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Cetotheriidae records from the Late Miocene of Patagonia expand the diversity of baleen whales from the Southwestern Atlantic Ocean

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CETOTHERIIDAE RECORDS FROM THE LATE MIOCENE OF PATAGONIA EXPAND THE DIVERSITY OF BALEEN WHALES FROM THE SOUTHWESTERN ATLANTIC OCEAN

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Abstract. The marine outcrops of the Patagonian Miocene (Argentina) encompass one of the most important assemblages of fossil mysticetes recorded worldwide, including key records of extant lineages. The Patagonian Late Miocene records comprise balaenids (right whales) or cetotheriids neobalaenines (pygmy right whales). In the last years, the increase of fieldwork efforts in Miocene outcrops of Patagonia has led to the discovery of new specimens, thus expanding our knowledge of mysticetes diversity from regional and global perspectives. In this work, we describe isolated ear bones collected from the Late Miocene Puerto Madryn Formation 12–2.7 Ma (Serravalian to Piacenzian), Península Valdés (Chubut Province), preliminarily attributed to Cetotheriidae. Although the lack of diagnostic elements precludes a more precise identification (at genus or specific level) within this family, our studies reveal a previously unknown diversity of morphotypes, indicating significant taxonomic diversity among these Patagonian mysticetes. In addition, the South Atlantic cetotheriid assemblage appears to be represented exclusively by large taxa, probably of pelagic habits, which may have facilitated their dispersal into the southern basins. Finally, these records suggest a rapid dispersion of cetotheriids from the Paratethys into the Southern Hemisphere during the Late Miocene, with the Southwest Atlantic Ocean representing their southernmost limit of distribution.

Key words. Miocene. Puerto Madryn. Mysticetes. Evolution. Neogene.

Resumen. REGISTROS DE CETOTHERIIDAE DEL MIOCENO TARDÍO EN PATAGONIA AMPLÍAN LA DIVERSIDAD DE BALLENAS BARBADAS DEL OCÉANO ATLÁNTICO SUDOCCIDENTAL. Los afloramientos marinos del Mioceno de Patagonia (Argentina) albergan uno de grupos faunísticos más importantes de misticetos de todo el mundo, incluyendo registros claves de linajes con representantes actuales. En particular, la mayoría de los registros del Mioceno Tardío comprenden balénidos (ballenas francas) o cetotéridos neobalenines (ballena franca pigmea). El incremento en los esfuerzos de muestreo de los últimos años en afloramientos miocenos de Patagonia ha resultado en el descubrimiento de nuevos ejemplares, ampliando así nuestro conocimiento regional y global de la diversidad de misticetos. En este trabajo describimos huesos del oído aislados colectados en la Formación Puerto Madryn del Mioceno Tardío 12–2,7 Ma (Serravaliense a Piacenzience), Península Valdés (provincia de Chubut), y referidos preliminarmente a Cetotheriidae. A pesar de que la falta de elementos diagnósticos impide una identificación más precisa de estos especímenes (a niveles genéricos o específicos) dentro de esta familia, nuestros estudios revelan una diversidad de morfotipos previamente desconocida que puede suponer una importante diversidad taxonómica para estos misticetos patagónicos. Además, los cetotéridos del Atlántico Sur parecen estar representados exclusivamente por taxones de gran tamaño, probablemente de hábitos pelágicos, lo que puede haber facilitado su dispersión en las cuencas australes. Por último, estos registros sugieren una rápida y amplia dispersión de los Cetotheriidae desde la región de Paratethys hacia el hemisferio sur durante el Mioceno Tardío, siendo el Océano Atlántico Sudoccidental el límite más austral de su distribución.

Palabras clave. Mioceno. Puerto Madryn. Misticetos. Evolución. Neógeno.

BALLEN WHALES (Mysticeti; Chaeomysticeti) are living cetaceans that play an important role in modern marine trophic webs as consumers of large amounts of food (*i.e.*, zooplankton and fish) through specialized filter-feeding methods. This group originated in the early Oligocene and reached its maximum diversification during the Miocene to Pliocene (*e.g.*, Marx & Fordyce, 2015; Bisconti *et al.*, 2023) when most of the lineages reached a worldwide distribution. Among these, cetotheriids are one of families of baleen whales with the most bizarre cranial morphology. Cetotheriids encompass a variety of small-to middle-sized extinct forms and, according to some phylogenetic hypotheses, one living species, *Caperea marginata*, grouped in the Neobalaeninae subfamily (Fordyce & Marx, 2013; Marx & Fordyce, 2016; Dutoit *et al.*, 2023). Cetotheriidae have a long and confusing taxonomic history due to taxa lacking diagnostic features of the living families, the reason why cetotheriids were considered a “wastebasket” group of baleen whales. During the last few years, cetotheriids have been the focus of many phylogenetic analyses (Marx *et al.*, 2017, 2019) providing the first attempts to elucidate the taxonomy of the group. There is broad consensus recognizing a monophyletic Cetotheriidae *stricto sensu* (*e.g.*, Bouetel & de Muizon, 2006; Steeman, 2007) including species more closely related to *Cetotherium rathkii*; and a variety of taxa of uncertain affinity including the “cetotheres’’ *sensu lato* (*e.g.*, Bouetel & de Muizon, 2006; Adli *et al.*, 2014; Marx *et al.*, 2016, 2017; Tanaka *et al.*, 2023).

The fossil record of cetotheriids is more abundant during the Neogene (Gol’din & Startsev, 2017), with a peak in diversity during the Late Miocene and a decline towards the Pliocene–Pleistocene (*e.g.*, Boessenecker, 2013). From a paleobiogeographic point of view, the eastern and central Paratethys was proposed as the biogeographical origin of Cetotheriidae before their dispersal and radiation worldwide (Steeman *et al.*, 2009; Gol’din *et al.*, 2014; Marx & Fordyce, 2015; Gol’din, 2018). During the Late Miocene, cetotheriids presented an almost global distribution, with records in the Paratethys, the North Pacific, the North Atlantic, and the Southeast Pacific (Gol’din & Steeman, 2015; Gol’din & Startsev, 2017; Marx *et al.*, 2017, 2019; Gol’din, 2018; Tarasenko *et al.*, 2020; Collareta *et al.*, 2021; Torcărescu, 2023). In South America, cetotheriids are well represented in the South Pacific Ocean, with undescribed specimens from Neogene deposits of the Bahía Inglesa Formation (Mid–Late Miocene), the Navidad Formation, and the Coquimbo Formation region (Miocene–Pliocene) in Chile (Gutstein *et al.*, 2015), as well as several taxa described for the Pisco Formation in Perú (Bouetel & de Muizon, 2006; Bisconti, 2012; Collareta *et al.*, 2015; Marx *et al.*, 2017). In contrast, the fossil record of cetotheriids from the Southwestern Atlantic Ocean, especially from Neogene deposits of Patagonia (Argentina), where other baleen whale groups are abundant (*e.g.*, Cabrera, 1926; Buono *et al.*, 2017; Cuitiño *et al.*, 2019; Viglino *et al.*, 2021, 2023), is only restricted to Neobalaenine (Buono *et al.*, 2014), preventing a better understanding of the evolution of cetotheriids in this region.

