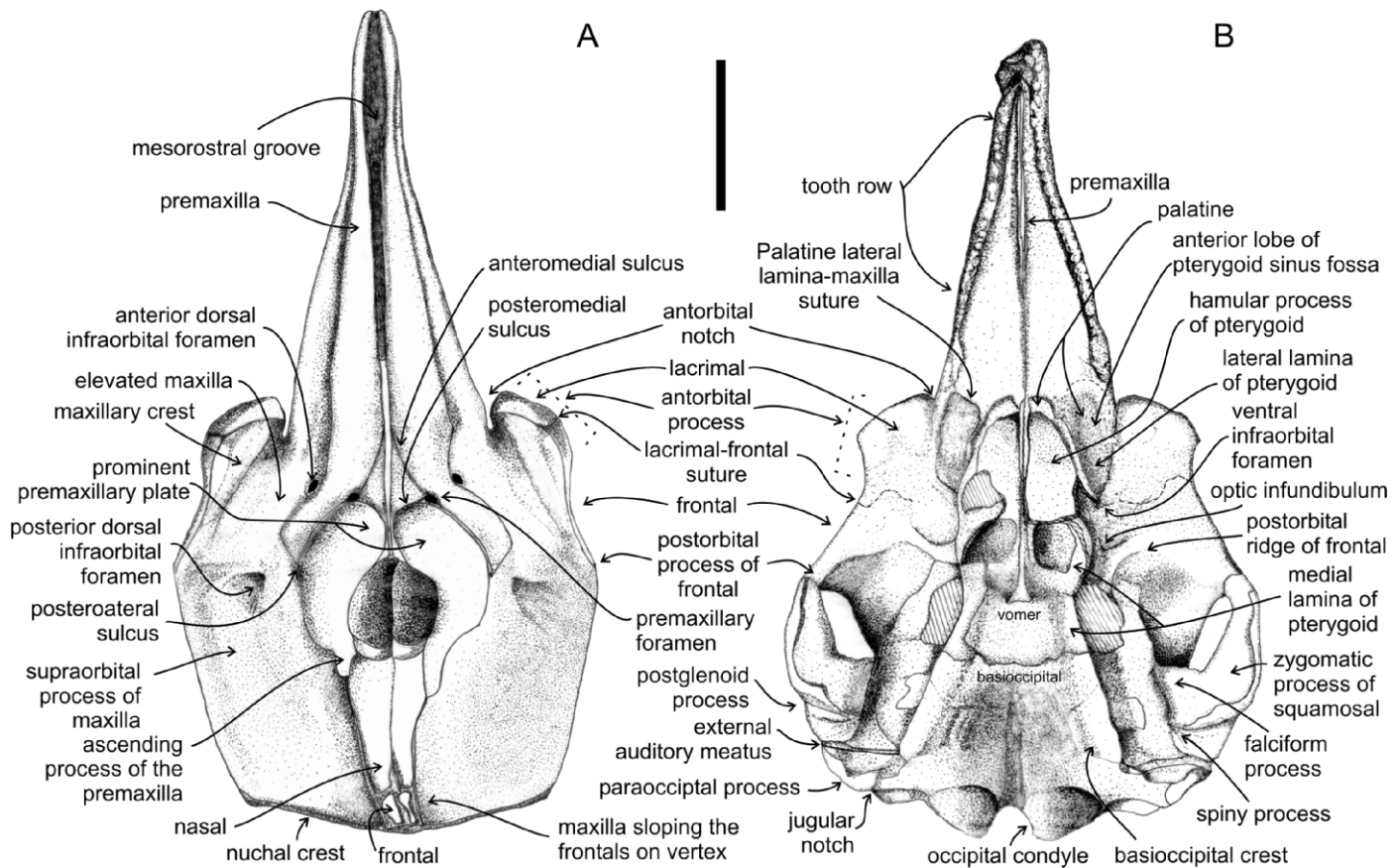
FIG. 4.—A) Dorsal reconstruction of mean shape for *Brachydelphis mazeasi*. B) Ventral view drawing from the most complete specimen (MUSM 565). Oblique lines are broken portions. Black bar = 50 mm.

in *Pliopontos*, *Pontistes*, and *Pontoporia*. It also is elevated, in a slender plate formed by the narrow curved frontals and a maxillary crest on the medial edge of the maxilla, similar to other Pontoporiidae and Iniidae and not as accentuated as in *Parapontoporia sternbergi* (Gregory and Kellogg, 1927), a member of the Lipotidae (sensu Muizon 1988b; Geisler and Sanders 2003). The vertex slopes posteriorly to this plate, in the contact of the nuchal crest and frontal.

The holotype (MNHN PPI 121), SGO-PV 746, and 748, have wide-open sutures (e.g., maxilla–frontal–lacrimal suture on lateral view); these materials plus specimen MUSM 593 all have a widely exposed lacrimal, not covered by maxilla, and low maxillary crests. In the other specimens (SGOPV 750, MPC 202, 377s, MUSM 565, ad 885–887), cranial sutures are visible but not open, maxillary crests are well developed, and the lacrimal is mostly covered by the maxilla in dorsal view. In all, the vertex is slightly elevated and asymmetric, with an inclined supraorbital process of the maxilla, being convex at the vertex and concave laterally.

Rostrum.—All specimens, including the holotype (MNHN PPI 121) and paratype (MNHN PPI 124) have a short triangular rostrum (1.24–1.29 times cranium length, for MUSM 565 and 887). Muizon (1988a) originally described the rostrum length as shorter than that of the cranium (braincase of this author). This was observed only in specimens SGO-PV 746 and 748 (0.8–0.99 times cranium length). However, these specimens, as

well as specimen MUSM 593, do not have individual alveoli but an alveolar or dental groove. The other specimens present at least some individualized alveoli. The base of the rostrum is flattened, but most of the specimens do not present the medial basin described for *P. sternbergi* and *Parapontoporia wilsoni*, except in SGO-PV 746, 748, and the holotype (MNHN PPI 121). The mesorostral groove at dorsal view is open along its extension. The vomer appears within it after the rostrum base (posteriorly) as observed in almost all specimens; however, its extension through the rostrum is variable.

The maxilla–premaxillary suture is not visible. Instead, a deep longitudinal groove across the rostrum is observed as in other Pontoporiidae and Lipotidae (*Parapontoporia* + Lipotes—sensu Muizon 1988b; Geisler and Sanders 2003). In ventral view, the flat-to-concave palate becomes narrower anteriorly, at the beginning of the longitudinal groove, where the premaxilla appears. The vomer and palatine form a deep, narrow keel posterior to the antorbital notches, between the internal nares, but not as deep as in *Parapontoporia*. The tooth alveoli are ventrally oriented at the extremity and more lateralized at its posterior end, where it curves upward, before the antorbital notches (SGO-PV 966, MUSM 565, 886, and 887).

