

# A new diminutive fossil ziphiid from the deep-sea floor off northern Chile and some remarks on the body size evolution and palaeobiogeography of the beaked whales

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The evolutionary history of the beaked whales (Ziphiidae), odontocetes nowadays adapted to deep diving, is well known thanks to a significant fossil record mainly from the deep ocean floors. A partial cranium of a ziphiid recovered from Plio-Pleistocene deep sea deposits (about 1000 m) off the port of Pisagua, northern Chile, during fishing activity is here described and referred to the new species *Ihlangesi changoensis*. *Ihlangesi changoensis* differs from the type species *Ihlangesi saldanhae*, from the sea floor off South Africa, by having a more elongated premaxillary sac fossa and consequently a more anteriorly located premaxillary foramen; dorsal margin of each premaxillary crest sloping markedly ventrolaterally and generating an acute dorsal profile of the vertex in anterior view; less anterolateral extension of the right nasal forming part of the premaxillary crest; lateral margins of the nasals not anteriorly diverging but weakly convex; nasofrontal suture anteriorly pointed. The phylogeny supports a sister-taxon relationship between *I. changoensis* and *I. saldanhae*, both members of the crown ziphiids Hyperoodontinae. *Ihlangesi changoensis* shares with *I. saldanhae* and other fossil ziphiids a small body size (estimated length 3.5 m) supporting the hypothesis that in the past small beaked whales (<4 m) were more common than today. Such recent shift of the ziphiids towards a larger size could be the result of a progressive change of diet from fish to cephalopods, to the competition with the delphinids, and the predatory impact of the white shark *Carcharodon carcharias* and/or of the killer whale *Orcinus orca*. This new Chilean ziphiid further supports the hypothesis that crown beaked whales originated and firstly dispersed in the oceanic waters of the Southern Hemisphere. Their radiation and geographical distribution could have been driven by the southern oceanic circulation and related localized concentration of trophic resources in high productivity upwelling areas.

Key words: Mammalia, Cetacea, Ziphiidae, Cenozoic, Southeastern Pacific, South America.

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## Introduction

The beaked whales (family Ziphiidae) are the most enigmatic among the cetaceans, due to the deep-sea habits and elusive behaviour of their extant species (Ellis and Mead 2017; MacLeod 2018). Their skulls are characterized by an elevated vertex, anteriorly well developed pterygoid hamuli and one or two pairs of apical or subapical mandibular teeth being more developed in the males (tusks) and generally combined with a rostral pachyostose (Moore 1968; Heyning

1989). Beaked whales also display an evolutionary tendency to reduce the number of functional teeth as an adaptation to suction feeding in deep waters (Bianucci et al. 2016b).

These medium to large-sized odontocetes comprise 24 extant species distributed in 6 genera (*Berardius*, *Hyperoodon*, *Indopacetus*, *Mesoplodon*, *Tasmacetus*, and *Ziphius*) (Mead 1989; Dalebout et al. 2002; Yamada et al. 2019) and, after Delphinidae, they represent the second richest family of cetaceans in species number.

The evolutionary history of beaked whales was almost unknown until a few decades ago, but recently many fossils

have been discovered and many new genera and species have been described highlighting that the extant high diversity of this family is the consequence of a large radiation having its maximum intensity towards the end of the Miocene (Bianucci et al. 2016b).

Many fossil remains of ziphiids come from Mio-Pliocene marine deposits exposed in Europe and North America, including both old (e.g., Bianucci 1997; Lambert 2005; Lambert and Louwey 2006, 2016) and recent acquisitions (Bianucci et al. 1992, 1994, 2016a, 2019; Bianucci and Post 2005; Fuller and Godfrey 2007; Post et al. 2008; Ramassamy 2016). Outside of these two continents, the remains found in Japan (Tanaka et al. 2019; Kawatani and Kohno 2021), Argentina (Buono and Cozzuol 2013) and Peru (Bianucci et al. 2016b) are the more significant. In particular, the fossils of beaked whales from the Upper Miocene deposits of the Pisco and Sacaco basins in Peru represent the best preserved remains of this family due their completeness and quality of preservation. Many of these fossils belong to the stem beaked whales *Messapicetus gregarius* and *Ninoziphius platyrostris*, two species featured by elongated rostrum and mandibles, both still bearing a complete set of functional teeth (Muizon 1984; Bianucci et al. 2010; Lambert et al. 2010, 2015, 2013; Ramassamy et al. 2018). The discovery of the presumed last meal associated with a *M. gregarius* skeleton allowed the authors to hypothesize a diet based on epipelagic fish of these basal beaked whales (Lambert et al. 2015). By contrast *Nazcacetus urbinai*, also from Peru, already displays an incipient dental reduction and was placed within the crown ziphiids (Lambert et al. 2009; Bianucci et al. 2016b).

Additionally, abundant cranial material has been recovered from the seafloor, mainly from phosphorites beds, of most oceans off Iberian Peninsula (Bianucci et al. 2013; Miján et al. 2017), Faroe Islands (Post and Jensen 2013), Florida and California (Whitmore et al. 1986), Japan (Horikawa et al. 1987; Tazaki et al. 1987; Miyazaki and Hasegawa 1992), Peru (Eastman 1906), Brazil (Ichishima et al. 2017), South Africa (Bianucci et al. 2007, 2008), New Zealand (Fordyce and Cullen 1979), Crozed and Kergelen islands (Robineau 1973; Lambert et al. 2018), and the Antarctic (Gol'din and Vishnyakova 2013). Such material indicates that the beaked whales in the past had an incredible disparity including bizarre morphologies, most having a restricted geographical distribution. Furthermore, many species and genera are represented by a single specimen suggesting that the diversity of the ziphiids in the past is still far from being fully understood.

Despite the existence of sedimentary basins off northern Chile (Fischer and Raitt 1962; Coulbourn and Moberly 1977; Coulbourn 1981) and extensive marine Miocene–Pleistocene formations within Chile itself, some of these bearing numerous cetacean fossils (Walsh 2001; Gutstein et al. 2008, 2015; Pyenson et al. 2014), beaked whale remains are documented only on the basis of three fragmentary poorly diagnostic remains (Sielfeld 1995; Walsh 2001; Gutstein et al. 2008, 2015).

The aim of this study is to describe a fossil skull of ziphiid collected off the Chilean coast at a depth of ap-

proximately 1000 m, while fishing for Patagonian toothfish *Dissostichus eleginoides*. The body size evolution and palaeobiogeography of beaked whales are also discussed.

*Nomenclatural acts.*—This published work and the nomenclatural acts it contains have been registered in ZooBank: [lsid:zoobank.org/pub:73F67704-27DA-4993-88D5-E5E1E-9A2EE13](https://zoobank.org/pub:73F67704-27DA-4993-88D5-E5E1E-9A2EE13).

*Institutional abbreviations.*—MUAP, Zoological Collection, Universidad Arturo Prat, Iquique, Chile; SAM, Iziko South African Museum, Cape Town, South Africa.

## Geological setting

As for other similar finds collected on the deep seafloor, providing a high-resolution stratigraphic overview of the fossil cranium of the ziphiid here examined is not easy, since it is difficult to carry out direct observations of the strata outcropping in the discovery area. Furthermore, the cranium is not associated with any sediment whose examination could have possibly allowed the identification of micro- or macrofossils useful for biostratigraphic analyses. However, the data provided by several articles on the tectonics and stratigraphy of the find area provide us with indirect but valuable information on the age of this fossil ziphiid. Indeed, the deep seafloor where the fossil cranium has been collected is located on the oceanward forearc of the northern Chile continental margin where the Nazca Plate subducts beneath the South American Plate (Armijo et al. 2015). This oceanward forearc deepens from 400 to 1500 m and holds a string of interconnected basins, named, from north to south, Arequipa, Arica, and Iquique basins (Coulbourn and Moberly 1977; Coulbourn 1981). Considering the geographical position and the depth of the sea where it was found, the fossil skull comes from the Iquique Basin or the southern part of the Arica basin.