In the present work, we report new baleen whales findings from the Late Miocene outcrops of the Puerto Madryn Formation, Patagonia, probably belonging to the Cetotheriidae, thus expanding our knowledge of the Mysticeti diversity in the Southwestern Atlantic Ocean.

GEOLOGICAL SETTING

During the Late Miocene, an extended region of Argentina was covered by a marine transgression known as the “Entrerriense or Paranense transgression”, which in Patagonia, deposited marine and estuarine facies restricted to the northeast of Chubut (Puerto Madryn Formation) and the east of Río Negro provinces (Facies Balneario La Lobería) (Haller, 1978; Scasso & del Río, 1987; Malumián & Náñez, 2011).

The Puerto Madryn Formation crops out in the surroundings of Puerto Madryn city and the Península Valdés (Fig. 1). It is mostly composed of shales, sandstones, and shell beds (especially mollusks), with abundant intercalations of pyroclastic material deposited in marine sediments (Scasso & del Río, 1987; Cuitiño *et al.*, 2017). It has been interpreted as a shallow marine to estuarine environment, registering frequent sea level oscillations (Scasso & del Río, 1987; Cuitiño *et al.*, 2017). Recent U-Pb geochronologic analyses suggest an interval between 11.17 ± 1.56 and 2.74 ± 0.11 Ma, from the Tortonian (Late Miocene) to the Piacenzian (Late Pliocene) (Cuitiño *et al.*, 2023).

The fossil vertebrates of the Puerto Madryn Formation are exceptional, not only for their diversity, but also for their excellent preservation. Bony fish, marine birds (Spheniscidae; Anserinae), and marine mammals (pinnipeds and cetaceans) are among the most outstanding groups represented in this unit (*e.g.*, Cozzuol, 2001; Buono *et al.*, 2016; Cuitiño *et al.*, 2017; Viglino *et al.*, 2021). Cetaceans comprise mostly balaenids and neobalaenines mysticetes, while odontocetes are represented by ziphiids and inioids (Buono & Cozzuol, 2013; Buono *et al.*, 2014, 2022; Cuitiño *et al.*, 2017; Viglino *et al.*, 2021).

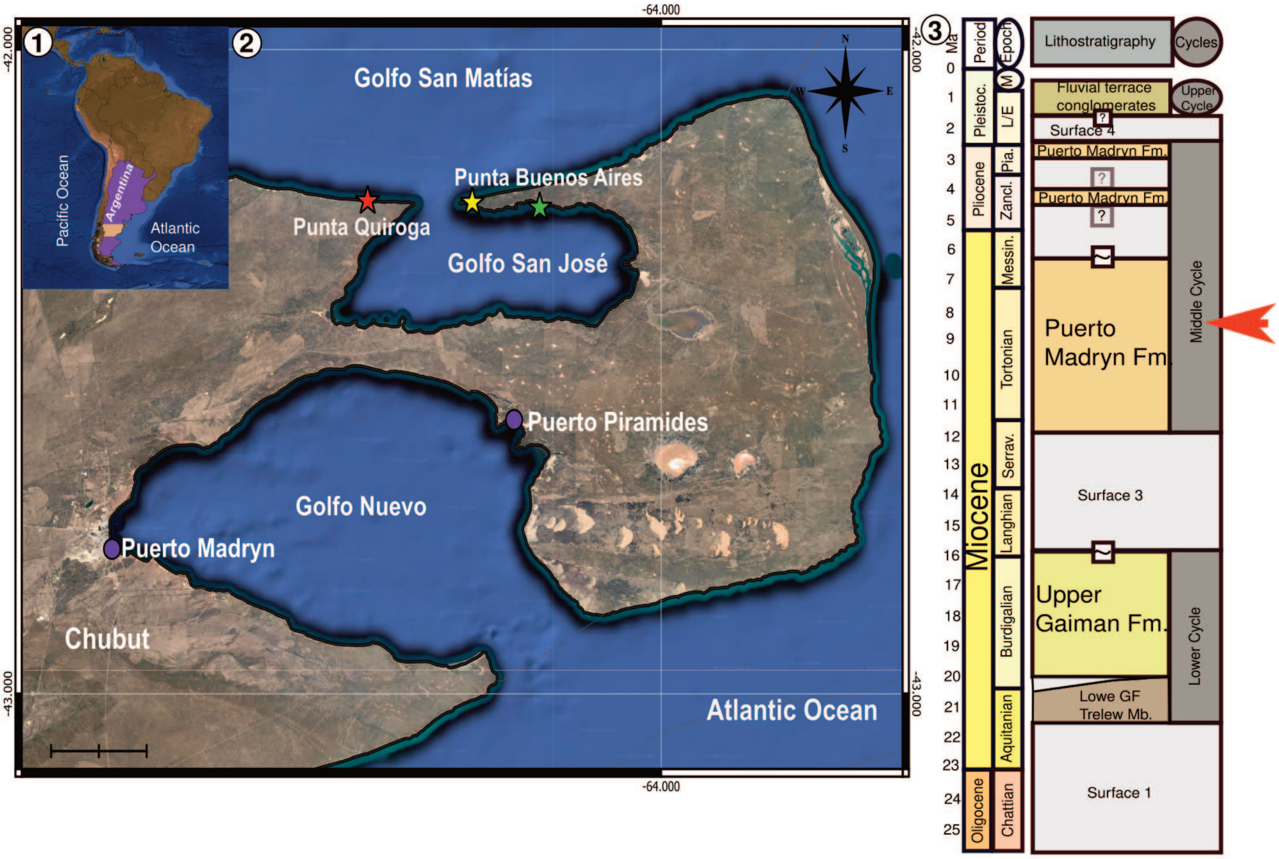

Figure 1. Geographic and stratigraphic occurrence of the studied specimens; **1,** map shows Argentina and highlights the Chubut Province; **2,** map of the northeast Chubut Province, including the localities in the Península Valdés area, where the specimens were collected; the green star corresponds to the **MPEF-PV-5603** locality, the yellow star corresponds to the **MPEF-PV-5914** locality, and the orange star corresponds to the **MPEF-PV-5928** locality; **3,** chronostratigraphic chart showing the chronological information of the Neogene and Quaternary deposits of Chubut; the red arrow marks the Late Miocene Puerto Madryn Formation, the unit where the specimens were collected. Taken and modified from Cuitiño *et al.* (2023). Scale bar= 20 km.