Premaxilla.—The premaxilla is constricted (more concave) in its lateral border at the level of the antorbital notches (Muizon 1988a). Actually, this feature corresponds to the medial position of the anterior dorsal infraorbital foramina (for
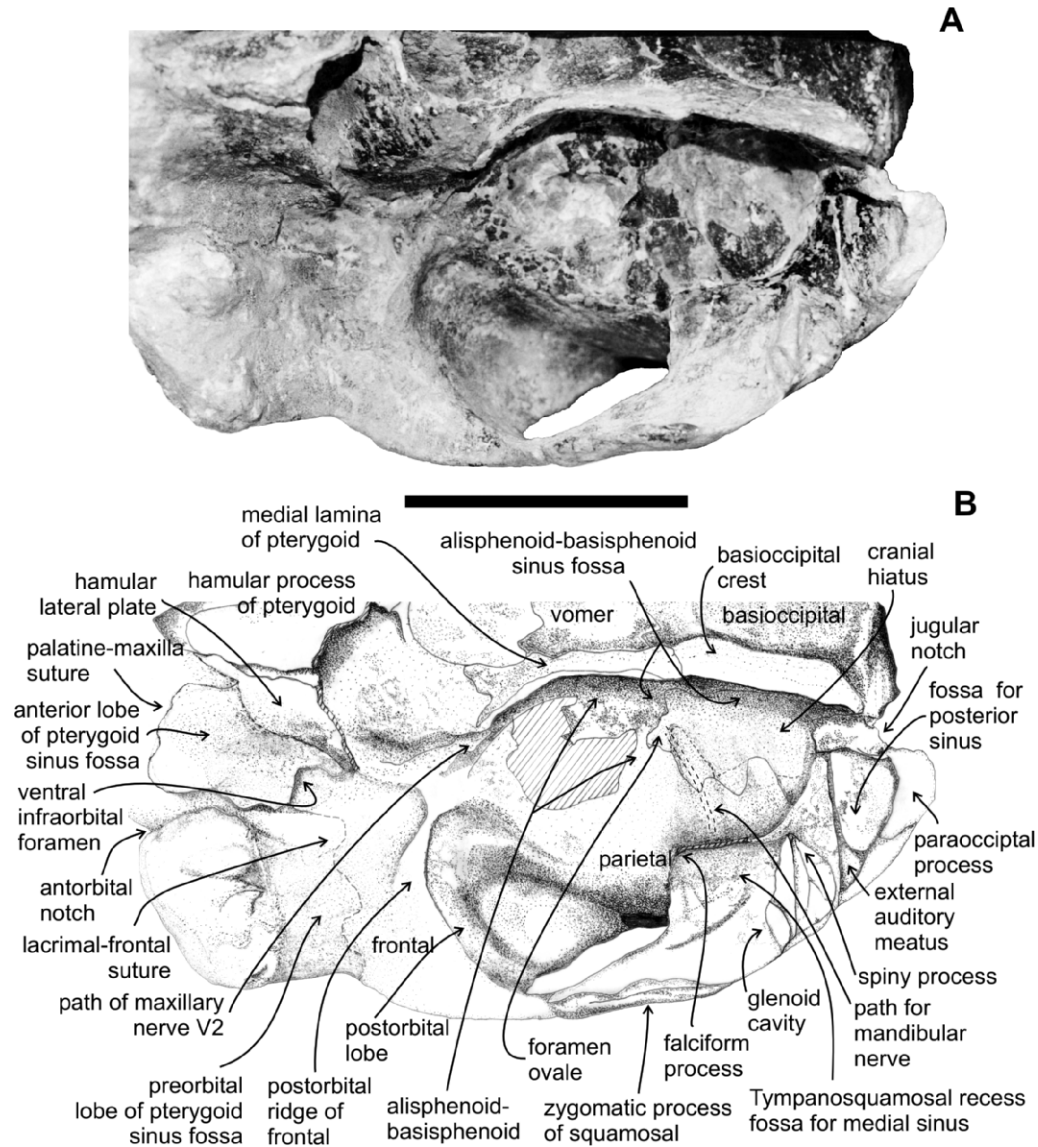
FIG. 5.—A) Ventrolateral view of right side of skull (MUSM 565) of *Brachydelphis mazeasi*. B) Drawing with structures indicated, dashed lines are for reconstruction based on left side. Oblique lines are broken portions. Black bar = 50 mm.

maxillary branch of trigeminal nerve V_2—sensu Fordyce 2002; Schulte and Smith 1918) and the convexity of the maxilla at this portion. In other genera observed (except *Pontistes*), this foramen lies more laterally and the maxilla presents a deep groove. In each premaxilla, anterior to the premaxillary foramina, lies a rough triangular surface, commonly interpreted as the nasal plug muscle attachment surface that is laterally limited by the associated sulci of these foramina (anteromedial sulcus for premaxillary artery). The posterolateral sulcus of this foramen is curved in an open angle and deviates laterally at the maximum width portion of the premaxilla, similar to *P. rectifrons*, *Parapontoporia*, and *L. vexillifer*, and without reaching the posterior part of the premaxilla, as in *P. blainvillei* and *P. littoralis*. The posteromedial sulcus of this foramen is not well marked in *B. mazeasi* but is not covered by bone as described for *Parapontoporia* (Barnes 1985).

The dorsolateral edge of the premaxilla is flattened and not markedly elevated as observed in *P. blainvillei*. At the orbital level, the premaxilla ranges the maximum width, corresponding to half of the maximum width of the skull, as in the holotype of *B. mazeasi*. The premaxillary plate (= spiracular plate—sensu Barnes 1985), the region that supported the premaxillary sacs (diverticula of the nasal passages—Mead 1975), is a prominent portion of the premaxilla between the nasal passage and the premaxillary foramen, delimited anterolaterally by the posterolateral sulcus for the premaxillary artery, similar to *P. blainvillei*. The posterior portion of the premaxilla contacts the nasal medially in the vertex, through a posteromedial ascending process. This configuration is unique among the Pontoporiidae, Iniidae, and Lipotidae; although a posteromedial ascending process is present in *P. rectifrons* and *Parapontoporia* together with a posterolateral one. In *L. vexillifer* the

posteromedial process appears but does not contact the nasal that is highly elevated.

The nasal passage has a variable form, from broad, with a rounded premaxillary suture (MPC 391s, SGO-PV 748, and 1109) to a slender, V-shaped premaxillary suture (MPC 377s, SGO-PV 746, and 750). This variation seems to be related to whether the premaxilla is highly elevated (inflated) on the premaxillary plate or not, respectively. MUSM 887 presents an intermediate pattern regarding both structures.

Maxilla.—The maxilla slopes from the vertex (higher), where it partially overlies the frontal bone, to the lateral edge (lower) at the level of the postorbital process of the frontal. *B. mazeasi* does not present a temporal crest above the temporal fossa; instead, the maxilla and frontal are fused in a smooth surface, differing from the adults of *P. blainvillei* and similar to the fetus of the same species (UFSC 1059). This last character also is observed in *Parapontoporia*.

At the level of the postorbital process lies a foramen that should correspond to the posterior dorsal infraorbital foramen (sensu Fordyce 2002), which was occupied by blood vessels and nerves. The maxillary branch of the trigeminal nerve (V_2) to the facial muscles (Fordyce 1994) lies at the postorbital process level, more posteriorly than in *P. blainvillei* and *P. littoralis*. In *P. blainvillei*, between the maxillary crest and the premaxilla border, lies a deep channel that extends well backward posterior to the naris. In *B. mazeasi* this channel does not exist and the region between the posterior and anterior dorsal infraorbital foramina is slightly elevated, also differing from the flattened surface of *P. rectifrons*. The anterior dorsal infraorbital foramen (sensu Fordyce 2002) is medially placed only in *B. mazeasi*. The maxillary crests (Muizon 1988a) above the orbit reach their maximum development at the preorbital process of the frontal and are asymmetric, similar to *P. blainvillei* and differing from the other genera. In ventral view, the posterior extremity of the maxilla is not so well defined, but the palatine suture is visible in MUSM 565 and the holotype (sensu Muizon 1988a), similar to *P. littoralis*, *L. vexillifer*, and *Parapontoporia* but differing from *P. blainvillei* and *Inia*. The maxilla also seems to articulate with the lacrimal, jugal, and palatine, without participation of the orbit. Medially, it contacts the palatines and the vomer anterior to the ventral keel (formed by the palatine, vomer, and hamular process of the pterygoid), but it differs from *P. blainvillei*, where the maxilla has a process within this keel between the pterygoid and palatines.