The analysis of seismic section profiles and a few collected samples indicate that these basins are filled by Cenozoic clays, muds, turbidites, pelagic, and hemipelagic marine sediments (Fischer and Raitt 1962; Coulbourn and Moberly 1977; Coulbourn 1981; Moberly et al. 1982; Henriquez et al. 1981; Von Huene et al. 1999; Geersen et al. 2015, 2018a, b; Ranero et al. 2006; Sallarès and Ranero 2005). More recently, Gonzáles et al. (2023), based on a seismic section profile off Pisagua, distinguished three stratigraphical units covering the seafloor, named, from bottom to top, SU1, SU2 and SU3, being SU3 the unit filling the Iquique Basin. According to the same authors SU3 has likely been deposited after most of the deformation took place in this region. Since Gonzáles et al. (2003) referred the last extensional deformations of the northern Coastal Cordillera of Chile to the Pliocene-Late Pleistocene, a Plio-Pleistocene age for the SU3 sedimentary unit containing the ziphiid cranium examined is here proposed.

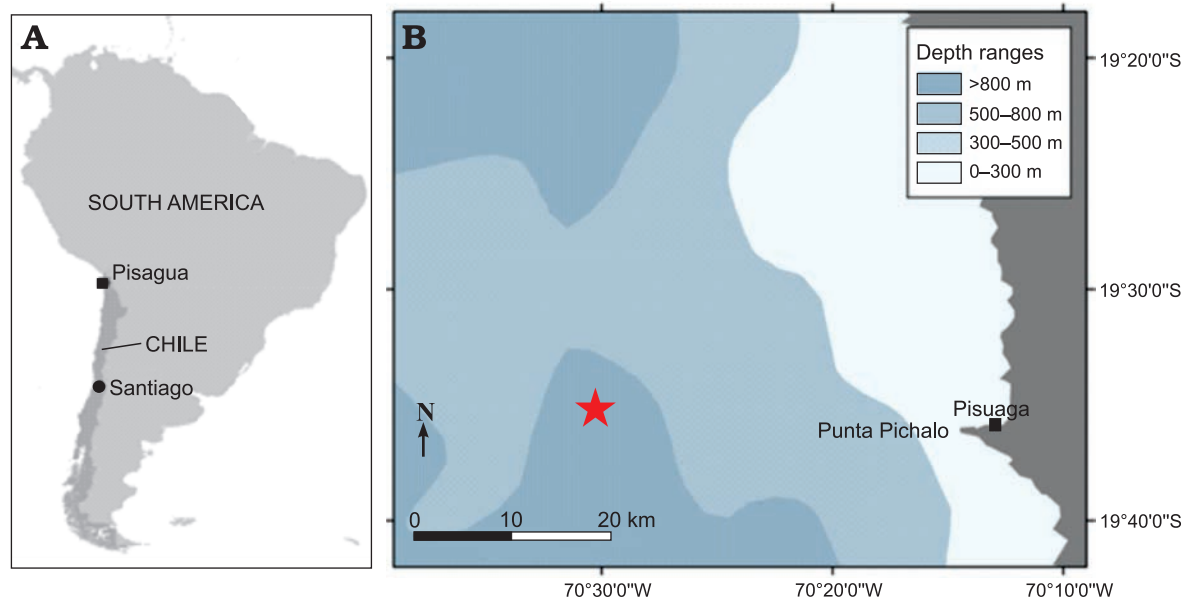


Fig. 1. A. Schematic map providing the position of Pisagua in South America. B. Schematic map of Northern Chile coast around Pisagua and sea floor bathymetry showing approximative discovery locality of the holotype MUAP(MM)-068 cranium of the beaked whale *Ihlangesi changoensis* sp. nov. at a depth of 1000 m (star).

## Material and methods

The fossil here examined is a partial cranium recovered from the ocean floor, at a depth of approximately 1000 m, while fishing for Patagonian toothfish *Dissostichus eleginoides* in May 2022. The collection area is located off the port of Pisagua, Northern Chile (Fig. 1). The fossil was collected by Dany Manzo in the fishing boat "La Huayca" and is deposited in the Zoological Collection of the Universidad Arturo Prat, Iquique, Chile. The fossil is strongly mineralized, as generally the ziphiid skull found in deep sea deposits, but it does not show phosphorite or manganese concretions adhering to the surface of bones.

The anatomical terms follow Mead and Fordyce (2009). The measurements mainly follow Ross (1984) and Lambert (2005).

**Phylogenetic analysis.**—The phylogenetic relationships of *Ihlangesi changoensis* with the other Ziphiidae are investigated here using the same methods and the same matrix as in Bianucci et al. (2016b), just adding, beside the new diagnosed *I. changoensis*, the two known species of *Khoikhoicetus* (*K. agulhasis* and *K. kergueleni*), both sharing several cranial similarities with *Ihlangesi* (see Appendix 1). The modified matrix includes 37 taxa (31 belonging to the family Ziphiidae), coded for 51 morphological characters (28 binary, 17 multistate and ordered, and six multistate and unordered) (see SOM, Supplementary Online Material available at [http://app.pan.pl/SOM/app68-Bianucci\\_etal\\_SOM.pdf](http://app.pan.pl/SOM/app68-Bianucci_etal_SOM.pdf)). The analysis was executed with the software PAUP (v. 4.0, Swofford 2002), using the branch-and-bound algorithm. The characters were analyzed under both equal and implied weight. In the phylogenetic analysis here proposed we have not modified the state of the characters of the

genera *Beneziphius* and *Berardius* to take into account the species *Beneziphius cetariensis*, *Berardius kobayashii*, and *Berardius minimus* recently described respectively by Miján et al. (2017), Kawatani and Kohno (2021), and Yamada et al. (2019). Indeed, these taxa are phylogenetically distant from *I. changoensis* and reviewing the entire phylogeny of the beaked whales is outside the aim of this work.

**Body size.**—The body size of the new ziphiid here described and of the other fossil beaked whale examined in the discussion paragraph are estimated using the following equation proposed by Bianucci et al. (2008: som: fig. b; see also Lambert et al. 2013):  $y = 9.464x + 1137$ , where  $y$  is the body length and  $x$  the width of the cranium (postorbital width), both in millimetres.

## Systematic palaeontology

Cetacea Brisson, 1762

Odontoceti Flower, 1867

Ziphiidae Gray, 1850

Hyperoodontinae Gray, 1866  
(sensu Bianucci et al. 2007)

Genus *Ihlangesi* Bianucci, Lambert, and Post, 2007

*Type species: Ihlangesi saldanhae* Bianucci, Lambert, and Post, 2007, by original designation; from the sea floor off Saldanha Bay, South Africa; age unknown.

*Species included:* Type species and *Ihlangesi changoensis* sp. nov.

**Emended diagnosis.**—*Ihlangesi* differs from all other Hyperoodontinae for the following unique combination of characters: narrow rostrum in dorsal view; presence of a distinct

maxillary tubercle and a wide and shallow prominent notch anteromedial to the antorbital notch; dorsal infraorbital foramen close to the prominent notch at the rostrum base; premaxillary foramen distinctly posterior to the antorbital notch; roughly flat dorsal surface of the preorbital area without distinct maxillary crest; moderate elevation of the vertex (less than in the other hyperoodontines but *Khoikhoicetus*); ascending process of the premaxilla in lateral view concave with posterodorsal portion partly overhanging the bony nares; transverse distance between the lateral margins of the premaxillary crests less than in the other hyperoodontines; wide space between the premaxillary crests (greater than in *Mesoplodon* and *Hyperoodon*); inclusion of the nasal into the premaxillary crest with the at least the left nasal covering about half the length of the median margin of the crest; deep anteromedian excavation of the nasals.

### *Ihlengesi changoensis* sp. nov.

Figs. 2–5, Table 1.

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*Etymology*: From “Changos”, the indigenous people and fishermen, who originally inhabited the coast of Northern Chile.

*Holotype*: MUAP(MM)-068, a partial cranium including the complete rostrum, the medial facial area (premaxillary sac fossae and vertex) and part of both supraorbital regions.

*Type locality*: Off the port of Pisagua (19°35'50"S; 70°12'48"W), Northern Chile, at a depth of 1000 m (Fig. 1), collected by Dany Manzo in May 2022.

*Type horizon*: Iquique Basin, Plio-Pleistocene (González et al. 2023).