MATERIAL AND METHODS

The materials described here were collected in 1996 and 2004 by Pablo Puerta and deposited at the Museo Paleontológico "Egidio Feruglio" (MPEF). The anatomical terminology follows Mead & Foryce (2009) unless indicated. Ear bones measurements follow Marx *et al.* (2019). The orientation of the periotic and tympanic *bulla* is based on the *in situ* anatomical position in the skull. The photographs of the specimen were digitally stacked in Photoshop CS4.

Institutional abbreviations. MPEF-PV, Colección de Paleontología de Vertebrados, Museo Paleontológico "Egidio Feruglio", Trelew, Argentina.

SYSTEMATIC PALEONTOLOGY

CETACEA Brisson, 1762
NEOCETI Fordyce & de Muizon, 2001
MYSTICETI Gray, 1864
CHAEOMYSTICETI Mitchell, 1989
PLIOCOGULAE Geisler, McGowen, Young & Gatesy, 2011
CETOTHERIIDAE Brandt, 1872 (*sensu* Marx *et al.*, 2019)

CETOTHERIIDAE indet. 1
Figures 2–3; Table 1

Referred material. MPEF-PV-5603, isolated left periotic.

Diagnosis. MPEF-PV-5603 differs from balaenids in having an anterior process mediolaterally compressed, with an acute triangular outline (in dorsal/ventral view); in lacking a lateral process and having a suprameatal area hypertrophied; and in having a *pars cochlearis* bulbous and not protruding cranially. MPEF-PV-5603 shares with Plicogulae taxa (*i.e.*, cetotheriids and some balaenopte-roids such as Balaenopteridae, Eschrichtiidae, some early diverging balaenopteroids) a well-developed anterior process with a triangular outline (Steeman, 2007; Gol'din & Startsev, 2017). Diagnostic Cetotheriidae characters, such as a distally expanded compound posterior process of the tympanoperiotic and enlarged paroccipital concavity extending on the compound posterior process cannot be determined due to missing parts. MPEF-PV-5603 differs from all cetotheriids in having a notably elongated anterior process of the periotic; and from the early diverging cetotheriids in the following features: from *Thinocetus arthitus* in the lack of a bulbous anterior process and the shape of lateral tuberosity is poorly developed; from

Figure 2. Photographs of the left periotic of Cetotheriidae (**MPEF-PV-5603**); **1,** dorsal view; **2,** ventral view; **3,** medial view; **4,** posteromedial view; **5,** lateral view; **6,** ventrolateral view. Scale bar= 1 cm.

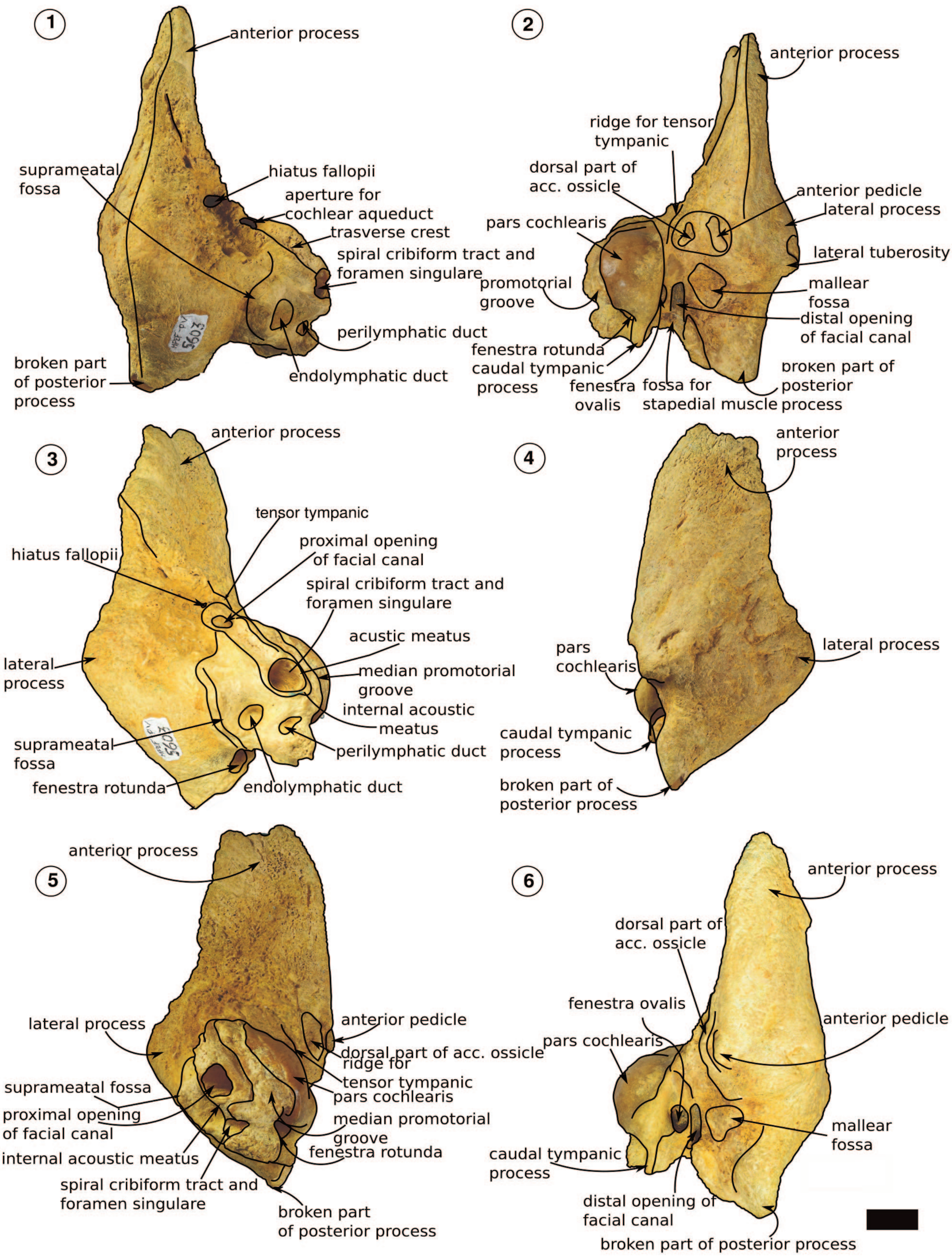

Figure 3. Interpretive drawings of the left periotic of Cetotheriidae (**MPEF-PV-5603**); **1,** dorsal view; **2,** ventral view; **3,** medial view; **4,** lateral view; **5,** posteromedial view; **6,** ventrolateral view. Scale bar= 1 cm.

