Unravelling the identity of the platanistoid *Notocetus vanbenedeni* Moreno, 1892 (Cetacea, Odontoceti) from the early Miocene of Patagonia (Argentina)

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Platanistoidea remains one of the most evolutionarily intriguing lineages of toothed whales (Odontoceti). The clade comprises mostly extinct species from the late Oligocene–early Miocene onward and a single extant riverine genus (*Platanista*). There is an ongoing debate as to the membership of Platanistoidea and the causes of their near extinction. In Patagonia (Argentina), the most abundant platanistoid recorded in the lower Miocene Gaiman Formation is *Notocetus vanbenedeni*, first described by Moreno in 1892 based on two individuals. The goal of the present contribution is to conduct an updated anatomical, palaeobiological and phylogenetic analyses of *Notocetus vanbenedeni* and hence contribute to an understanding of the evolutionary history of the Platanistoidea. Our analyses, including at least 26 individuals (12 undescribed), show that *Notocetus vanbenedeni* is a valid platanistoid taxon, recovered as part of a new clade. Among its most outstanding features, this taxon has an elevated dorsal tubercular supraorbital crest formed mainly by the frontal, the precursor of the pneumatized crest of the extant *Platanista*. *Notocetus vanbenedeni* also shows initial stages of the plesiomorphic bony connection between the earbones and skull as in *Platanista*, although the functional implications for hearing remain elusive. The nasal sac system, pterygoid sinus system and morphology of the earbones suggest that this species was able to hear high-frequency sounds and echolocate underwater, similar to extant odontocetes. Thus, *Notocetus vanbenedeni* presents a mosaic of features that suggest an intermediate platanistoid morphotype. Anatomical differences and phylogenetic analyses suggest that Peruvian specimens could not be referred to this species. The feeding apparatus of *Notocetus vanbenedeni* makes it the only combination suction-feeder recorded in the early Miocene of Patagonia and among the smallest odontocetes. Finally, the abundant records of *Notocetus vanbenedeni* in an inner shelf environment with freshwater influence suggest a possible early preference for such protected habitats.

**Keywords**: evolution; Platanistoidea; palaeobiology; Odontoceti; time-calibrated phylogenetic hypothesis; Gaiman Formation

**Introduction**

The South Asian river dolphin *Platanista gangetica* is the last member of an early diverging lineage within Odontoceti, the Platanistoidea (e.g. de Muizon 1987; Fordyce & de Muizon 2001; Barnes et al. 2010; see the recent taxonomic revision of the genus by Braulik et al. 2021). The International Union for Conservation of Nature (IUCN) classified *Platanista gangetica* as an endangered species (Braulik & Smith 2019), highlighting the need to understand the evolutionary history of this dolphin. Fossil Platanistoidea species appeared in the late Oligocene and were once major components of global marine ecosystems (e.g. Fordyce 1994; Lambert et al. 2014; Tanaka & Fordyce 2017 and references therein; Boersma et al. 2017; Viglino et al. 2018a, b; Gaetán et al. 2019). There is an ongoing debate as to the contents of the clade Platanistoidea and the causes of its diversity decline from the middle Miocene onward.