*Diagnosis*.—*Ihlengesi changoensis* sp. nov. differs from *Ihlengesi saldanhae* in the following characters: more elongated premaxillary sac fossa and consequently premaxillary foramen more anteriorly located (ratio between the longitudinal distance between the right premaxillary foramen and the rostrum base and the width of rostrum base equals 0.10 contra 0.32 in *I. saldanhae*); dorsal margin of each premaxillary crest sloping markedly ventrolaterally and generating an acute dorsal profile of the vertex in anterior view (rounded profile in *I. saldanhae*); less anterolateral extension of the right nasal forming part of the premaxillary crest; lateral margins of the nasals not anteriorly diverging but weakly convex; nasofrontal suture not convex posteriorly but anteriorly pointed.

*Description*.—Judging from the size of the cranium (Table 1), *Ihlengesi changoensis* was a small ziphiid which, like *Ihlengesi saldanhae*, did not reach 4 m in length. Indeed, by roughly estimating the postorbital width of the cranium to 250 mm and applying the aforementioned equation proposed by Bianucci et al. (2008), the body length results to be 3.5 m, a value close to that estimated for *I. saldanhae* (3.1 m). Therefore, based on these estimations, species of *Ihlengesi* were smaller than all extant ziphiids with the exception of the pygmy beaked whale *Mesoplodon peruvianus* (maximum body length 3.72 m; Reyes et al. 1991).

The complete rostrum is moderately elongated and, similarly to the paratype of *Ihlengesi saldanhae* (SAM PQ

Table 1. Measurements (in mm) of the crania of *Ihlengesi changoensis* sp. nov. and *Ihlengesi saldanhae* (measurements from Bianucci et al. 2007). Abbreviations: e, estimate; –, no data.

	<i>Ihlengesi changoensis</i> sp. nov.		<i>Ihlengesi saldanhae</i> Bianucci, Lambert, and Post, 2007	
	MUAP(MM)-068 (holotype)		SAM PQ 2792 (holotype)	SAM PQ 69673 (paratype)
Length of rostrum	540		–	–
Width of rostrum at mid-length	38		–	–
Width of rostrum base at prominent notch	104		108	104
Width of rostrum base at antorbital notch	180		e143	e142
Width of premaxillae at rostrum base (anterior notch)	55		47	–
Distance rostrum base—anterior apex of palatine	120		–	–
Preorbital width of skull	e230		–	–
Longitudinal distance right premaxillary foramen—antero-median corner of naris	47		31	–
Width of premaxillary sac fossae	130		105	101
Width of right premaxillary sac fossa	69		51	e52
Width of left premaxillary sac fossa	55		46	44
Width of bony nares	45		49	–
Minimum width of right ascending process of premaxilla	32		25	–
Width of premaxillary crests	110		103	–
Width of right premaxillary crest	59		47	–
Width of left premaxillary crest	42		38	–
Minimum distance between premaxillary crests	34		34	–
Maximum width of nasals	41		52	–
Length of medial suture of nasals on vertex	45		e45	–
Minimum posterior distance between maxillae	37		32	–

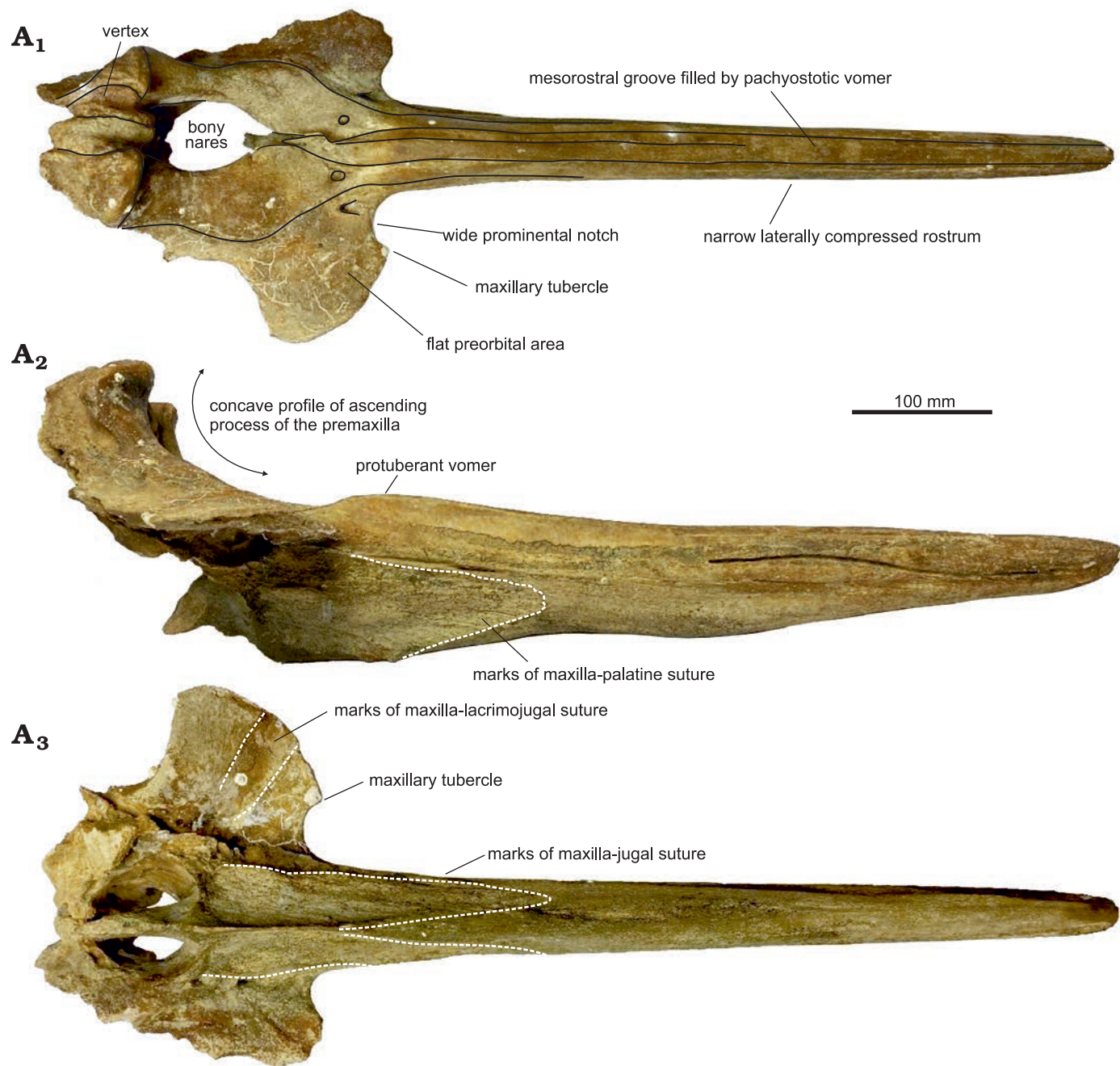


Fig. 2. Holotype of the beaked whale *Ihlangesi changoensis* sp. nov. (MUAP(MM)-068) from the sea floor off Pisagua, Northern Chile; Plio-Pleistocene. Cranium in dorsal (A<sub>1</sub>), right lateral (A<sub>2</sub>), and ventral (A<sub>3</sub>) views.

69673), shows a strong lateral compression generating a narrow dorsal profile and a transverse section with a height significantly greater than its width (Figs. 2, 5). Due to its narrow dorsal shape, the rostrum of *Ihlangesi changoensis* clearly differs from *Khoikhoicetus* spp. Indeed, the rostrum of this latter genus is significantly transversely wider than in *I. changoensis*, a feature particularly marked in *Khoikhoicetus kergueleni* having a triangular outline of the rostrum in dorsal view (Lambert et al. 2018).

The medial margins of the premaxillae on the rostrum never contact medially and the mesorostral groove is filled by the pachyosteosclerotic vomer along its whole rostral

portion (Fig. 2A<sub>1</sub>), a feature that, at least in the extant ziphiids, is only observed in adult males (Bianucci et al. 2016b). The vomer greatly inflates towards the posterior portion of the rostrum as in the holotype of *Ihlangesi saldanhae* (SAM PQ 2792). A median longitudinal suture between the lateral walls of the vomer in the rostrum base area is visible as in all hyperoodontines.