TABLE 1 – **Measurements of left periotic MPEF-PV-5603 in cm.**

Periotic	MPEF-PV-5603
Maximum width of the anterior process	3.1
Thickness of the anterior process	1.9
Anteroposterior length of the *pars cochlearis*	4.6
Anteroposterior length of *pars cochlearis*	2.6
Dorsoventral width of the proximal opening of facial canal	1.6
Diameter of the proximal opening of facial canal	2.8
Anteroposterior length of internal acoustic *meatus*	3.1
Transverse wide of the internal acoustic *meatus*	0.5
Anteroposterior diameter of the endolymphatic duct	0.96
Anteroposterior diameter of the perilymphatic duct	0.1
Anteroposterior length of suprameatal *fossa*	1.9
Anteroposterior diameter of the *fenestra rotunda*	1.88
Thickness of the caudal tympanic process	0.3
Anteroposterior length caudal tympanic process	0.6
Width of the pedicle of the tympanic *bulla*	0.4
Width of accessory ossicle of the *bulla*	0.3
Width of the stapedial *fossa*	1.0
Dorsoventral height of the tympanic caudal process	0.4

Diorocetus hiatus by having a globose *pars cochlearis*, not elongated anteroposteriorly and by having an anterior process strongly compressed and relatively deep anteroposteriorly. MPEF-PV-5603 also differs from herpetocetines and *Caperea* in lacking an irregular, L-shaped external outline of the anterior process of the periotic and in having a well-developed caudal tympanic process; from *Miocaperea* in lacking a well-developed lateral tuberosity, from *Cetotherium rathkii* in having a squared-shape anterior process of the periotic in lateral view, and anterior process transversely compressed and blade-like absent; from *Piscobalaena*, *Brandtocetus*, and *Joumocetus* in having the perilymphatic duct smaller than the endolymphatic duct; from *Caperea marginata* in lacking the cranial elongation of the anterior part of the anterior process, in having a broad connection between the anterior process and the *pars cochlearis*, a long caudal tympanic process and the spiral cribiform tract separated by a sulcus form the proximal opening of the facial canal; from *Metopocetus* by having a shallow and not well-defined mallear *fossa*. It differs from Balaenopteridae in lacking a medial elongation of the *pars cochlearis*, in having a dorsal extension of the *tensor tympani*c muscle on the medial side of the anterior process; from *Aglaocetus patulus*, *Uranocetus*, *Isanacetus*, and *Parietobalaena* in having a transversally compressed and blade-like anterior process, and in lacking the anteroposterior alignment of the opening of the perilymphatic duct and the endolymphatic duct (except *B. acutorostrata*, *B. bonaerensis*, and *Uranocetus*). MPEF-PV-5603 also differs from *Aglaocetus patulus*, *Isanacetus laticephalus*, *Parietobalaena*, *Uranocetus gramensis*, and *Tiphyocetus temblorensis* by having a well-defined promontorial groove. The preservation of the periotic of MPEF-PV-5603 precludes a more precise taxonomic assignment than its inclusion in Cetotheriidae until new specimens are discovered and described.

Description. The isolated left periotic is well preserved (Figs. 2–3), lacking the compound posterior process. In the ventral view (Fig. 3.2), the anterior process is elongated, mediolaterally compressed, and has an acute triangular outline. It has a straight anteroposterior orientation, without twists. Posteriorly, the broken base of the anterior pedicle of the tympanic *bulla* is observable on the surface of the anterior process. The mallear *fossa* is a shallow depression on the ventral surface of the periotic, without well-defined margins. The lateral tuberosity is a poorly developed lateral projection with a rounded outline posteriorly to the anterior pedicle. The *pars cochlearis* is anteroposteriorly elongated, bulbous with a well-defined convex profile (in medial view), and represents 50 % of the length of the anterior process. The *pars cochlearis* has a smooth ventral surface. A deep promontorial groove runs across the medial margin of the *pars cochlearis* and terminates anteriorly to the fenestra cochleae. The ventral surface is smooth but a shallow promontorial groove is developed. The caudal tympanic process is elongated, triangular-shaped, and thin in posterior view. The *fossa* for the stapedial muscle is broad and has a shallow depression; it is delimited laterally by a slight ridge and medially by the caudal tympanic process. The sulcus for *tensor tympani* muscle is identified on the ventral surface of the anterior process, anteriorly to the *pars cochlearis*, as a slightly concave surface, and the insertion of the *tensor tympani* muscle extends along the medial surface of the anterior process. Two structures are also identified in the ventral surface of the anterior process: the anterior pedicle of the tympanic *bulla* and part of the accessory ossicle of the *bulla*. The ventrolateral tuberosity is a small and triangular projection. In ventrolateral view (Fig. 3.6), a deep distal opening of the facial canal runs in the posterior direction, and it is medially flanked (but separated) by a large *fenestra ovalis*. In dorsal view (Fig. 3.1), the suprameatal *fossa* is a well-defined depression, not hypertrophied, dorsal to the internal acoustic meatus. The *foramina* of the internal acoustic *meatus* are well separated by a long *sulcus* (1.5 cm), which connects both the proximal opening of facial canal and the spiral cribiform tract (VIII). The proximal opening of the facial canal is rounded and smaller than the rounded dorsal vestibular area; both *foramina* are aligned.

The aperture for the cochlear aqueduct is circular and smaller than the vestibular aqueduct, and it does not converge with the cochlear fenestra. The superior process is low and delimits ventromedially the suprameatal *fossa*. In posteromedial view (Fig. 3.5), the *crista transversa* is indistinguishable. A large and oval *Hiatus Fallopii* is identified posterior to the ridge for the *tensor tympanic* muscle. In lateral view (Fig. 2.4), a strong concavity corresponding to the epitympanic hiatus connects the lateral tuberosity and the broken base of the compound posterior process. In this view, the anterior process is almost square and wide. The lateral process has a moderate development with a convex profile. Part of the posterior pedicle of the tympanic *bulla* is preserved.

Geographic and Stratigraphic Occurrence. Punta San Román (42° 14′ 42″ S; 64° 13′ 42″ W), Península Valdés, Golfo San José, Chubut Province (Argentina); Puerto Madryn Formation, Tortonian (Late Miocene; Cuitiño *et al.*, 2023) (Fig. 1).

CETOTHERIIDAE indet. 2

Figures 4–5; Table 2

Referred material. MPEF-PV-5928, left tympanic *bulla* (Figs. 4–5).