Within the Platanistoidea, the late Oligocene–early Miocene marine family Squalodelphinidae (Dal Piaz 1917) includes species such as *Squalodelphis fabiani*, *Medocinia tetrarhina*, *Phocageneus venustus*, *Huaridelphis raimondii* and *Macrosqualodelphis ukapachai* (e.g. Barnes et al. 2010; Lambert et al. 2014; Bianucci et al. 2018). Yet there is still some debate as to the content and monophyly of this family (e.g. Boersma & Pyenson 2016; Tanaka & Fordyce 2017 and references therein; Viglino et al. 2018a, b; Gaetán et al. 2019). In Patagonia (Argentina), squalodelphinids are represented by the early Miocene *Notocetus*...
vanbenedeni, the most abundant odontocete species in the Gaiman Formation (Haller & Mendía 1980; Cuitiño et al. 2019). The species was first described by Moreno (1892), from fairly complete skulls with associated postcranial bones of two individuals. Since then, the exact affinities of Notocetus vanbenedeni have remained uncertain, varying among Squalodelphinidae, Platanistidae, Squalodontidae, Ziphiidae and Physeteridae (e.g. Lydekker 1893; True 1910; Dal Piaz 1917; Cabrera 1926; Kellogg 1928; Simpson 1945; de Muizon 1987). Recently, new putative records of the species from the early Miocene of Peru were described (Bianucci et al. 2014, 2020). Even though Notocetus vanbenedeni has been included in different morphological phylogenetic matrices (e.g. Fordyce 1994; Geisler et al. 2011; Lambert et al. 2014; Boersma et al. 2017; Godfrey et al. 2017; Tanaka & Fordyce 2017 and references therein; Bianucci et al. 2018; Viglino et al. 2018a, b; Gaetán et al. 2019), a modern and more comprehensive palaeobiological study would help elucidate the phylogenetic relationships of the species among Platanistoidea.

Thus, the goal of the present contribution is to conduct an updated palaeobiological and phylogenetic study of Notocetus vanbenedeni and to clarify the phylogenetic relationships and evolutionary history of the Platanistoidea. It should also help us understand the early Miocene radiation of platanistoids in the southwestern Atlantic and the resulting origins of Platanista gangetica, thus explaining how this species may have evolved into its present nearly ‘dead end’ as the single extant endangered representative of the clade.

Material and methods

Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA; CNPMAMM, Colección de Mamíferos Marinos del Centro Nacional Patagónico (CCT CONICET-CENPAT), Puerto Madryn, Argentina; GMNH, Gunma Museum of Natural History, Tomioka, Gunma Prefecture, Japan; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; MACN, Colección de Mastozoología, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Ciudad Autónoma de Buenos Aires, Argentina; MLP, Colección de Paleontología de Vertebrados, Museo de La Plata, La Plata, Argentina; MNHN, Muséum national d'Histoire naturelle, Paris, France; MPEF-PV, Colección de Paleovertebrados, Museo Paleontológico ‘Egidio Feruglio’, Trelew, Argentina; MUSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marco, Lima, Peru; NMNZ, Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; OU, Geology Museum, University of Otago, Dunedin, New Zealand; USNM, Department of Paleobiology & Department of Vertebrate Zoology (Division of Mammals), National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

Other abbreviations

BIZYG, bizygomatic width; CBL, condylobasal length; ch., character; GC, difference in frequency of Groups present/contradicted; ICZN, International Code of Zoological Nomenclature; MPT, most parsimonious tree; OTU, operational taxonomic unit; TBR, tree bisection and reconnection; TL, total length.

Sample, description and methods of palaeobiological inference

The present study is based on 15 incomplete skulls, six mandibles (two of them nearly complete), 13 pteriotics, 15 tympanic bullae, two incudae and stapedes, 37 vertebrae, at least 18 ribs, and one right scapula, which are identified as Notocetus vanbenedeni based on direct comparison with the holotype (Moreno 1892) and two previously published specimens confidently assigned to this species (True 1910; de Muizon 1987). We also compared the specimens against known odontocete species recorded in Patagonia. It should be noted that the holotype (MLP 5-5) is covered with old glue, as it was prepared almost 150 years ago, so sutures and specific structures are hard to identify; a modern preparation was not permitted due to its taxonomic value. Thus, recently collected specimens were key pieces that allowed a thorough and complete palaeobiological study of the species as presented here. Therefore, we based the following description of Notocetus vanbenedeni on at least 26 specimens, of which 12 were undescribed prior to this work. Data from the included specimens, literature, and specimens used in the comparative and phylogenetic studies are listed in Supplemental material S1.