Lacrimal and jugal.—The lacrimals are robust and the antorbital notches are deep, delimiting the facial nerve trajectory (VII—sensu Schulte and Smith 1918). Only in SGO-PV 746, and 748 the lacrimals are dorsally exposed almost their entire extension, and a small portion of the jugal is preserved ventrally at the base of the rostrum. In this case, the jugal lies within the antorbital notch posteriorly, and articulates with the lacrimal on both the antorbital notch and the base of the rostrum, similar to *Parapontoporia*.

Frontal.—The frontals in the vertex are very thin and short (>3 times shorter than the nasals), curved to the right (SGO-PV 746, MUSM 565, 887, and MPC 203), being asymmetric and thus differing from all other Pontoporiidae. Anteriorly,
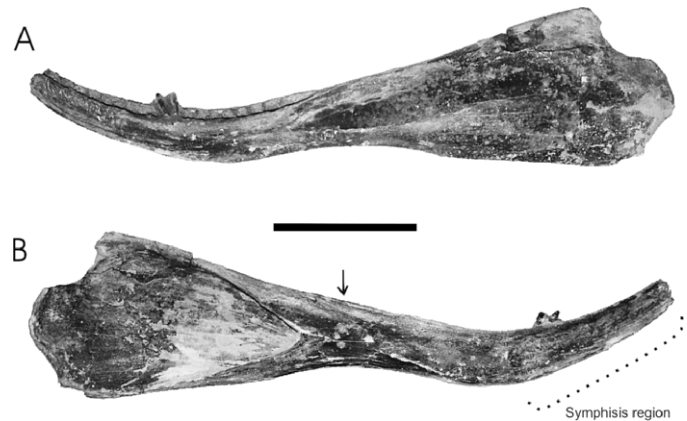

Fig. 6.—Mandibles of MUSM 565 referred to *Brachydelphis mazeasi*. A) Lateral view. B) Medial view. The black arrow indicates the end of the toothrow and beginning of deflection of coronoid process. Black bar = 50 mm.

they are inserted between the nasals in a V-shaped (posteriorly opened) suture, as in Pontoporiidae, but more similar to *Pontistes*. The nuchal crest is slightly projected anteriorly, differing substantially from *Pliopontos*. The maxilla covers the frontal in almost its entire dorsal extension, except the vertex, it only appears above the orbits, laterally to the maxillary crest, being less apparent than in other Pontoporiidae, and similar to *Inia*, *Lipotes*, and *Parapontoporia*. In lateral view, there is a visible suture with the lacrimal and maxilla at the antorbital process. The triangular postorbital process of the frontal contacts the zygomatic process of the squamosal extremity (MUSM 565), which is upwardly inclined. In ventral view, the optic infundibulum is limited at postorbital level by the postorbital ridge (MUSM 565). Anteriorly, the preorbital ridge is well marked only in the specimen of a senile individual (MUSM 565). The optic infundibulum is visible in ventral view and the optic foramina are very deep (SGO-PV 966). In this specimen, there is a foramen in front of the preorbital ridge, below the proximal lateral lamina of the palatine, which is interpreted here as the ventral infraorbital foramen (sensu Fordyce 2002), but it is anterolaterally oriented and is not evident as in *Pontoporia* and *Parapontoporia*. The sphenopalatine foramen was not observed. The orbit and the postorbital sinus are markedly bigger than in adults of *Pontoporia*, being similar to the fetal condition in the latter species. The frontoparietal suture could not be observed.

Nasal.—The nasal is elongated, narrow, mostly curved to the right, and is triangular to rectangular in shape, apparently depending on the alignment of the nasofrontal suture, which also is variable in *P. blainvillei*. In MUSM 565 and MUSM 887 the distal portion of the nasal that contacts the frontal is less than one-third of the thickness of its own proximal portion, being highly triangular in shape. In MPC 377s the nasal is markedly rectangular in shape. In most cases, the anterolateral corner of the nasal is truncated by the posterior process of the premaxilla that contacts the nasal, as in *P. rectifrons*. In *P. blainvillei* this feature was only observed in specimens of juveniles that do not have fully developed nasals, but these did

not present contact with the premaxilla. The nasal is somewhat elevated and deflected, being more similar to *Lipotes* and *Parapontoporia*, but to a lesser degree. This slight elevation of the face, at nasal level, may indicate a moderate development of the maxillo-naso-labialis muscle.

Mesethmoid.—In the posterior wall of the nasal passage, the mesethmoid is inclined but not as inclined as the nasals, as in *Parapontoporia*. It definitely does not support nor elevates the nasals as in Delphinidae, Ziphiidae, and other modern dolphins. The olfactory nerve's fossa was not observed. The mesethmoid septum has an irregular dorsal end that could indicate a cartilage continuation (Fordyce 1994). Its septum is slightly deviated to the right, giving an asymmetric profile to the nasal passage, differing from *P. blainvillei* and *P. littoralis*, but similar to *P. sternbergi*.

Palatine, vomer, pterygoid, and pterygoid sinus.—In the basicranium, the extension of the lateral lamina of the palatine is unknown, because only its proximal portion is preserved in all specimens analyzed. The same is observed for the lateral lamina of the pterygoid, differing from the original interpretation of *B. mazeasi* (Muizon 1998a:111, figure 53). In the holotype and paratype, a thin posterior portion of the palatine and the lateral lamina of the pterygoid are preserved, reaching the posterior margin of the internal naris; see Muizon (1988a:118, figure 59).

Specimen MUSM 565 has part of the hamuli processes of the pterygoid preserved, which almost contact each other medially. The pterygoid articulates in its dorsal lamina with the keel of the vomer and the anterior portion of the basioccipital, as in the holotype. Anteriorly, an anterolateral process of the palatine articulates with the maxilla in a rounded shape. Medially, a very thin lamina of the palatine appears between the pterygoid bones. Anteriorly, the maxillary insertion between the palatines makes it difficult to distinguish which one is in contact with the vomer. The keel is thinner than in *P. blainvillei*.

The pterygoid sinuses are well developed in this species. The fossa for the anterior lobes are very well marked over the palatine, having an elongated shape from just anterior to the antorbital notch to well posterior to the lateral palatine–maxillary suture (MUSM 565, 887, and SGOPV 966—sensu Fraser and Purves 1960). The fossa for the pre- and postorbital lobe lies anteriorly and posteriorly from the postorbital ridge of the frontal, respectively (Fordyce 1994). These fossae are rounded and vary from deeply (MUSM 565) to slightly (SGOPV 966) marked. The fossa for the middle lobe of the pterygoid sinus occupies the tympanosquamosal recess, a poorly excavated fossa, lateral to the falciform process and anterior to the glenoid fossa (MUSM 565, 887, and holotype—sensu Fraser and Purves 1960). There also are excavations for the posterior lobe on the paroccipital process of the exoccipital (sensu Fraser and Purves 1960) and on the lateral border of the basioccipital crest; the alisphenoid–basisphenoid sinus fossa for the sinus pterygoid lies in the homonymous bones (sensu Fordyce 1994 [= peribullary sinus—sensu Fraser and Purves 1960). No subcircular fossa (sensu Muizon 1987) or periotic fossa (sensu Fordyce 1994) were observed.

Medially, the keel of the vomer forms the nasal passage septum. Posteriorly, it contacts the basioccipital (the basisphenoid–basioccipital suture could not be observed), and laterally, it contacts the pterygoids medial laminas, which are robust and also articulate with the basiocciptal (posteriorly). The path for the maxillary branch of the trigeminal nerve (V_2) is visible and runs parallel to the medial lamina of the pterygoid up to just below the postorbital ridge (Fig. 5).