In ventral view the rostrum does not show a distinct alveolar groove whereas a clear maxilla-palatine suture extends about 12 cm anterior to the antorbital notch (Fig. 2A<sub>3</sub>).

Medial to the narrow antorbital notch, a distinct maxillary tubercle is visible. The position the suture between the

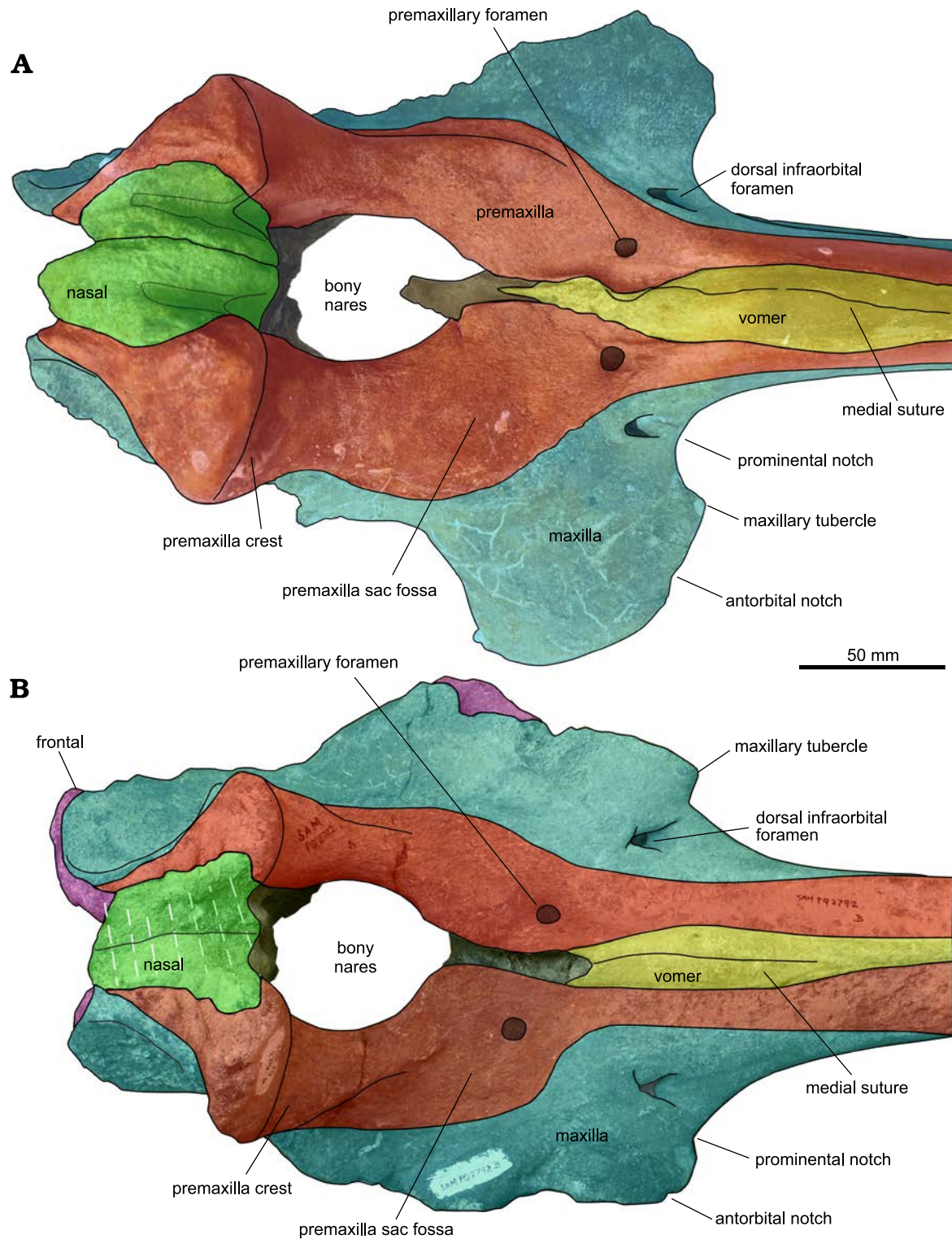


Fig. 3. Comparison of the neurocrania and the posterior portion of the rostra in dorsal view in two beaked whales. **A.** The holotype of *Ihlengesi changoensis* sp. nov. (MUAP(MM)-068) from the sea floor off Pisagua, Northern Chile; Plio-Pleistocene. **B.** The holotype of *Ihlengesi saldanhae* (SAM PQ 2792) from the sea floor off Saldanha Bay, South Africa; age unknown.

maxilla and the missing lacrimojugal complex, well visible in the ventral surface of the left side of the neurocranium, supports that this tip, apparently laterally located to the rostrum base, is actually the maxillary tubercle. Indeed, this suture is located well lateral to the lateral margin of

the rostrum, leaving exposed ventrally a wide portion of the maxilla that anteriorly bears what we interpret as maxillary tubercle. The presence of a well-defined maxillary tubercle separated from the lateral margin of the rostrum by a distinct prominent notch is a feature shared by most