We took photographs with a Nikon D800 DSLR camera with a 105 mm microlens, a Nikon D3000 camera with a 16–35 mm lens, and a Canon Powershot G16 camera, and used the image-stacking technique (Bercovici et al. 2009). Descriptions are based on the right or left side, whichever was more informative, with differences between them mentioned only if directional asymmetry is evident. For the skull terminology, we followed Mead & Fordyce (2009), and postcranial terms followed Rommel (1990) and Rommel & Reynolds (2008) unless otherwise noted. We followed Perrin’s
Notocetus vanbenedeni from the early Miocene of Patagonia (Argentina)

Phylogenetic analyses

The morphological matrix used here was based on Viglino et al. (2018b), incorporating the codings for Prosqualodon australis (Gaetán et al. 2019), and was constructed using Mesquite 2.75 (Maddison & Maddison 2011). We expanded the matrix by adding the following species based on the literature (up to April 2020): Arktocara yakataga, Dilophodelphis fordycei, Arcaedelphis natator, Huaridelphis raimondii, Aloddelphis pratti, Zarhinoctes errabundus, Goedertius oregonensis and Macrosqualodelphis ukupachai. We coded the following species from direct observation of the specimens: Medocinia tetrarhorhina and Ninjadelphis ujiharai. Based on all the available specimens and the present re-description, we thoroughly revised the codings for Notocetus vanbenedeni. We acknowledge this is not an exhaustive list of possible platanistoids to include, but we have included as many taxa as possible to capture the diversity of the group. Finally, based on preliminary differences observed, we included Peruvian specimens MUSM 1395 (Bianucci et al. 2014) and MUSM 3896, 3897 and 1484 (Bianucci et al. 2020) assigned to Notocetus vanbenedeni, to test their phylogenetic relationship with the Patagonian specimens analysed here. The list of characters and coding modifications is provided in Supplemental material S3. The resulting matrix has 99 OTUs and 285 chs. (226 craniomandibular, 28 postcranial and 31 soft-tissue). Notocetus vanbenedeni has 20% missing data (including soft-tissue chs.; for the full matrix, see Supplemental material S4).

We conducted a heuristic parsimony analysis of the dataset in TNT version 1.5 (Goloboff & Catalano 2016) under equal and implied weights (K = 1–100). All chs. were treated as unordered. We applied the New Technology search with the default parameters and 100 hits to the minimum-length. The MPTs obtained at the end of the replicates were subjected to a final round of TBR branch swapping, and summarized as consensus trees with zero-length branches collapsed (i.e. rule 1 of Coddington & Scharff 1994). We illustrated the frequency with which key nodes and clades were recovered during equal and implied-weight searches using grids derived from sensitivity analyses (Wheeler 1995; Giribet 2003). For branch support, we estimated Bremer and GC values of jackknife resampling analyses (using p = 0.30 and 1000 pseudoreplicates; Goloboff et al. 2003). To identify unstable taxa, we applied the IterPCR procedure (Pol & Escapa 2009) over the entire set of MPTs. Finally, we merged species in the more-diverse clades crownward of Squaloziphius and Xiphiacetus for ease of illustration (for the full cladograms see Supplemental material S5).

Time-calibrated phylogenetic hypothesis

For the time-calibrated tree, based on the literature, we determined the chronostratigraphical range (oldest and youngest records) for each OTU included in the morphological matrix (see Supplemental material S6). Then, we chose an MPT (see the Phylogenetic analyses section below) that was calibrated using the timephylo function of the paleotree package (Bapst 2012) for R (R Core Team 2017), applying the minimum branch length (mbl) method with a branch length of 0.1 million years.

Geological setting

The specimens studied in this work were collected from two main areas. Most were recovered from outcrops in the north-east region of Chubut Province (Gaiman Formation; Fig. 1). On the other hand, one specimen comes from outcrops in the south-east of Santa Cruz Province, i.e. roughly 800 km south of the former region (Monte León Formation; Fig. 1).