Squamosal.—In dorsal view, the zygomatic process of the squamosal is barely seen on MUSM 565 (the only specimen with a complete squamosal) and it is not laterally projected as in *Lipotes*, which is broadly apparent in dorsal view. It is upwardly oriented as in *Parapontoporia* and *Pontoporia*, but to a greater degree. The squamosal–parietal suture is lower, in lateral view, than in *Pliopontos* and *Pontoporia*, being more similar to that of *Parapontoporia*. The anteroventral squamosal seems to present an articular facet for the jugal. In ventral view, above the external auditory meatus and posttympanic process lies the zygomatic process fossa, where at least the sternomastoideus and mastohumeralis muscles should have attached (Schulte and Smith 1918:31, figure 8). The postglenoid process is robust, pointed, and ventrally projected, being similar to that of *Parapontoporia* and not rounded as in *Pontoporia*.

The falciform process, anteromedial to the glenoid cavity, is barely medially projected. The posterior spiny process (sensu Muizon 1987) is not accentuated, but may be broken. The glenoid fossa is wide and delimited by lateral and posterior ridges. The posterior ridge marks the beginning of the postglenoid process. The external auditory meatus is deep and lies between the postglenoid process and a rough surface that must correspond to the posttympanic process (Fordyce 1994), where the tympanic articulates with the squamosal.

Alisphenoid, basisphenoid, orbitosphenoid, and parietal.—In lateral view, through the temporal fossa the parietal appears, with a visible squamosal–parietal suture. The lambdoid crest gives an elongated aspect for the temporal fossa by being more posterior than the occipital condyle. This fossa is very high and it is roofed by the maxilla and frontal dorsal expansions, being excavated by the postorbital lobe of the pterygoid sinus (MUSM 565 and 887), differing from *Lipotes*.

The other sutures are poorly delimited because the only specimen that has a well-preserved basicranium (MUSM 565) seems to be senile, with most of the bone sutures fused. In ventrolateral view, the bone sutures and foramina seem to be fused or combined; only the cranial hiatus (Fraser and Purves 1960) is recognized, with all foramina unified, as in many other derived odontocetes. The foramen ovale is not well defined; its possible location is in front of the cranial hiatus and above the bony bridge that should correspond to the alisphenoid–basisphenoid bones; nevertheless, these bones are fused and broken. Therefore, the foramen ovale may not be separated from the cranial hiatus but this could be due to the nonpreservation of this thin bony lamina. Laterally, the parietal articulates with the alisphenoid–basisphenoid. The orbitosphenoid was not recognized. The path for the mandibular nerve (3rd branch of trigeminal nerve, V_3—sensu Fordyce 1994; Romer 1962; Schulte and Smith 1918) is not evident, but seems

to be present in a bony bridge that may correspond to the alisphenoid.

Basioccipital.—The basioccipital has a high and relatively thin crest (= falcate process of authors), anteriorly continued by the medial lamina of the pterygoid; continuous to this crest, lies the fossa for alisphenoid–basisphenoid sinus. The suture of these bones with the basisphenoid–alisphenoid cannot be confidently recognized. The basiocciptal–vomer and basioccipital–pterygoid lateral lamina sutures are evident medially. Laterally, the carotid foramen seems to appear at the level of the inferred foramen ovale, but it is not well preserved.

Supraoccipital, paroccipital, and exoccipital.—The occipital shield is almost vertical and presents a longitudinal sulcus separating the bulges for the cerebral hemispheres and an oblique mediolateral depression that splits the paroccipital process from the supraoccipital. This configuration differs substantially from the globoid aspect observed in *Pontoporia* and *Pliopontos*. The exoccipital is larger and more robust than in *Pontoporia* and *Pliopontos* and is similar to *Parapontoporia*; the paroccipital process of this bone is ventrally projected and longer than the basioccipital, differing from *Pontoporia* and similar to *Pliopontos*, *Parapontoporia*, and *Inia*. The jugular notch is broad and profound; it splits the paroccipital from the exoccipital ventrally. The hypoglossal foramen lies within the jugular notch (MUSM 565).

Mandible.—The mandibles are short, lateromedially compressed, and curved upward, as does the rostrum. The symphysis is not fused; instead there is a contact region in the anterior extremes from where the bony axis deflects laterally, in contrast to the long, fused symphysis present in all Pontoporiidae, Iniidae, and Lipotidae. The mandibular foramen (fossa of some authors) is wide and occupies most of the posterior end of each mandible, between the condyle and the anterior portion of the coronoid (dorsal) and angular (ventral) processes. The condyle is only preserved in MUSM 887 and it is articulated with the skull, making it possible to observe that it is rounded. The toothrow ends at the base of the coronoid process, which is very high. Approximately 18 alveoli are present in MUSM 565. In the anterior extremity, in lateral view, there is only a shallow sulcus, not accentuated as in Pontoporiidae.

Teeth.—The shape of the teeth is similar to that of other Pontoporiidae but they are smaller in size (9.91 mm maximum length). Only 1 tooth root could be observed (MUSM 887), which is deviated backward, similar to *P. littoralis* and *P. blainvillei*. In MUSM 886 the teeth seem to be all laterally oriented to some degree, from the anterior extremity to the base of the rostrum.

cf. *Brachydelphis* new form

Referred materials localities and age (Fig. 7).—Materials include incomplete ventral and dorsal parts of skulls (SGO-PV 972 and MUSM 884), a dorsal portion of skull (SGO-PV 1109), and a rostrum fragment (SGO-PV 759). We referred specimen MUSM 884 from Ocucaje, Ica, Pisco Formation (Peru) to a middle–late Miocene age. The Chilean specimens (SGO-PV) are from Mina Fosforita locality, late Miocene (Messinian–Tortonian stage—Bahía Inglesa Formation).
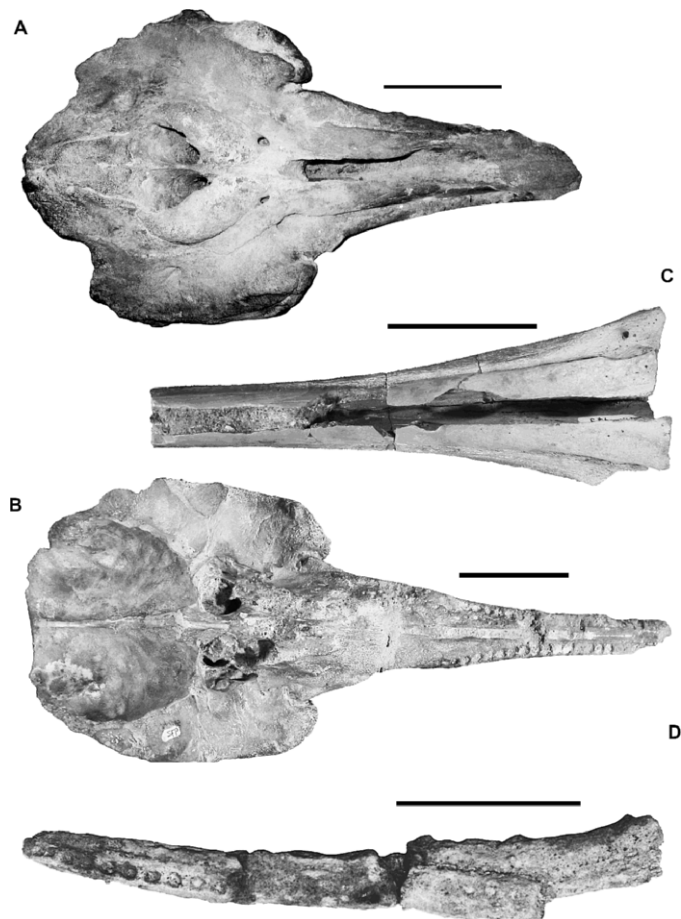

Fig. 7.—Specimens referred to cf. *Brachydelphis* new form. A) Dorsal view of SGO-PV 1109. B) Ventral view of SGO-PV 972. C) Dorsal view of rostrum (SGO-PV 759). D) Mandibles of MUSM 884 in dorsal view. Black bar = 50 mm.