Diagnosis. MPEF-PV-5928 shares with Cetotheriidae a squared anterior edge of the tympanic *bulla* (as most of the cetotherid taxa); shallow lateral furrow, anterior portion of the tympanic *bulla* narrower than the posterior half (observed in some cetotheriids such as *Piscobalaena*); a well-developed conical process. MPEF-PV-5928 also shares some characteristics with balaenids, such as a squared anterior margin of the tympanic *bulla*; an involucral ridge posteriorly and medially retracted, and a dorsoventral compression in the anteroventral corner of the *bulla*. However, it differs from Balaenidae in lacking a rhomboid-shaped *bulla* (typical of, for example, *Eubalaena*), in lacking a prominent longitudinal groove, and in having a prominent inner posterior prominence and a well-developed conical process. Differs from Balaenopteridae by having a more rectangular body profile, with a squared anterior margin, lacking a medially retracted involucral ridge and antero-lateral shelf, having a well-developed inner posterior prominence defining a convex *involucrum* surface, and having a high conical process. The lack of more diagnostic features precludes a more precise taxonomic assignment of MPEF-PV-5928.

Description. The tympanic *bulla* of MPEF-PV-5928 has an anteroposterior length of 9.6 cm (Figs. 4–5), almost completely preserved and only lacking the sigmoid process. In ventral view (Fig. 5.1), the anterior margin of the tympanic *bulla* is markedly squared, while the main ridge is convex. The anterior lobe is narrower than the posterior. The lateral furrow is a well-defined *sulcus*, ventrally oriented, and is placed on the anterior 1/3 of the length of the tympanic *bulla*. The sigmoid cleft is weak. The *bulla* presents a slight but evident dorsoventral compression on the anteroventral surface. The anteroposterior outline of the medial margin of the *bulla* is strongly convex. In dorsal view (Fig. 5.2), the opening of the tympanic cavity is wide anteriorly and narrows posteriorly, with an evident step separating a posterior and an anterior involucral region. The involucral ridge is laterally retracted. The *involucrum* surface presents few transversal crests. The opening of the Eustachian outlet is wide and has a slightly triangular shape. The inner posterior prominence is pronounced, forming a well-defined convex surface. The conical process is well-developed and anteriorly oriented, with a protruding convex shape in the dorsal view. In the medial view, the main ridge is well-defined and develops anteroposteriorly, being separated by the *involucrum* ridge by a wide space. The involucral ridge is anteroposteriorly directed. In medial view (Fig. 5.4), the convex inner posterior prominence define a sinusoidal involucral surface. The ventral surface of the *bulla* is convex. In lateral view (Fig. 5.5), the sigmoid process and part of the lateral margin of the *bulla* are missing; in this view is evident a general quadrangular profile of the *bulla*, with a dorsoventrally narrower anterior lobe, a pointed anteroventral angle, and a flat anterior surface. The posterior lobe has a truncated posterior margin.

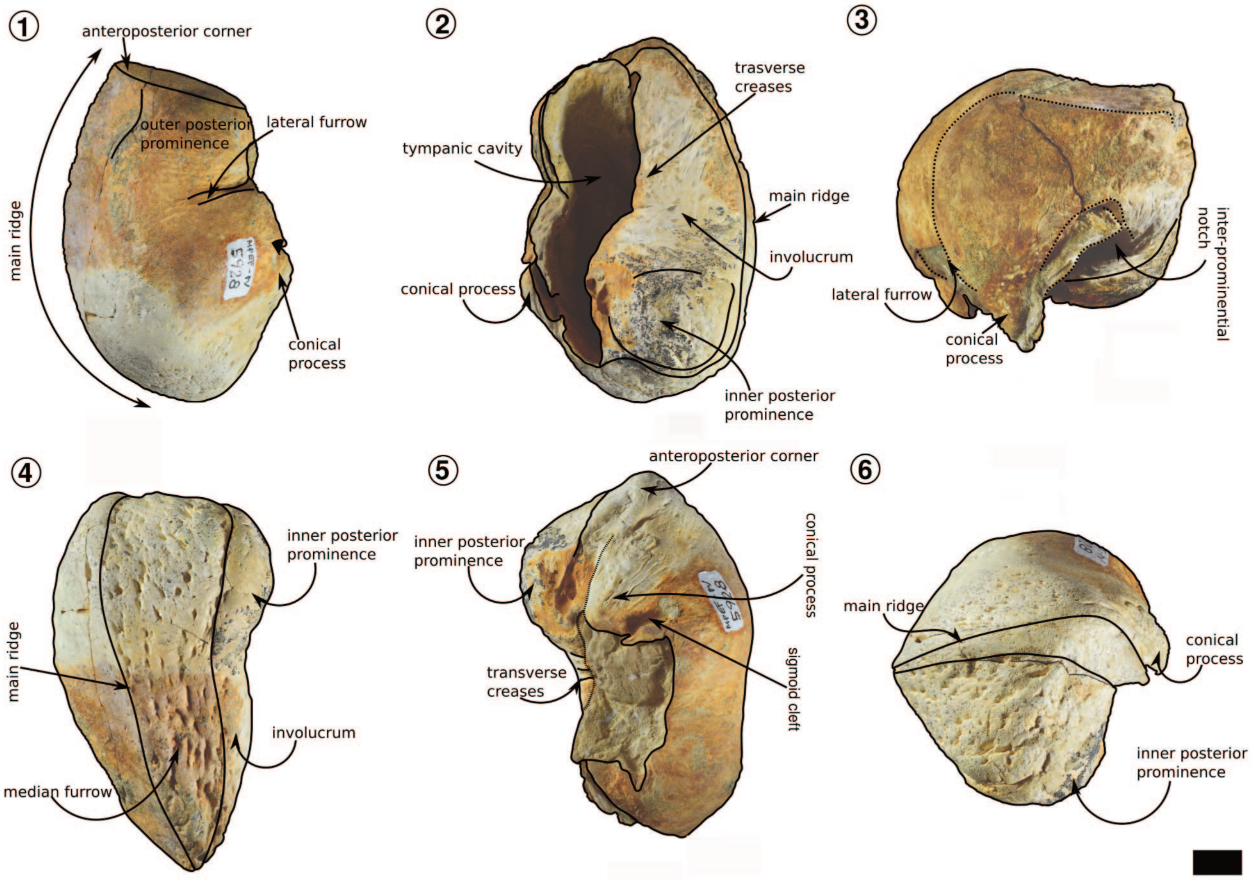

Figure 4. Interpretive drawings of the left tympanic *bulla* of Cetotheriidae (**MPEF-PV-5928**); **1,** ventral view; **2,** dorsal view; **3,** anterior view; **4,** medial view; **5,** lateral view; **6,** posterior view. Scale bar= 1 cm.