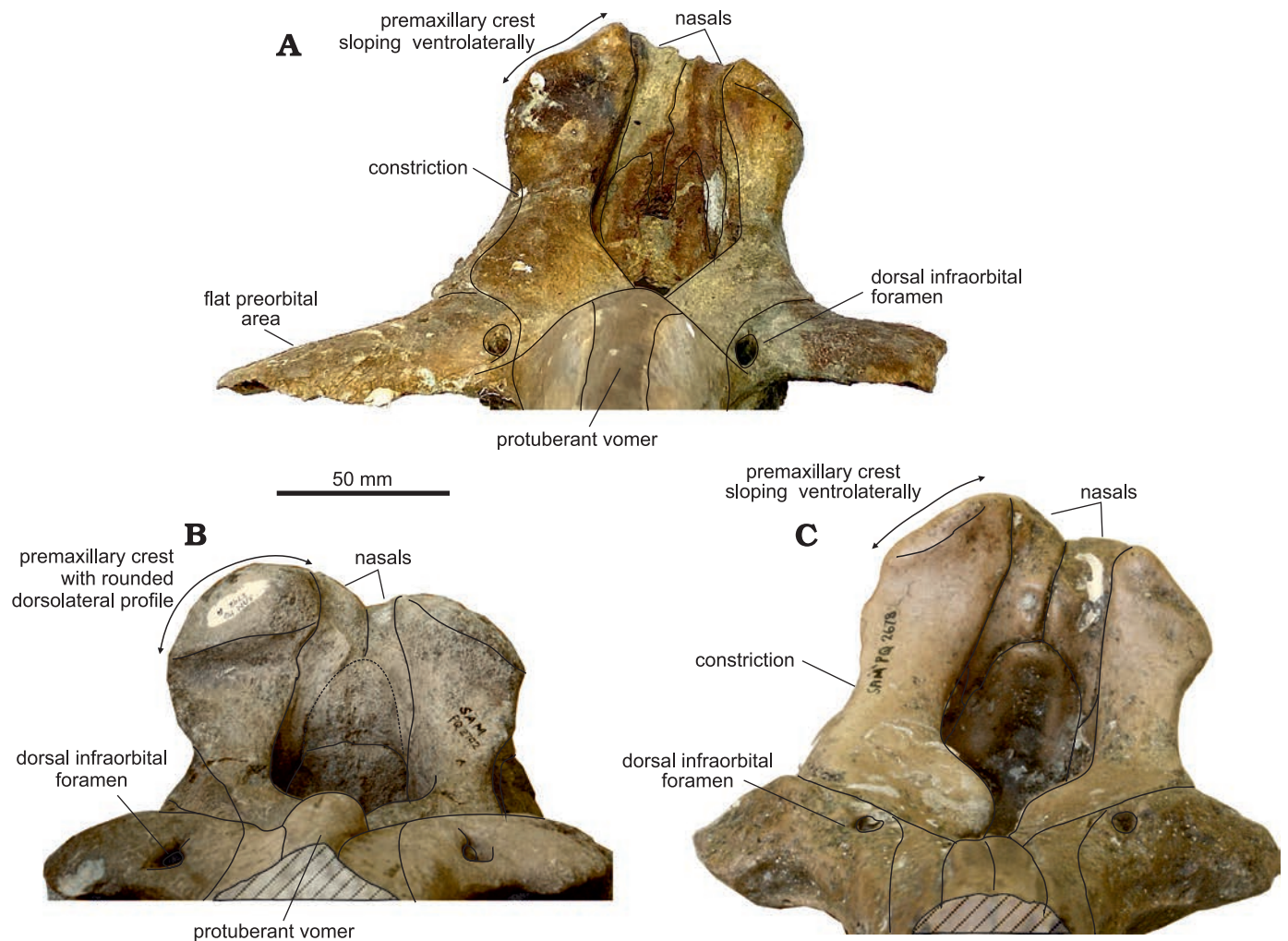


Fig. 4. Comparison of the crania in anterior view of the holotype of three beaked whales. **A.** *Ihlengesi changoensis* sp. nov. (MUAP(MM)-068) from the sea floor off Pisagua, Northern Chile; Plio-Pleistocene. **B.** The holotype of *Ihlengesi saldanhae* (SAM PQ 2792) from the sea floor off Saldanha Bay, South Africa; age unknown. **C.** The holotype *Khoikhoicetus agulhasis* (SAM PQ 2678) from the sea floor off Cape Agulhas, South Africa; age unknown. Diagonal lines represent broken surfaces.

hyperoodontines including *Ihlengesi saldanhae* but absent in *Khoikhoicetus* spp.

The prominent notch of the *Ihlengesi changoensis* holotype is transversely wide, U-shaped and shallow as in the paratype of *I. saldanhae*, whereas in the *I. saldanhae* holotype this notch is V-shaped and transversely shorter, suggesting that this character is subject to intraspecific variation (Fig. 3).

The dorsal surface of the preorbital area is roughly flat without a distinctive maxillary crest, as in *I. saldanhae*, while in most of the other crown Ziphiidae, including *Khoikhoicetus*, the maxillary crest is present and generally elevated to form a peculiar dome.

Both the right and the left maxilla are pierced by a single dorsal infraorbital foramen near the prominent notch, 13- and 7-mm posterior to the rostrum base, respectively. Similar dorsal infraorbital foramina are observed in *Ihlengesi saldanhae* but more posteriorly located in *I. saldanhae* paratype.

The right and the left premaxillary foramina are distinctly posterior to the rostrum base (5 mm) but less than in *Ihlengesi saldanhae* as well quantified by the ratio between the longitudinal distance between the right premaxillary foramen and the rostrum base and the width of rostrum base, being this ratio equal to 0.10 in *I. changoensis* against 0.34–0.32 in *I. saldanhae*. This significant difference in the position of the premaxillary foramina is related to the greater anteroposterior extension of the premaxillary sac fossae in *I. changoensis* compared to *I. saldanhae*. Indeed, the premaxillary sac fossae of *I. saldanhae* are unusually short so that this feature was previously considered an apomorphy of the *Ihlengesi* (Bianucci et al. 2007). Interestingly, in *I. saldanhae* the premaxillary foramina are distinctly posterior to the dorsal infraorbital foramina, an unusual condition in beaked whales. The premaxillary foramina of *I. changoensis* are posteriorly located to the dorsal infraorbital foramina but to a lesser degree than *I. saldanhae*. Regardless the position of the foramina with respect to the

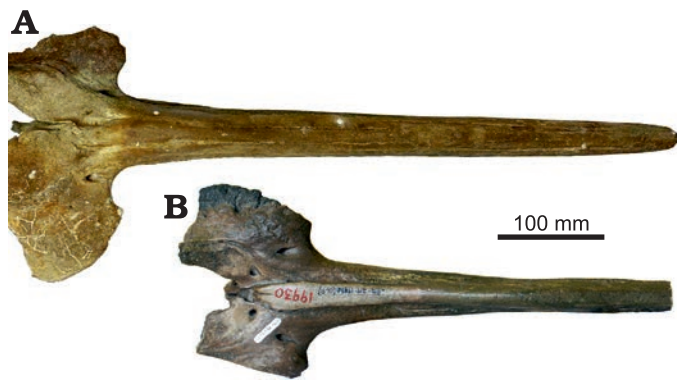


Fig. 5. Comparison of the rostra and posterior portion of the neurocrania in dorsal view of two beaked whales. **A.** The holotype of *Ihlengesi changoensis* sp. nov. (MUAP(MM)-068) from the sea floor off Pisagua, Northern Chile; Plio-Pleistocene. **B.** The paratype of *Ihlengesi saldanhae* (SAM PQ 69673) from the sea floor off Saldanha Bay, South Africa; age unknown.

rostrum base, in all hyperoodontines, except some species of *Mesoplodon* (e.g., *Mesoplodon grayi* von Haast, 1876), the premaxillary foramina are always roughly at the same level or weakly anterior to the maxillary foramina.

The weakly concave premaxillary sac fossae of *I. changoensis* are distinctly asymmetrical as in *I. saldanhae*, being the right fossa transversally wider than the left fossa (ratio between the widths of the left and right premaxillary fossae = 0.78).

The ascending process of the premaxilla rises towards the vertex with its posterodorsal portion partly overhanging the bony nares (Fig. 2A<sub>2</sub>). Therefore, with the cranium in lateral view, the anterior profile of this portion of the ascending process of the premaxilla is clearly concave in *Ihlengesi changoensis* as in *I. saldanhae*, not straight and vertical as in *Khoikhoicetus* spp.

The vertex is moderately elevated as in *Ihlengesi saldanhae* and *Khoikhoicetus* spp. (ratio between the vertical distance between the dorsal margin of the maxilla at the rostrum base and the top of the vertex and the width of the premaxillary sac fossae between 0.70 and 1.0). All other hyperoodontines have a higher vertex (ratio > 1.0).

The ascending process of the premaxilla displays a strong constriction between premaxillary sac fossa and premaxillary crest (ratio between the minimal width of ascending process of the right premaxilla and the width of right premaxillary crest = 0.56).

As in *Ihlengesi saldanhae* and *Khoikhoicetus agulhasis*, the posterolaterally directed premaxillary crests are transversally narrower than in the other hyperoodontines (ratio between the transverse width of the premaxillary crests and the width of premaxillary sac fossae = ca. 1.0), whereas the distance between the premaxillary crests is greater than in *Mesoplodon* and *Hyperoodon* (ratio between the minimum distance between the right and left premaxillary crests and the width of the premaxillary sac fossae = 0.3).

The dorsal margin of each premaxillary crest slopes markedly ventrolaterally generating an acute dorsal profile of the vertex in anterior view, similarly to species of

*Mesoplodon*, *Hyperoodon*, *Khoikhoicetus* but not *Ihlengesi saldanhae*, this latter having premaxillary crests with a rounded dorsolateral profile (Fig. 4).

The elongated nasals (ratio between the length of medial suture of nasals on vertex and the maximum width of nasals = 1.1) show a deep anteromedial excavation on their joined dorsal surface as in the other hyperoodontines but *Indopacetus pacificus* (Longman, 1926). Due to a significant anterolateral expansion of the nasals forming part of the premaxillary crests, a deep notch is visible on the dorsal margin of each nasal, a feature not discernible in *Ihlengesi saldanhae* holotype due to the bad preservation of the vertex. The inclusion of the nasals in the premaxillary crests is significant, although less for the right than for the left nasal, a condition shared with *Khoikhoicetus* spp. rather than with *I. saldanhae* having a greater anterolateral expansion of the right nasal.

The lateral margins of the nasals are weakly convex as in *Khoikhoicetus* spp., not anteriorly diverging as in *Ihlengesi saldanhae*. The nasofrontal suture is anteriorly pointed as in *Khoikhoicetus* spp., not convex posteriorly as in *I. saldanhae*.