Measurements (Fig. 2B).—TL, 290a; LC, 101.78; LR, 176.9a; WR, 60.3; WPo, 106.8; WPx, 60.75b; WN, 30.05; LN, 25.65b; WNh, 6.5b; WM, 117.6b; LO, 53.95 (where a is SGOPV 972 only, and b is SGOPV 1109 only).

General description.—These specimens have basically the same features observed above for *B. mazeasi*; therefore, only the differing features will be summarized here.

Rostrum.—These specimens differ from *B. mazeasi* basically by the rostrum, that is longer (more than 1.63 times larger than the cranium's length in SGO-PV 972, which is not complete), more slender, and not upwardly curved. In lateral view, the rostrum presents a thinner base with a higher premaxilla. In ventral view, the palate is also thinner and continuously decreases in width instead of the abrupt decrease that gives the triangular shape of the rostrum in *B. mazeasi* (see below).

The vomer and palatine form the keel between the internal nares, but the fossa for the anterior sinus over the palatine is poorly marked and the keel is less accentuated than in *B. mazeasi*. Specimen SGO-PV 972 presents more than 26 circular to squared alveoli that mark a polydonty when compared to *B. mazeasi* but presenting less teeth than *Lipotes*, *Pontoporia*, and *Parapontoporia*, although the real extent of the rostrum is unknown.

Cranium.—As demonstrated in *B. mazeasi* (above), the cranial characteristics can be confusing when comparing all ontogenetic and individual variation. Consequently, such features could not be discarded to reflect the individual variation rather than diagnostic characters. These are a narrower cranium, preorbital process more robust; a more marked concavity in the supraorbital process (cranial portion) of maxilla which is dorsolaterally rather than laterally oriented, as observed in *B. mazeasi*; and an almost symmetric and more elevated vertex, triangular nasal in SGO-PV 1109 and MUSM 884, but never so narrow as described for some specimens of *B. mazeasi* (MUSM 565 and MUSM 887). In ventral view, the anterior, pre-, and postorbital lobes of the pterygoid sinus are less marked than observed in *B. mazeasi*. The infraorbital foramina on the ventral portion of frontal have a different configuration, the fossa below the palatine lateral lamina is elongated in SGO-PV 972, whereas it is more circular in *B. mazeasi*. The optic infundibulum, on the frontal, is barely marked compared to *B. mazeasi* and, at postorbital level, the postorbital ridge of the frontal (Fordyce 1994) is more anterior than in *B. mazeasi*, having a smaller and narrower orbit, as well as pre- and postorbital sinus fossae. The foramen rotundum is visible, dorsal to the optic foramen, and is the passage for the maxillary branch of the trigeminal nerve (V_2). The squamosal, occipitals, parietals, and other bones of the basicranium are not preserved.

Mandibles.—Specimen MUSM 884 presents a fragment of mandible that is much deteriorated and it is not strongly upwardly curved; instead it presents a long, fused symphysis (presumably more than one-half of the total length of the mandible). It differs from *B. mazeasi* and is similar to the Pontoporiidae, *Lipotes*, and *Parapontoporia*.

cf. *Brachydelphis* indet

Referred materials, localities, and age.—The Peruvian specimens are from beds provisionally referred to the middle–late Miocene of the Pisco Formation and the Chilean specimens are from late Miocene beds of the Bahía Inglesa Formation (Messinian–Tortonian stage). The materials are dorsal portions (SGO-PV 747, 968, MPC 203, and 391s—Mina Fosforita, Caldera, Chile) and a ventral portion (MUSM 590—Cerro Los Huesos, Ica, Peru) of skulls and a partial rostrum (MUSM 591—Cerro Tres Pirámides, Ica).

Measurements.—TL, 145.65i; LC, 91.5; LR, 52.45i; WR, 57.15; WPo, 106.3; WPx, 57.3; WN, 27.3; WNh, 9.0; WM, 116.1; LO, 48.55 (only based on SGO-PV 747; I indicates incomplete).

Description.—It is not possible to determine if these specimens have a long or short rostrum. They are close to *Brachydelphis*, presenting deep antorbital notches, with large lacrimals and a thick antorbital process, an elevated and asymmetric to near symmetric vertex, large and narrow nasals and slender frontals, a flat palate, and a triangular postorbital process.

Ontogenetic comparisons.—Some specimens (SGO-PV 746 and 748), including the holotype of *B. mazeasi* (MNHN PPI 121), have wide-open sutures and present a dental groove instead of alveoli in the rostrum, which indicates their juvenile

condition, summed with other morphological features. Still, when relative size of the structures is compared between fetal, juvenile, and adult specimens of *P. blainvillei*, and the juvenile and adult specimens of *B. mazeasi*, the fossil specimens have some features more similar to fetuses and juveniles than to adults of the living species (Fig. 8), such as relatively broader cranium; slightly larger size of the orbit, which is even bigger in the holotype, SGO-PV 746, and 748; a more posterior position of the nasals; higher vertex; markedly shorter and upwardly curved rostrum; longer paraocciptal process (MUSM 565); thicker zygomatic process in MUSM 565 and more slender in MUSM 887, but both shorter, resembling the fetal condition in *P. blainvillei*; and anterior position of the squamosal in its base and well-marked fossae for musculature (m. sternomastoideus and mastohumeralis).

Geometric morphometrics.—The results of the principal component analysis of the landmarks partitions the data set into 2 groups, differentiating *P. blainvillei* and *Brachydelphis*, with some variation within both groups (Fig. 9). The NPMANOVA gives a significant value to this principal component analysis ($P < 0.01$). The 1st component, which describes 60.1% of the variance, splits the 2 taxa into negative (*Brachydelphis*) and positive values (*P. blainvillei*). The 1st component should not reflect size (corrected to Procrustes coordinates); instead, landmarks 6 and 30 have an important (approximately -0.5) participation, corresponding to maximum width of the premaxillae on the cranial portion, with higher values in *Brachydelphis*. This confirms the morphological character, that maximum width of the premaxillae on the level of the postorbital process constitutes one-half of the maximum width of the cranium. These landmarks also correspond to the lateral ending of the posterolateral sulcus for the premaxillary foramen, which is posterior in *P. blainvillei*, where this species shows the maximum width of the premaxillae but never so accentuated as in *Brachydelphis*, as this analysis has corroborated.

Landmarks 4 and 32 also contribute to this axis (approximately 0.20), reflecting a major difference between the species as well; the posterolateral process of the premaxilla in *P. blainvillei*, instead of posteromedial as in *Brachydelphis*. Landmarks 8 and 28 ($0.17 < x < 0.20$) correspond to the medial position of the anterior dorsal infraorbital foramen in *Brachydelphis* and the more lateral position in *P. blainvillei*, respectively. This confirms the character diagnostic for the species: concave lateral premaxilla edge at the antorbital notch level. The next higher landmark (0.19) is 36, which corresponds to the nasofrontal medial suture; 17 and 19 (0.16–0.13) correspond to the width of the cranium at the postorbital process; and 10 and 11 (0.15–0.16) correspond to the width of the maxilla and the premaxilla at the most anterior point marked on the rostrum.