Figure 5. Photographs of the left tympanic *bulla* of Cetotheriidae (**MPEF-PV-5928**); **1,** ventral view; dorsal view; **3,** anterior view; **4,** medial view; **5,** lateral view; **6,** posterior view. Scale bar= 1 cm.

TABLE 2 – Measurements of the tympanic *bulla* of MPEF-PV-5914 and MPEF-PV-5928 in cm.

Measurement	MPEF-PV-5914	MPEF-PV-5928
Anteroposterior length	8.4	9.6
Maximum transverse width, taken just before the sigmoid process	5.2	5.3
Width of the sigmoid process	0.8	-
Anteroposterior length of the sigmoid process	1.7	-
Thickness of the conical process	2.2	2.4
Width of the main ridge (taken in the middle of the *bulla*)	1.7	1.8
Maximum anteroposterior length of the tympanic cavity	6.7	7.5
Maximum width of the tympanic cavity in the anterior region	0.7	0.8
Lateromedial width of inner posterior prominence	3.4	3.8
Anteroposterior length of the inner posterior prominence	3.6	4.5

Geographic and Stratigraphic Occurrence. Punta Quiroga, Península Valdés, Golfo San José (42° 14′ 05.6′′ S; 64° 33′ 06.8′′ W), Chubut Province (Argentina); Puerto Madryn Formation, 12–2.7 Ma (Serravalian to Piacenzian; Cuitiño *et al.*, 2023) (Fig. 1).

CETOTHERIIDAE indet. 3

Figures 6–7; Table 2

Referred material. MPEF-PV-5914, left tympanic *bulla*.

Diagnosis. MPEF-PV-5914 shares with cetotheriids a squared anterior edge of the tympanic *bulla* (most of the cetotherid taxa) and an anterior portion of the tympanic *bulla* narrower than the posterior half (shared with *Tranatocetus*, *Piscobalaena*, and *Metopocetus*). MPEF-PV-5914 differs from balaenids in lacking a rhomboid shape, a marked dorsoventral compression of the *bulla*, and transverse creases on the dorsal surface of the *involucrum*, and in having a shallow lateral furrow and an *involucrum* ridge not retracted from the posterior margin. Differs from Balaenopteridae in having a globose outline with a quadrangular anterior margin, in lacking an *involucrum* ridge retracted from the medial margin, and a large anterolateral shelf. The lack of more diagnostic characters prevents a more accurate taxonomic assignment.

Description. In ventral view (Fig. 7.1), the general profile of

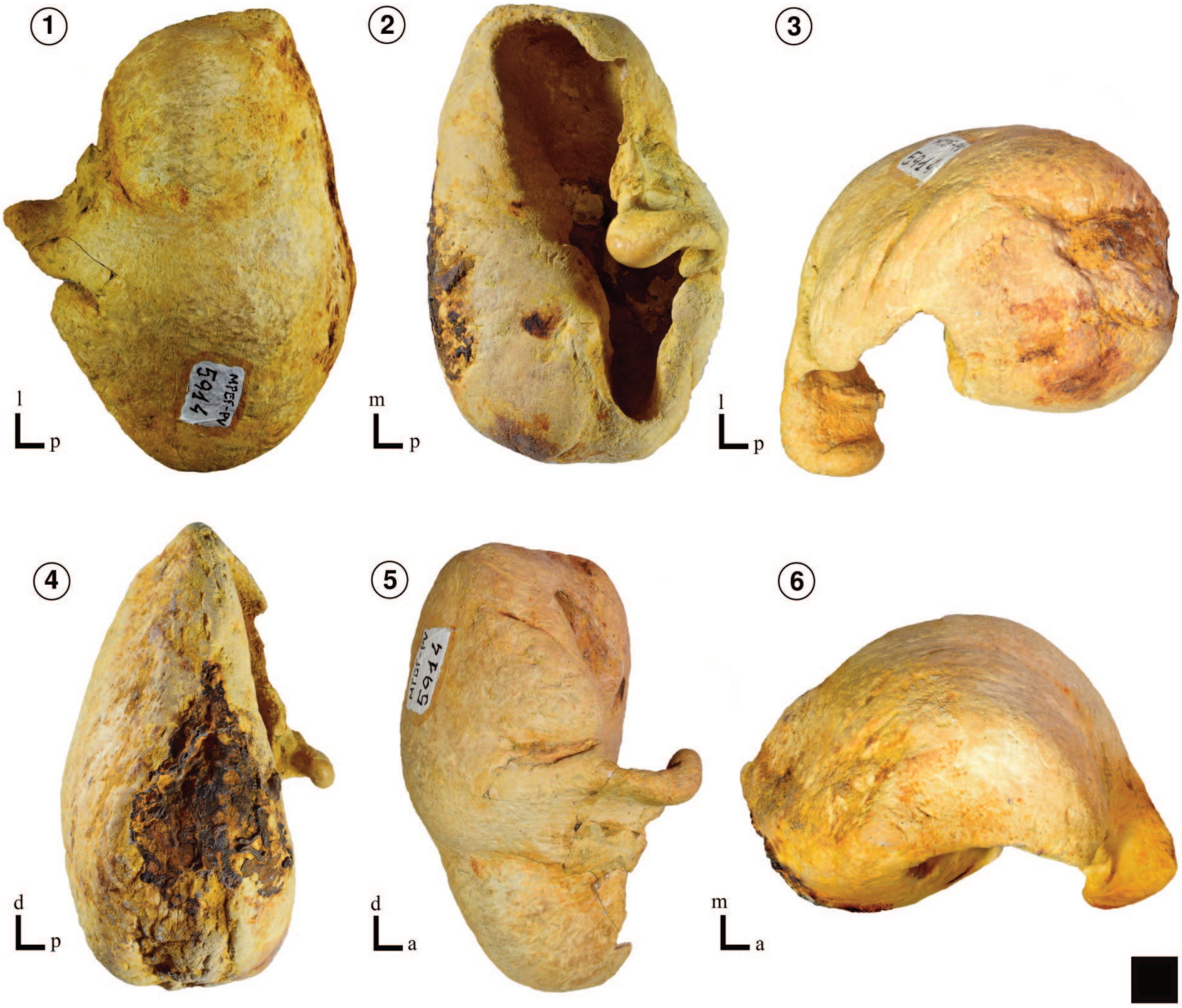

Figure 6. Photographs of the right tympanic *bulla* of Cetotheriidae (**MPEF-PV- 5914**); **1,** ventral view; **2,** dorsal view; **3,** posterior view; **4,** medial view; **5,** lateral view; **6,** anterior view. Scale bar= 1 cm.