**Remarks.**—All characters listed in the diagnosis separating *Ihlengesi changoensis* from *Ihlengesi saldanhae* are shared with *Khoikhoicetus* spp. Indeed *Khoikhoicetus* is a hyperoodontine with a cranium roughly similar to *Ihlengesi* (i.e., for the size and for the moderate elevation of the vertex). Nevertheless *Khoikhoicetus* does not show many of the character above listed of the genus *Ihlengesi* (i.e., rostrum narrow in dorsal view, presence of a distinct maxillary tubercle and a wide and shallow prominent notch anteromedial to the antorbital notch; premaxillary foramen distinctly posterior to the antorbital notch, roughly flat dorsal surface of the preorbital area without distinct maxillary crest; ascending process of the premaxilla in lateral view concave with posterodorsal portion partly overhanging the bony nares) and therefore we consider reliable the appurtenance of the new Chilean species to *Ihlengesi* rather than *Khoikhoicetus*, being also supported by the phylogenetic analysis.

**Stratigraphic and geographic range.**—Type locality and horizon only.

## Phylogeny

As for the phylogeny in Bianucci et al. (2016b), the best result was obtained using implied weight analysis with constant  $K = 3$  (Goloboff 1993). This analysis generated a single most parsimonious tree, with tree length = 172, Goloboff fit = -37.65, CI = 0.48, and RI = 0.77 (Fig. 6). The addition of *Ihlengesi changoensis*, *Khoikhoicetus agulhasis*, and *Khoikhoicetus kergueleni* did not change the topology of the tree compared to the tree published in Bianucci et al. (2016b). Indeed, *I. changoensis* results to be sister taxon of *I. saldanhae* and *Ihlengesi* to be sister taxon of *Hyperoodon*, both in derived position within the Hyperoodontinae. *Khoikhoicetus*



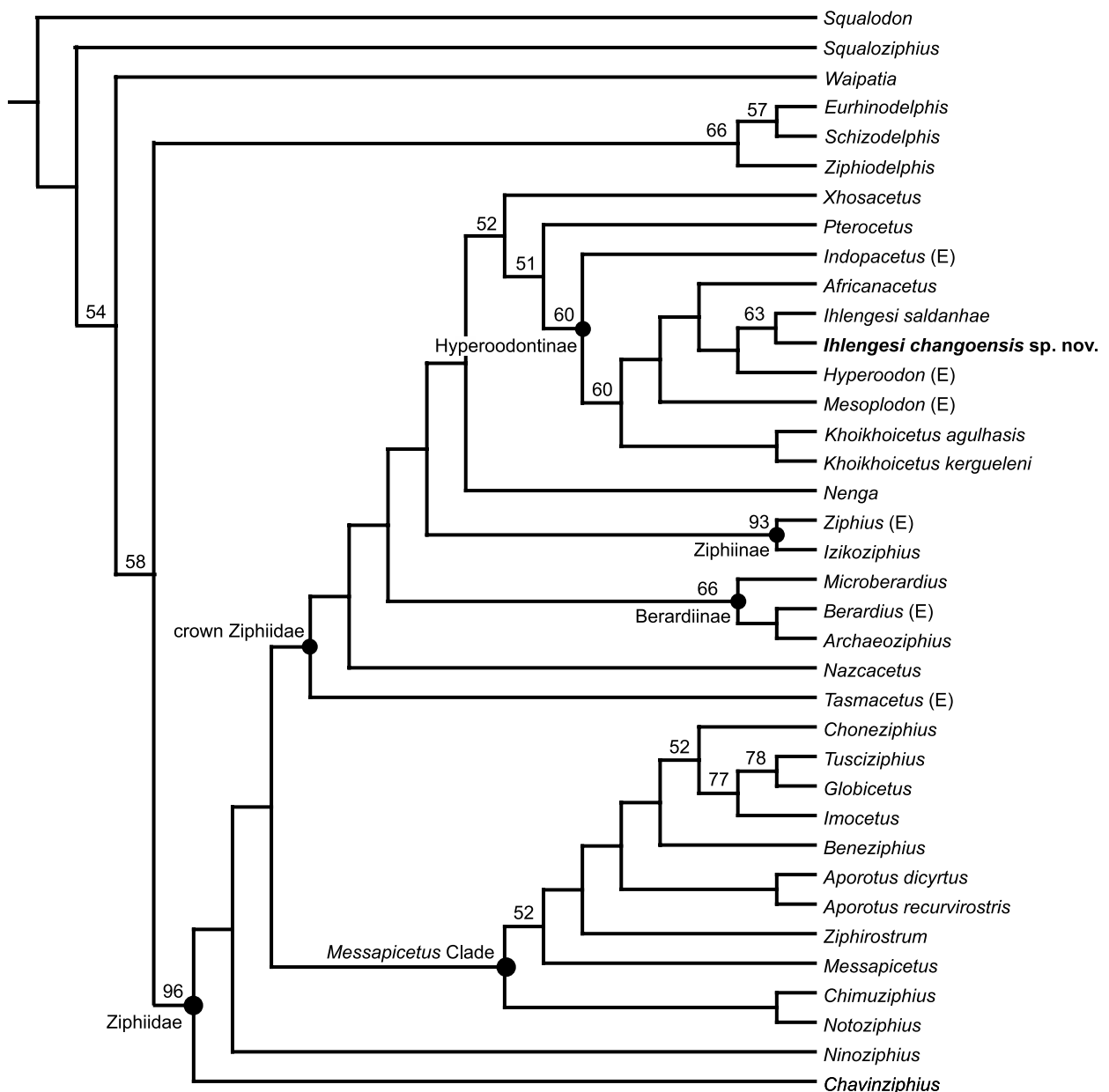


Fig. 6. Single most parsimonious tree of the heuristic search with downweighted homoplastic characters ( $K = 3$ ) showing the relationships of *Ihlengesi changoensis* sp. nov. (in bold) with the other ziphiids. Numbers associated with branches are bootstrap values. (E) genera with extant species. See text, Appendix 1, and Bianucci et al. (2016b) for data matrix and description of characters.

*kergueleni* is confirmed to be congeneric with *K. agulhasis*, both forming a clade basal to *Mesoplodon*. *Khoikhoicetus* was not included in the analysis by Bianucci et al. (2016b), whereas in the consensus tree of five most parsimonious cladograms published in Bianucci et al. (2007) it shows the same position than the

*Khoikhoicetus agulhasis* + *Khoikhoicetus kergueleni* clade of the analysis here proposed.

The two following reversals, that define the *Ihlengesi* clade, also support the close relationship of *Ihlengesi changoensis* with *I. saldanhae*:

- character 9 (elevation of the vertex) from state 2 to state 1: ratio between the vertical distance between the dorsal margin of the maxilla at the rostrum base and the top of

the vertex and the width of the premaxillary sac fossae between 0.7 and 1.0;

- character 11 (width of the premaxillary crests) from state 1 to state 0: ratio between the width of premaxillary crests and the width of premaxillary sac fossae  $< 1.0$ .

## Discussion

**Body size evolution.**—The estimated body size of *Ihlengesi changoensis* is compared with those of the other ziphiids and the evolution of body size amongst ziphiids is analysed putting this character in the most parsimonious cladogram pro-

duced by the phylogenetic analysis. This approach is similar to that in Lambert et al. (2013: fig. 16) but the selected body size categories are different: small size (3–4 m); medium size (4–5 m); medium-large size (5–7 m); and large size (6–11 m).

The obtained graph (Fig. 7) evidences a low disparity of body size within the stem ziphiids being all medium-sized apart from the small-sized *Chimuziphius* and the medium-large-sized *Imocetus* and *Tusciziphius*. The size disparity in the crown beaked whales appears greater being this wide clade represented by all four body size categories from the small size (e.g., *Ihlengesi*), to the large size of *Hyperoodon* and *Berardius*. These different sizes were independently achieved by parallel evolution several times during the evolution of the crown beaked whales.

Such changes in body size among extant and fossil ziphiids have been related, by Bianucci et al. (2008), to a dietary niche partitioning (different prey size) of species living in the same area (MacLeod et al. 2003) and to a wider exploration of the water column for foraging. The development of a larger body, in fact, improves the dive capacity of air-breathing vertebrates (Schreer and Kovacs 1997). Moreover, the progressive global climatic cooling culminating in the Quaternary glaciations could have contributed to the origin of the extant large beaked whale (i.e., *Berardius* and *Hyperoodon*) confined to the cold waters at high latitudes (Lambert et al. 2013; Bianucci et al. 2016b).