An important variation in components 2 and 3 for the fossil specimens could reflect the existence of the 2 forms described above. Because of this variation it was not possible to differentiate *Brachydelphis* and *P. blainvillei* through these components, but they describe only 18% of the total variance (9.6% and 7.3%, respectively). Because for all multivariate analyses the specimens of cf. *Brachydelphis* new form and
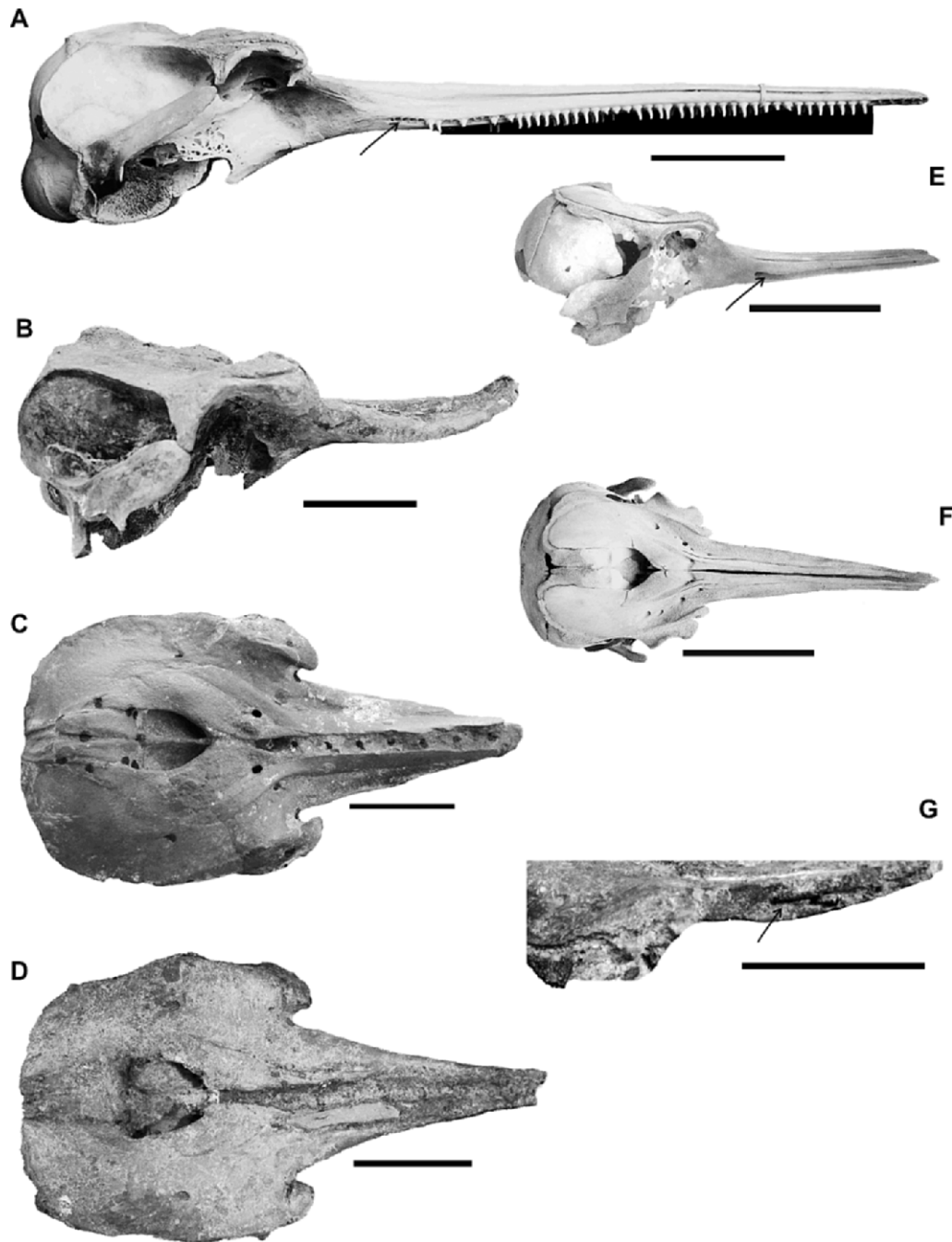
Fig. 8.—Comparison between skulls of *Pontoporia blainvillei* and *Brachydelphis mazeasi*. A) Adult form of *P. blainvillei* (UFSC 1037). B, C) Adult form of *B. mazeasi* (MUSM 887 and MPC 377s). D) Juvenile form of *B. mazeasi* (SGO-PV 746). E, F) Fetal form of *P. blainvillei* (UFSC 1059) in dorsal and lateral view, respectively. G) Detail of juvenile form of *B. mazeasi* in laterodorsal view (SGO-PV 746). Note the similarity between the juvenile skulls of both species but not the adult ones. Black bar = 50 mm.

B. mazeasi were grouped together, independent of locality and whether they have a long or short rostrum, this group shows more variation than *P. blainvillei*. Both fossil groups have not been split from each other in this analysis. This could be explained by the fact that the main differences of rostrum morphology are found after 7–9 cm from its base, where no landmarks were defined for this study. The differences between *P. blainvillei* and the fossil species are due to an interaction of almost all points, including nasal–frontal–maxillary suture

(1 and 37), posterior process of premaxillae (4 and 32; lateral position and growth), maximum width of premaxillae (6 and 30) and maxillae (17 and 19), width and shape of rostrum (10, 11, 25, and 26), orbit anterior processes (16 and 20), lacrimals, and maxillae–frontals suture (15 and 21). *P. blainvillei* shows almost no variation within component 3.

The juvenile specimens SGO-PV 746 (*B. mazeasi*) and UFSC 1059 (fetus of *P. blainvillei*) are distant from the rest of the specimens (in both species) mainly due to the influence of
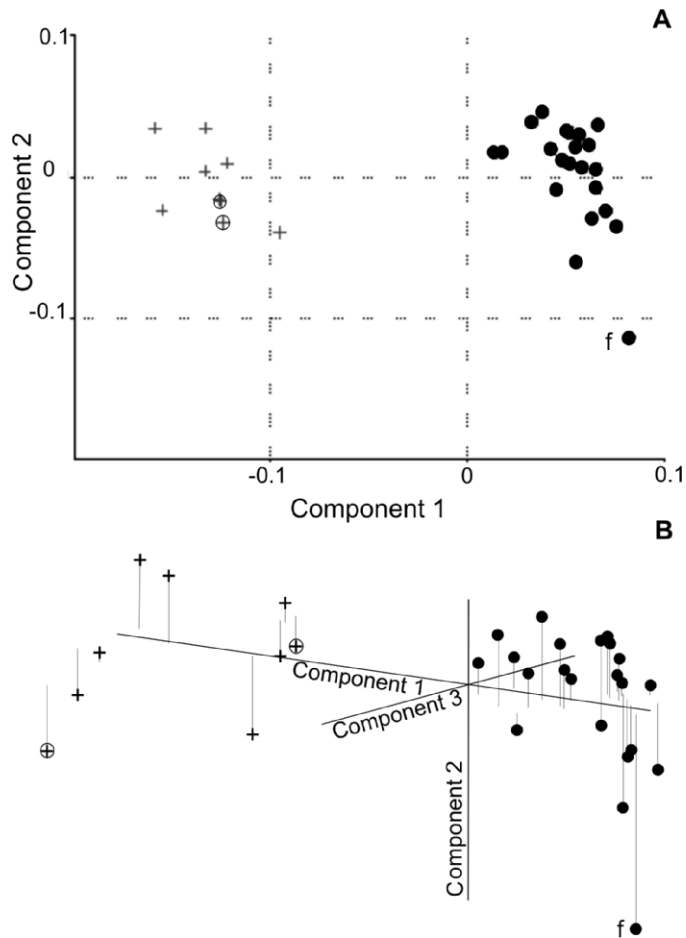
Fɪɢ. 9.—Principal component analysis shape analysis scatter diagram from landmarks (2-dimensional) of fossil specimens (+) and specimens of *Pontoporia blainvillei* (closed circles). Note the greater variation within the fossil group and significant differentiation from *P. blainvillei* ($P < 0.01$). A) Principal component analysis scatter diagram with components 1 and 2. B) Three-dimensional plot landmarks from 3 main components rotated in principal component axes 1 and 2 (x and y). The juvenile (juv) and fetal specimens are indicated (open circles).

landmarks 4 and 32. The premaxilla process becomes more posterior with age and growth in specimens of *P. blainvillei*, where the relative ontogenetic sequence is known. This observation led us to maintain specimen SGO-PV 746 in the analysis, even though we were not sure if it is broken on this portion, using the interpretation of Muizon (1988a) for the holotype (MNHN PPI 121). Additionally, running the principal component analysis without it showed no difference in the positions of the other specimens. The holotype specimen (MNHN PPI 121) and SGO-PV 746 are not separated by components 1 and 2, but lie on opposite extremes of variation on component 3 by the influence of the same landmarks (4 and 32), because the holotype shows (following reconstruction by Muizon [1988a]) the posterior process of the premaxilla reaching the nasal as observed in other adult specimens. The specimen MUSM 887, considered an adult with all alveoli formed, also lies together with these juvenile specimens.