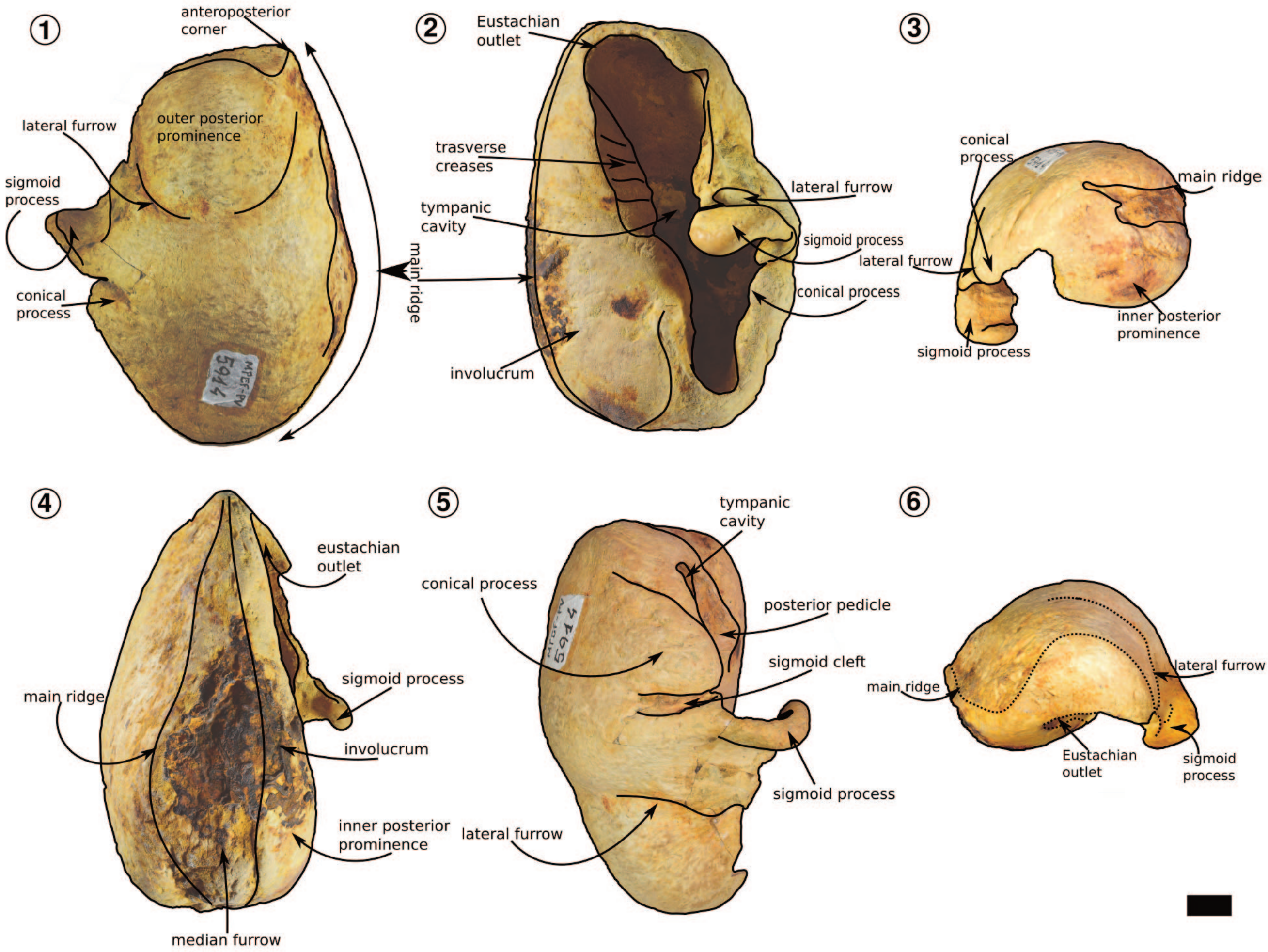

Figure 7. Interpretive drawings of the right tympanic *bulla* of Cetotheriidae (**MPEF-PV- 5914**); **1,** ventral view; **2,** dorsal view; **3,** posterior view; **4,** medial view; **5,** lateral view; **6,** anterior view. Scale bar= 1 cm.

the tympanic *bulla* is globose, with a quadrangular anteromedial corner. The main ridge extends anteroposteriorly along the medial surface of the tympanic *bulla* and describes a convex medial outline. The posterior margin of the *bulla* is convex. There is no anterolateral shelf. In dorsal view (Fig. 7.2), the *involucrum* surface is narrow anteriorly and becomes wider in the posterior direction. Anterodorsally, the *involucrum* bears transverse crests. The Eustaquian outlet is rounded and wide and the tympanic cavity narrows posteriorly. The *involucrum* ridge extends anteroposteriorly reaching the posterior margin of the *bulla*. Medially, it does not contact the main ridge. The sigmoid process is observed slightly twisted in the posterior direction. In medial view (Fig. 7.4), the *involucrum* and main ridge do not meet medially and are separated by a wide median furrow. The surface of the *involucrum* described a slight convex outline, while the ventral surface of the *bulla* is convex. In lateral view (Fig. 7.5), the anterior 1/3 portion of the *bulla* is markedly narrower than the posterior 2/3. The sigmoid process is high, robust, and wide at the base, and it is slightly twisted toward the posterior side. The conical process is broad and low, with a convex outline; it is anteriorly delimited by a deep sigmoid cleft. The lateral furrow is weak and runs in a straight line in the ventral direction.

Geographic and Stratigraphic Occurrence. Punta Buenos Aires, Península Valdés, Golfo San José (42° 14′ 14.582″; 64° 21′ 18.5″ W), Chubut Province (Argentina); Puerto Madryn Formation, 12–2.7 Ma (Serravalian to Piacenzian; Cuitiño *et al.*, 2023), (Fig. 1).