Interestingly, a small body size characterizes not only *Ihlengesi changoensis* and *I. saldanhae*, but also other four fossil species of crown ziphiids: *Archaeoziphius microglenoideus*, *Khoikhoicetus agulhasis*, *K. kergueleni*, *Microberardius africanus*, and *Nazcacetus urbinai*. Instead among the extant ziphiids only the pygmy beaked whale *Mesoplodon peruvianus* does not reach 4 m in length (Reyes et al. 1991). Based on few stomach contents analysed, *M. peruvianus* feeds only on fish (Reyes et al. 1991) while a diet preferentially based on cephalopods was observed in larger extant ziphiids (MacLeod et al. 2003). These data seem to suggest that *Ihlengesi changoensis* and other small fossil beaked whales had a predominantly piscivorous diet and that the drastic reduction in number of small species and concomitant appearance of large species in the extant ziphiid could at least in part be related to a shift towards a diet based mainly on octopuses and squids. In turn, this partial change of diet in the extant ziphiids could be due to feeding competition with the mainly fish-eater delphinids which have a recent explosive radiation. A similar but older competition had already been claimed, when observing that the extinction of the epipelagic feeder stem ziphiids coincides with the radiation of the delphinids (Lambert et al. 2015). Nevertheless, the case here reported concerns a more recent competition between bottom feeder crown ziphiids and ecologically related delphinids.

Predatory pressure may have also contributed to the extinction of small-sized beaked whales. Analysing the documented cases of active predation on cetaceans by the white shark *Carcharodon carcharias*, Long and Jones

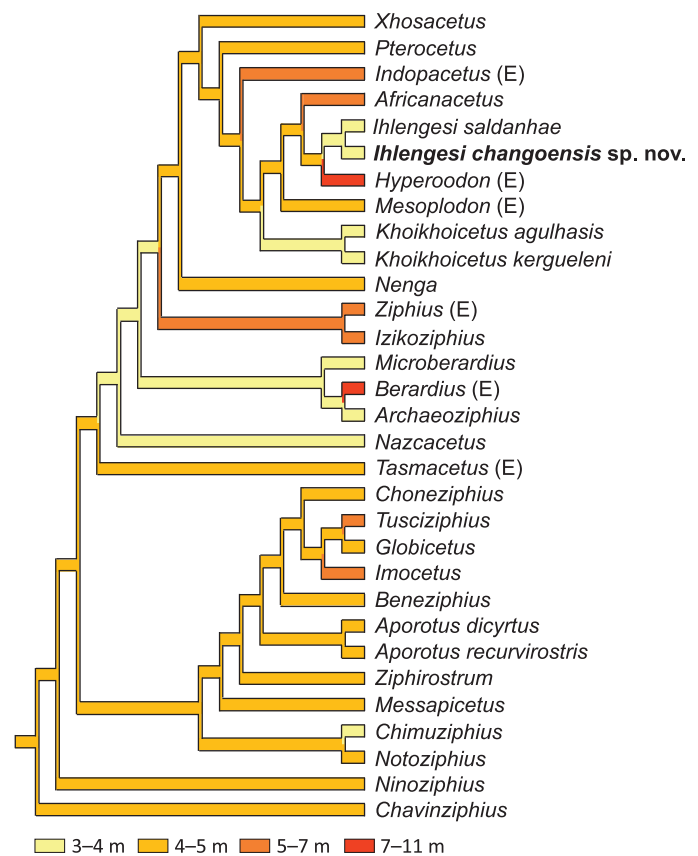


Fig. 7. Body size evolution amongst ziphiids. The tree is the single most parsimonious as presented in Fig. 6. (E) genera with extant species. See text and Lambert et al. (2013: fig. 16) for details.

(1996) noted that the biggest reported preys are two juvenile *Mesoplodon stejnegeri* and *Ziphius cavirostris*, about 3 m long. According to the same authors this datum implies an upper limit for the prey of white sharks due to their maximum body size that generally does not exceed 6 m. The shift of the minimum size towards 4 m in the extant beaked whales could therefore be interpreted as a consequence of the predatory impact of white shark whose appearance is reported toward the end of Messinian (Ehret et al. 2012). The weakness of this hypothesis is that it is not possible to well correlate the change in size of the beaked whales with the evolution of *C. carcharias* and other large predatory sharks due to the poor constrain of the ages of *Ihlengesi changoensis* and of most of the other small fossil beaked whales. It should be also considered that other macropredatory sharks lived before and some (e.g., the giant *Carcharocles megalodon*) also together with *C. carcharias*, becoming extinct well after the appearance of the white shark (Pimiento and Clements 2014; Boessenecker et al. 2019). The selective pressure on beaked whales by these large sharks may have been very strong, shifting the lower limit of body size of the beaked whale even higher than today. Therefore, the impact of the shark predation on the evolution of the size of the beaked whales is still far from being clarified.

Another macropredator that could have driven the recent evolution of beaked whales is the killer whale *Orcinus orca*

(Aguilar de Soto et al. 2020). Indeed, Bianucci et al. (2022) suggested that the ability to prey on tetrapods, including other cetaceans, has been achieved quite recently (possibly during the Pleistocene) in the *O. orca* lineage. However, even if there are some documented evidences of predation by killer whales on beaked whales (Jefferson et al. 1991; Wellard et al. 2016), it is unclear how much this predatory pressure may have directly influenced the reduction in the number of species of small ziphiids. In fact, unlike sharks, killer whales can attack prey much larger than themselves by hunting in groups (Ford 2018). However, the predation by *Orcinus orca* could have indirectly favoured the increase in body size of beaked whales by progressively pushing them towards deeper waters. Indeed, as mentioned above, the diving capacity is greater in larger cetaceans and therefore beaked whales might have suffered an indirect selective pressure towards their present large size.

**Palaeobiogeography.**—The attribution of the Chilean fossil skull to a hyperoodontine further supports the hypothesis that the crown beaked whales originated and radiated in the oceanic waters of the southern hemisphere. In fact, all the beaked-whale fossil assemblages found on the sea floor of the southern oceans (Fig. 8) are characterized by the absence of stem ziphiids (Whitmore et al. 1986; Bianucci et al. 2007; Gol'din and Vishnyakova 2013; Ichishima et al. 2017; Lambert et al. 2018), while stem ziphiids are abundant and diversified in the deep sea assemblages of North Atlantic (Bianucci et al. 2013; Miján et al. 2017). This geographic difference has been related to a phenomenon of convergent evolution in disjunct antitropical areas that would have led to similar adaptations to deep-sea feeding (Bianucci et al. 2007, 2016b; Lambert et al. 2018). Interestingly, all the ziphiid remains found on the sea floor of the Southern Hemisphere, including the cranium here described, were collected in an area presently characterized by high productivity due to oceanic circulation and upwelling (Bianucci et al. 2008). These areas, where even today beaked whales are abundant and quite diversified (Ross 1984; Mead 1989), could have contributed to past radiation of crown beaked whales in the Southern Hemisphere oceanic environments. In particular, the cold Humboldt Current, which originated during the Eocene or Oligocene and intensified between 15 to 10 Ma, generates coastal upwelling activity along the Peruvian and Chilean margins which still today represents one of the most productive marine areas (Karstensen and Ulloa 2009; Armijo et al. 2015; Collareta et al. 2021). Therefore it is not surprising that, even in the eastern South Pacific off the coast of Chile, beaked whales show a high diversity today, although, as usual for beaked whales, their record is rather scarce and fragmentary. In particular, information on present species in this area has been summarized by Aguayo-Lobo et al. (1998) who reported *Berardius arnouxii*, *Hyperoodon planifrons*, *Tasmacetus shepherdi*, *Ziphius cavirostris*, *Mesoplodon densirostris*, *M. grayi*, *M. hectori*, *M. layardii*, *M. peruvianus*, and *M. traversii*. The occurrence of