The analysis of adult specimens gives the same results with more confidence (component 1 explains 66.8% of variance and splits the 2 species with 95% confidence ellipses). In the relative warps scores the 2 species also were split in a 95% confidence ellipse; *P. blainvillei* was bounded to negative values in warp 1 (or score 1) and specimens of *B. mazeasi* were all highly positive (>1).

The cluster analysis showed 2 groups, 1 composed by specimens of *P. blainvillei* and the other with specimens of *B. mazeasi* and cf. *Brachydelphis* (indet. and new form). When keeping all ontogenetic series available, the fetus and juveniles appeared on the base of both groups. The new form cf. *Brachydelphis* also lies in a basal position of the cluster in both algorithms used (single and paired linkage), between the juveniles of *B. mazeasi* (SGO-PV 746 and MNHN PPI 121 [holotype]).

Traditional morphometrics.—The short- and long-rostrum forms (*B. mazeasi* and cf. *Brachydelphis* new form) were not well differentiated by simple morphological observations or by geometric morphometrics, because there are few specimens with a complete rostrum and a virtually complete cranium at the same time (Fig. 10). Nevertheless, 2 main tendency lines of width loss were recognized (short and long rostrum known a priori; Figs. 10A and 10B). This analysis allowed us to define some specimens as having a short or long rostrum, considering their shape variation. The MPC 377, 391, MUSM 887, and SGO-PV 749 were classified after this analysis as short-rostrum type. SGO-PV 747 remains a possible long-rostrum type because it is broken near its base and it was not possible to define it better.

Some ontogenetic variation was detected here because the fetus of *P. blainvillei* was classified as a transitional form. It is more similar to the short-rostrum type of *Brachydelphis* than the long-rostrum type of adult specimens of *P. blainvillei* (Fig. 10C).

Dɪsᴄᴜssɪᴏɴ

The comparison of different specimens of *B. mazeasi* with specimens from known ontogenetic stages of *P. blainvillei* allowed us to assess ontogenetic variation. The holotype (MNHN PPI 121) of *B. mazeasi* presents several similarities to a fetus and juveniles of *P. blainvillei* (from postnatal stage to before sexual maturity—Ramos et al. 2000a). These similarities include: the late (delayed) ossification of the teeth alveoli in the rostrum as observed in fetuses and juveniles of *P. blainvillei*; the wide-open suture of the maxilla, frontal, and lacrimal in lateral view, observed in juvenile individuals of *P. blainvillei*; the low maxillary crests and proportionally large orbits compared with the temporal fossa, as observed in fetuses of *P. blainvillei*; and the rostrum length shorter than the braincase length (Muizon 1988a). These are interpreted here as juvenile characters for *B. mazeasi* because there is major growth of the rostrum from the fetuses to juvenile and adult specimens of *P. blainvillei*. These traits lead us to conclude that the holotype (MNHN PPI 121) of *B. mazeasi* is a juvenile specimen and that some of these traits were confused with traits diagnostic for the species (Muizon 1988a).
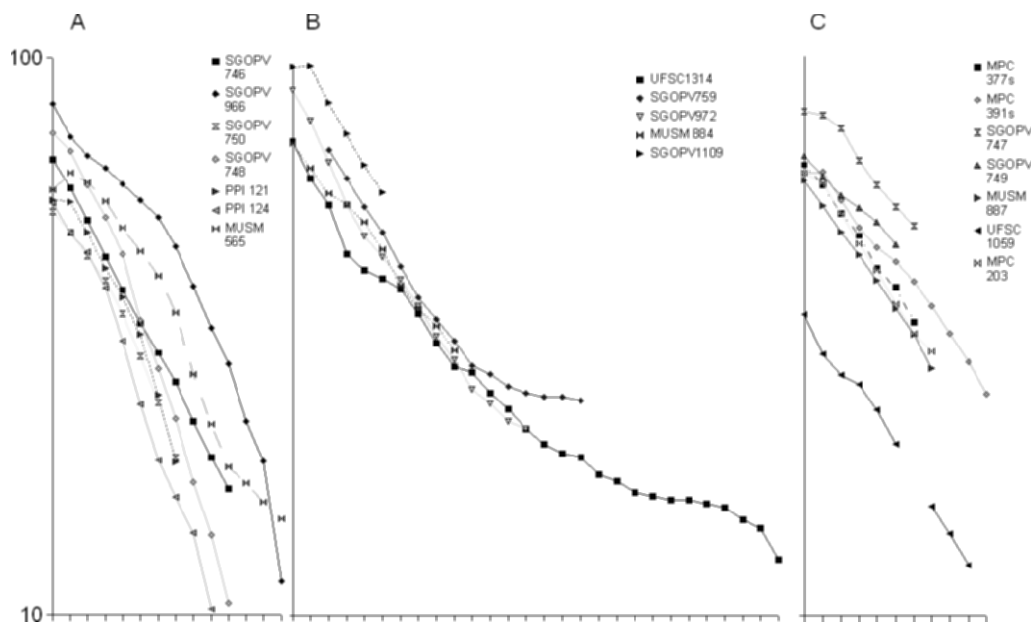
FIG. 10.—Curves of rostrum width across the rostrum axis; in y: the width of rostrum transformed to logarithmic scale (10–100), in x: distance from rostrum base in centimeters (each interval corresponds to 1 cm). A) Known short-rostrum specimens of *Brachydelphis mazeasi*. B) Known long-rostrum specimens of cf. *Brachydelphis* new form and *Pontoporia blainvillei* (UFSC 1314). C) Dubious fossil specimens and fetus of *P. blainvillei*. Note that MUSM 887 and MPC 377s have short-rostrum tendencies.

Other allegedly diagnostic characters of *B. mazeasi*, such as the discontinued lateral lamina of the pterygoid ranging well posterior to the level of the postorbital process, and the small paroccipital process of the exoccipital, were not confirmed here because they were not observed in any of the new specimens. Actually, they can be confirmed in neither the holotype nor the paratype (Muizon 1988a: figures 52 and 59). The constriction of the premaxilla at the antorbital level was found to be variable, absent, or poorly marked in some specimens, but still unique to *B. mazeasi*. The cranial features of the diagnosis provided by Muizon (1988a) for *B. mazeasi* were revised and amended here (above).

A new form was recognized, cf. *Brachydelphis* (new form), from specimens from the Pisco and Bahía Inglesa formations. This form was characterized by having a longer rostrum with a long mandibular symphysis. There is not much evidence that this may be a sexually dimorphic character. In *P. blainvillei*, it has been observed that the female has a larger size (reflected in the size of skull and teeth—Higa et al. 2002; Ramos et al. 2000b) but there are no known cases in odontocetes that have demonstrated differences in the size of the rostrum as a sexually dimorphic character. Additionally, a long or short rostrum could be interpreted to imply different feeding habits (Werth 2006), but still these inferences are difficult to delimit in living species and may be less crucial in the animal's life than has been generally thought. Goodall and Galeazzi (1985) have pointed out that the diets thought to be specific in some species and higher groups (e.g., family) of cetaceans actually vary according to food supplies and geographic displacement. More simply, the different rostrum types could be related to the greater diversity of the whole Inioidea clade during the middle

to late Miocene as shown so far in the fossil record with respect to the South American coast (Cozzuol 1985, 1996; Fordyce and Muizon 2001; Muizon 1983, 1988a).