DISCUSSION AND CONCLUSIONS

During the Miocene, mysticetes diversity underwent a marked turnover event associated with global climatic and oceanographic fluctuations, during which many archaic lineages were drastically reduced, and the modern fauna began to flourish and establish (*e.g.*, Marx & Fordyce, 2015; Berta & Lanzetti, 2020). In particular, the marine Miocene outgroups from Patagonia (Argentina) contain one of the most important fossil assemblages of mysticetes worldwide, partially documenting this shift in the taxonomic composition of global mysticetes communities (Viglino *et al.*, 2023). The Patagonian Early Miocene records of mysticetes house an important and abundant diversity of archaic balaenids and early diverging balaenopterids (Lydekker, 1894; Cabrera, 1926; Buono *et al.*, 2017; Cuitiño *et al.*, 2019), while during the Late Miocene mysticetes are mostly represented by cetotheriids neobalaenines and balaenids (Buono, 2014; Buono *et al.*, 2014, 2016; Cuitiño *et al.*, 2017). Here, we expand the diversity of mysticetes during the Late Miocene of Patagonia by describing new specimens with similar morphology to cetotheriids. Although the specimens lack diagnostic elements that would allow a more precise taxonomic identification within the Cetotheriidae, comparison with other cetotheriid taxa shows no evidence of affinities with Neobalaeninae (*i.e.*, *Caperea* and *Miocaperea*). In this sense, these new records document a previously unknown diversity of morphotypes for Patagonian mysticetes that may represent an important taxonomic diversity, especially regarding non-neobalaenines cetotheriids. Anatomical comparisons with non-neobalaenine cetotheriids are not conclusive but show similarities with some coetaneous taxa. For example, the periotic of MPEF-PV-5603 shares with *Herentalia nigra* a strongly compressed and elongated anterior process of the periotic in ventral view, not twisted posteriorly. However, MPEF-PV-5603 differs from *H. nigra* in having a more elongated and anteroposteriorly rounded *pars cochlearis*, and a well-defined promontorial groove. Conversely, MPEF-PV-5603 shares with *Herpetocetus* sp. a well-defined lateral projection of the anterior process, and in having the aperture for cochlear and the vestibular aqueduct aligned anteroposteriorly. However, MPEF-PV-5603 differs from *Herpetocetus* in the larger size of the periotic, and in lacking a blade-like anterior process. The tympanic *bulla* of MPEF-PV-5928 resembles that of *Piscobalaena nana* having a pear shape in ventral view, with the posterior region of the *bulla* wider than the anterior, and a strongly convex inner posterior prominence (Bouetel & de Muizon, 2006). However, MPEF-PV-5928 differs from *P. nana* in lacking a pronounced main ridge and an anterior spine of the tympanic. It also shares with *Tiucetus rosae* (Marx *et al.*, 2017) a well-developed conical process and an involucral and main ridges separated by a broad medium furrow. It differs from *T. rosae* by having a highly convex inner posterior prominence, a dorsal surface of the *involucrum* separated by a well-defined step, and obliqued oriented anterior and posterior faces of the *bulla*. The tympanic *bulla* of MPEF-PV-5914 exhibits a different morphology to MPEF-PV-5928, suggesting different taxa: a flat involucral surface with a poorly developed inner posterior prominence, a low conical process, and a more pronounced narrow anterior region of the *bulla*. Compared to other cetotheriids, MPEF-PV-5914 is morphologically close to *Tranatocetus maregermanicum* (Marx *et al.*, 2019): it has a ventral surface transversely convex throughout, a wider posterior region, a conical process located entirely posterior to the sigmoid process, and a transversely oriented and not twisted sigmoid process, located at two-thirds of the total length of the *bulla*. In summary, the anatomy of the specimens suggests some similarities with other known cetotheriids, but they are not conclusive for confident taxonomic assignment; the discovery of more complete specimens with associated skulls will help to determine the taxonomic status of these specimens.

Cetotheriids whales are mostly restricted to Late Miocene–Pleistocene taxa that are well represented in eastern and central Paratethys localities where cetotheriids evolved before their global dispersal and radiation (*e.g.*, Uhen & Pyenson, 2007; Boessenecker, 2011; Bisconti, 2015; Gol'din & Startsev, 2017; Marx *et al.*, 2019; Collareta *et al.*, 2021; Figueiredo *et al.*, 2024). However, sampling biases in rocks from northern global localities (Viglino *et al.*, 2023) may affect the interpretation of the diversity and biogeographic distribution of this group of mysticetes. The fossil record of cetotheriids from the Global South is less abundant but significant, and is primarily associated with Neobalaeninae and, to a lesser extent, non-neobalaenines cetotheres. These include records from the Late Miocene of

Perú (Bisconti, 2012), South Africa (Marx *et al.*, 2018), and Australia corresponding to *Caperea* sp. (Govender & Marx, 2023), and other less diagnostic identified as Neobalaeninae indet. from the Late Miocene of Argentina (Buono *et al.*, 2014) and Australia (Fitzgerald, 2012). Non-neobalaenid cetotheres have been exclusively recorded from the Middle–Late Miocene of Perú (Marx *et al.*, 2017) and the Late Miocene of Chile (Gutstein *et al.*, 2015). Our study reinforces the idea of a rapid dispersal of cetotheriids from their Paratethys origin, reaching their southernmost distribution in the Southwest Atlantic Ocean at least in the Late Miocene. Although the presence of non-neobalaenines in the southwestern Atlantic is not unexpected, given the widespread distribution of this group in many global northern localities during the Middle–Late Miocene, these findings raise new questions about the dispersal routes of cetotheriids into the Southern Hemisphere, *e.g.*, does the invasion of the subsequent ocean basins from the Paratethys centre of origin first proceed via the North Pacific and North Atlantic, then spread to the South Pacific and finally reach the South Atlantic basin?

Most large cetotheriids (7–8 m) are mainly from the early Late Miocene, whereas smaller forms (less than 5 m) are more common in the Latest Miocene and Pliocene (*e.g.*, Marx *et al.*, 2019). The ear bones described here are closer in size to larger cetotheriids such as *Herentalia*, *Tranatocetus*, and *"Cetotherium" megalophysum*, reinforcing the idea that these forms, with possible more pelagic habits, were more restricted to the Early Late Miocene (Cope, 1895; Bisconti, 2015; Marx *et al.*, 2019). Regionally, the South Atlantic cetotheriid assemblage appears to be represented exclusively by large taxa (*e.g.*, Buono *et al.*, 2014), differing on this point from the South Pacific assemblage, which appears to be more characterized by small forms (*e.g.*, Bisconti, 2012; Gutstein *et al.*, 2015, 2020; Marx *et al.*, 2017).

Despite the incomplete state of the mysticetes specimens described here, these new records provide insights into some palaeobiogeographic and palaeobiological aspects of cetotherian evolution. It is possible to hypothesize that the final conquest of the South Atlantic by cetotheriids was facilitated by the dispersal of large-sized and pelagic forms. Moreover, these records document a previously unknown diversity of mysticetes in the Patagonian assemblage during the Late Miocene, which needs to be confirmed by the discovery of more diagnostic specimens. Therefore, collection efforts should continue in the Miocene outcrops of Patagonia to improve our understanding of the taxonomic and palaeobiological composition of the Mysticetes assemblage, and also to test hypotheses of paleogeography dispersal to the Southern Hemisphere.

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