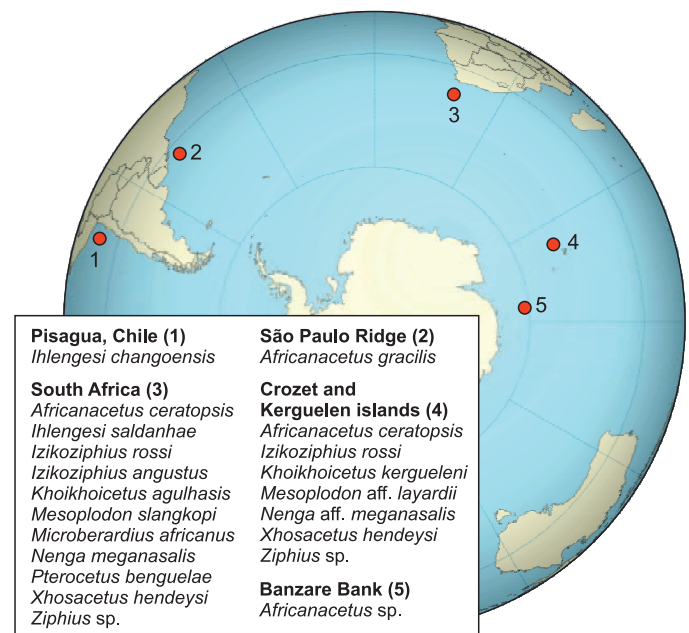


Fig. 8. Geographic distribution of the main fossils of ziphiids recovered from the seafloor of the Southern Hemisphere. Data from: 1, this study; 2, Ichishima et al. (2017); 3, Bianucci et al. (2006, 2007); 4, Lambert et al. (2018); 5, Gol'din and Vishnyakova (2013).

*B. arnouxii* is based on direct observations in Antarctic waters (Aguayo-Lobo 1994) and skeletal remains stranded in the eastern Strait of Magellan (Goodall 1978; Sielfeld 1983). *Hyperoodon planifrons* presents sightings off 33°S (Aguayo 1966) and Antarctic waters (Mörch 1911). *Ziphius cavirostris* has been sighted between Valparaíso and Easter Island (Aguayo-Lobo et al. 1998) and off central Chile (Hucke-Gaete 1998; Findley et al. 1998). Strandings of *Z. cavirostris* have been reported for the coast of Concepción (Oliver-Schneider 1946), Robinson Crusoe Island (Cárdenas and Yáñez 1988) and the eastern outlet of the Strait of Magellan: Cabo Espiritu Santo (Venegas and Sielfeld 1978; Sielfeld 1983). *Tasmacetus shepherdi* has only been reported from carcasses stranded on Gable Island: Beagle Channel (Goodall 1978) and Alejandro Selkirk Island (Brownell et al. 1976). *Mesoplodon densirostris* has been reported based specimens stranded in Puerto Montt: Bahía Pargua (Pastene et al. 1990) and Isla de Pascua (Aguayo-Lobo et al. 1998). The presence of *M. grayi* has been recorded on the basis of bone remains collected in the Strait of Magellan: Punta Wreck and Punta Catalina: Bahía Munió (Sielfeld 1979, 1983). The inclusion of *M. hectori* in the ziphiid list of the Chilean waters is supported by a skull stranded on the Atlantic coast of Tierra del Fuego (Goodall 1978) and Bahía Windhond: Isla Navarino (Sielfeld 1979). *M. layardii* has a stranding on the north coast of the Strait of Magellan: Rio Seco (Venegas and Sielfeld 1978), Tierra del Fuego: Cabo Espiritu Santo (Goodall 1978), and Isla Navarino: Bahía Windhond (Venegas and Sielfeld 1978; Sielfeld 1979). *M. peruvianus*, firstly described only for the coast of Peru (14°S) (Reyes et al. 1991; Reyes and Van Wawarebeek 2018),

Table 2. Extant species of beaked whales recorded along the coast of Chile and their geographical distribution in the other main circumantarctic areas. For detailed references of the Chilean record see the text whereas the other data are from MacLeod et al. (2006).

	Chile	South Africa	Antarctic	Australia	New Zealand
<i>Berardius arnouxii</i>	×	×	×	×	×
<i>Hyperoodon planifrons</i>	×	×	×	×	×
<i>Mesoplodon densirostris</i>	×	×		×	×
<i>Mesoplodon grayi</i>	×	×	×	×	×
<i>Mesoplodon hectori</i>	×	×		×	×
<i>Mesoplodon layardii</i>	×	×	×	×	×
<i>Mesoplodon peruvianus</i>	×				
<i>Mesoplodon traversii</i>	×				×
<i>Tasmacetus shepherdi</i>	×			×	×
<i>Ziphius cavirostris</i>	×	×	×	×	×

afterwards was sighted south of Iquique (Tarapacá) and off Punta Choros (Atacama) and also reported through a skull stranded on Playa Choros (Sanino et al. 2007). *M. traversii* (= *M. bahamondi*) was reported on the basis of a skull found on Robinson Crusoe Island (Reyes et al. 1995). Most of these species of beaked whales found off the Chilean coasts have also been reported off South Africa, Australia, and New Zealand (Table 2), evidencing a circumpolar distribution (McLeod et al. 2006). A similar distribution can be hypothesized for the fossil genus *Ihlangesi* which, in addition to being reported in Chile, was previously known from Cape Columbine, west coast of South Africa, in the Atlantic Ocean (Bianucci et al. 2007). But unfortunately, the Chilean beaked whale fossil record is too scarce to analyse its biogeographic relationships and more generally to reconstruct the mode and tempo of the evolution of beaked whales in this part of the eastern south Pacific Ocean. Indeed, besides the described cranium, the Chilean fossil record of ziphiids is represented only by three fragmentary remains from the Upper Miocene–lower Pliocene Bahía Inglesa Formation (Caldera, Atacama Region). These fossils consist of an indeterminate rostrum (Sielfeld 1995), an incomplete tympanic bulla attributed to *Ninoziphius* aff. *N. platyrostris* by Walsh (2001) but that does not actually retain sufficient characters for a generic attribution (GB personal observation), and an unfigured tooth referred to Ziphiidae indet. (Gutstein et al. 2008, 2015).

## Conclusions

Morphological characters and phylogeny support affinities, but also distinctive differences, of the Chilean fossil cranium described in this study with the fossil hyperoodontine *Ihlangesi saldanhae*. Therefore this cranium is here described as holotype of the new specie *I. changoensis*.

The small body size of *Ihlangesi changoensis* (estimated length 3.5 m) supports the hypothesis that in the past small beaked whales (body length under 4 m) were more common

than at present. The following reasons for the recent shift towards larger body sizes in the ziphiids have been hypothesized: (i) a progressive change of diet with a greater component of cephalopods rather than fish partially related to the competition with delphinids; and (ii) the predatory impact of white sharks and killer whales.

Given that the new Chilean fossil ziphiid is an hyperoodontine, the previously formulated hypothesis that the crown beaked whales originated and radiated in the oceanic waters of the Southern Hemisphere is further supported. In particular, the fossil and extant record of beaked whales of the whole Southern Hemisphere suggests that the radiation and the geographical distribution of crown beaked whales may have been driven by the oceanic circulation and related localized concentration of trophic resources in high productivity upwelling areas. Even if the high diversity observed in the extant beaked whales off the coast of Chile and the fossil specimen here described seem to support this evolutionary and paleogeographic pattern, new fossil remains from the ocean floor as well as from inland outcrops (e.g., the fossil-rich Bahía Inglesa Formation) will better clarify the rise of the southeastern Pacific current beaked whale assemblage.

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## Appendix 1

Coding for *Ihlangesi changoensis* sp. nov., *Khoikhoicetus agulhasis*, and *Khoikhoicetus kergueleni* in the morphological matrix by Bianucci et al. (2016). Abbreviations: a, variable between 1 and 2; ?, missing character.

<i>Ihlangesi changoensis</i>	22000	03212	0013a	200??	?????	?1??0	01021	?????	?????	??100	?
<i>Khoikhoicetus agulhasis</i>	?2000	0221a	00a31	200??	?????	?1??0	01011	?????	?????	??100	?
<i>Khoikhoicetus kergueleni</i>	22000	02212	20a31	200??	?????	?1??0	01011	?????	?????	??100	?