We should also remark that some characters described as diagnostic of different groups within the Delphinida (Muizon 1988b:23) were found to be variable in *B. mazeasi* and *P. blainvillei*. For example, the shape of the nasal passage, used to differentiate Lipotidae (*Parapontoporia* + *Lipotes*) and Pontoporiidae, varies from broad with a semicircular premaxillary suture to slender with a V-shaped or cordiform premaxillary suture in different specimens of *B. mazeasi*.

The morphometric study revealed greater variation within the fossil specimens, which could be interpreted as ontogenetic variation in shape (the juveniles are peripheral in the distribution of specimens on the principal component analysis scatter chart). In the cluster analysis, the greater variation also is attributed to the new form of cf. *Brachydelphis* that is placed near the base of the cluster of fossil specimens, together with the juveniles. This analysis also showed a higher similarity between the fetus and juveniles of *P. blainvillei* and *B. mazeasi*, respectively. Geometric morphometrics has been used to elucidate confusing cases of existence of living species or subspecies of Delphinidae (Monteiro-Filho et al. 2002) and the existence of subpopulations of *P. blainvillei* (Higa et al. 2002).

Generally, the variation within *P. blainvillei* has been attributed to a north–south disjunction in geographic distribution resulting in 2 subpopulations (Pinedo 1991; Ramos et al. 2002; Secchi et al. 1998). However, this distributional hiatus, often mentioned for Santa Catarina State (Brazil), cannot be supported because regular records of the species (Cherem et al. 2004) and a resident population have been recently reported

(Cremer and Simões-Lopes 2005). In the case of *Brachydelphis*, this pattern of variation does not appear to exist, because specimens from both of the formations that were studied are placed together in the principal component analysis and cluster analysis.

Evolutionary implications.—The presence of a short rostrum was cited as an autapomorphic character that has defined the subfamily Brachydelphininae (Fordyce and Muizon 2001; Muizon 1988b). The occurrence of cf. *Brachydelphis* new form, with a long rostrum, implies that the validity of this subfamily might need to be reevaluated and a new phylogenetic approach should be provided. The short rostrum concomitant with the brachycephalic skull and big orbits (Figs. 8 and 9) are probably a consequence of a paedomorphic trend (Gould 1977; McKinney and McNamara 1991), which is suggested by the transitional rostrum shape of the fetus of *P. blainvillei* (Fig. 9). In other Inioidea and Lipotidae such as *Inia*, *Lipotes*, and, to a lesser degree, *Pontoporia*, there is apparently a peramorphic trend (Gould 1977; McKinney and McNamara 1991) that presents a very large rostrum. The paedomorphic short rostrum can be used to diagnose the short-faced form of *B. mazeasi*, but not a rostrum shorter than the braincase as suggested by Muizon (1988a), an artifact of using a juvenile as holotype. In adults of the short-faced *B. mazeasi*, the rostrum and braincase are of about equal length.

The dendogram of Muizon (1988b:164–166, figure 1) apparently was not constructed using cladistic algorithms, generating only 1 hypothesis with no consistency measures (i.e., consistency index, retention index, and most parsimonious trees). Following Muizon's approach, the characters that define Pontoporiinae are the reappearance of a lateral lamina of the pterygoid (character 33) and acquisition of a symmetrical vertex (character 34). However, the 1st character is not well known in *Pontistes*, *Pliopontos*, and *Brachydelphis*. On the other hand, the symmetry found in the vertex of *Brachydelphis* is variable and the extant *P. blainvillei* and specimens from the Pleistocene have a slightly asymmetrical vertex (Ribeiro et al. 1998; C. S. Gutstein, pers. obs.). The interpretation of this character (symmetry) as a derived state in the Pontoporiidae was broadly used because Heyning (1989) described soft tissue of *Pontoporia* as asymmetric (see also Cranford et al. 1996). Nevertheless, these studies also show a disconnection between soft-tissue and bony asymmetry or symmetry of the odontocete face. These observations caution us against using this trait until its actual variability is better understood.

The Inioidea clade was defined by Muizon (1988b:164–166, figure 1) by presenting the following cranial characters: lateral lamina of palatine fused to maxilla (character 21); prominent premaxillary plate (= inflated spiracular plate; character 22); premaxilla nearly in contact medially with medial borders equidistant along all their length (character 23), dorsal erection of lateral border of maxilla above temporal fossa and orbit and reduction of the roof of temporal fossa (character 24), and narial fossa semicircular and not cordiform (character 25). From these characters, the only one surely present in *B. mazeasi* is character 22. Character 21 is absent because a visible suture of the maxilla and palatine was observed even

in a senile specimen; characters 23 and 25 were found to be variable. Actually character 23 is essentially not well known because the rostrum and premaxillae medial borders are often broken; and character 24 also is absent, by presenting a wide roof for the temporal fossa and not the erection of the border of the maxilla. We found that the variability of several cranial characters does not fit their previous use to argue phylogenetic relationships of clades related to *B. mazeasi* and *P. blainvillei*.

In contrast with the conclusions of Muizon (1988a, 1988b), a recent phylogenetic proposition places *Brachydelphis* as the sister group of Inioidea + Lipotoidea + platanistoids (Geisler and Sanders 2003). The characters that support this hypothesis were corroborated in this revision (see diagnosis). However this analysis is not conclusive because fossil taxa probably related to *Brachydelphis* are not included.

The problems with grouping the Platanistoidea are the paleobiogeographic implications. Geisler and Sanders (2003) claimed a single marine ancestry and hypothesized that most extinct platanistoids had a high tolerance for freshwater. The records of *Brachydelphis* and *Pliopontos* are from shallow marine sediments of Peru (Pisco Formation—Muizon 1988a; Muizon and DeVries 1985) and marine environment of Chile (Bahía Inglesa Formation) with influence of the Copiapó fluvial system (Achurra 2004). *Pontistes* comes from the epicontinental sea of the Paraná Formation (Argentina—Cione et al. 2000). This environmental characterization is consistent with the biology of *P. blainvillei* (Cremer and Simões-Lopes 2005). The recent records of Pontoporiidae-related taxa (*P. minima*—Lambert and Post 2005) from the North Sea show that these taxa probably were more widespread during the Neogene. However, a phylogenetic analysis with all the possible related fossil taxa should be performed to clarify this issue.

RESUMEN

Brachydelphis mazeasi Muizon, 1988a, de la Formación Pisco (Mioceno Medio, Perú), es un odontoceto originalmente conocido sobre la base de dos cráneos incompletos y unos pocos elementos post-craneales asociados, asignados a la familia Pontoporiidae, y a la subfamilia Brachydelphininae (= Brachydelphinae) creada para incluir a este género. En el presente trabajo, el holotipo es considerado un juvenil ya que no presenta septos alveolares y presenta suturas craneales ampliamente abiertas. Consecuentemente, algunos de los caracteres diagnósticos, más bien corresponden a características juveniles y no tienen significado taxonómico. Aquí, ofrecemos un enfoque más detallado de la morfología y variación de este taxón, con nuevos especimenes de las formaciones Pisco y Bahía Inglesa (Mioceno Tardío, Chile). Se plantea una revisión de la descripción original del género, comparada a otros taxa del clado Inioidea. Adicionalmente, es llevada a cabo una comparación con *Pontoporia blainvillei* (Pontoporiidae viviente) por análisis de morfometría (geométrica y tradicional). La variación de formas de especimenes de fetos, juveniles y adultos de *P. blainvillei* fue comparada a lo observado en especimenes juveniles y adultos de *B. mazeasi* para evaluar la variación ontogenética, individual, y interespecífica.

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