North-East Chubut Province: Gaiman Formation

According to Moreno (1892), the holotype (MLP 5-5) and MLP 5-17 are from ‘Bahía Nueva’, a small bay where the city of Puerto Madryn is located and where the Gaiman Formation outcrops extensively (see Paolucci et al. 2020 for further details about this locality). In turn, AMNH 29026 and MLP 5–10 come from Cerro Castillo, located within the Chubut River Valley just south of the city of Trelew, with abundant exposures of the Gaiman Formation (see Buono et al. 2017 for further geographical and stratigraphical details about this locality). Specimens MPEF-PV 681, 683, 1117, 1118, 1119, 1120, 1375 and 1804 come from Bryn Gwyn (= Loma Blanca), within the southern margin of the Chubut River Valley, 8 km south-east of the city of Gaiman (approximately 43.355°S, 65.456°W). MPEF-PV 1660 comes from Playa Santa Isabel, 13 km south-east of the city of Rawson. Finally, MPEF-PV 2580
comes from Estancia La Redonda, about 30 km southwest of the city of Rawson (43.554°S, 65.224°W).

The collection cards for both MLP 5-52 and MLP 76-VI-11 read ‘F.P.M., Chubut’. In north-east Chubut, marine Miocene outcrops belong to either the Gaiman Formation or the Puerto Madryn Formation (Cuitiño et al. 2017, 2019). Given that *Notocetus vanbenedeni* has never been recorded in the Puerto Madryn Formation (Buono et al. 2016), and that the area surrounding Puerto Madryn and Trelew has been historically the most prospected, we conservatively propose that the note indicates the specimens were collected in north-east Chubut Province, from outcrops of the Gaiman Formation. MLP 76-IX-2-5, MLP 76-IX-2-9/11/12 and MLP 87-XII-20-1 lack a detailed stratigraphical and geographical provenance. Based on the note on the collection card that reads ‘Patagoniano?’ – an old stratigraphic name for the Gaiman Formation (Haller & Mendía 1980; Cione 1986) – they are proposed to have been collected from outcrops of this formation, in Chubut Province (Scasso & Castro 1999; Cuitiño et al. 2019).

The Gaiman Formation (Haller & Mendía 1980) consists of a succession of tuffaceous mudstones, tuffaceous fine sandstones and sparse shell-beds, deposited in inner shelf to coastal marine environments (Scasso & Castro 1999; Lech et al. 2000; Cuitiño et al. 2019). It crops out in the north-eastern Chubut Province, especially in the surroundings of the city of Puerto Madryn, the lower reaches of the Chubut River Valley, and the coastal region some kilometres south of Playa Unión (Fig. 1).
The maximum age of the Gaiman Formation is constrained by the fossils contained in the underlying Trelew Member of the Sarmiento Formation, which is assigned to the Colhuehuapian (lower Miocene) South American Land Mammal Age (Goin et al. 2007; Dunn et al. 2013). A lower Miocene age (probably Burdigalian) is estimated for the Gaiman Formation based on stratigraphical correlation and comparison to better-dated equivalent marine successions (Cuitiño et al. 2015, 2017). Evidence from extinct fishes, penguins (Cione et al. 2011), cetaceans (Buono et al. 2017; Viglino et al. 2018a, b; Paolucci et al. 2020) and a palynological assemblage recovered from the study area (Palazzesi et al. 2006) also indicates a lower Miocene age. The minimum age is constrained by the overlying late Miocene Puerto Madryn Formation (Scasso & Castro 1999; Cuitiño et al. 2017).

South-East Santa Cruz Province – Monte León Formation

One specimen (AMNH 9485) comes from the mouth of the Santa Cruz River, Santa Cruz Province (True 1910; Fig. 1). The area is the type locality of the Punta Entrada Member of the Monte León Formation, which is composed of tuffaceous mudstones and tuffaceous sandstones deposited in inner shelf environments (Parras & Griffin 2009; Parras & Cuitiño 2018). The age of the Punta Entrada Member at the mouth of the Santa Cruz River is constrained by Sr isotopes at about 18–19 Ma (Burdigalian; Parras et al. 2012).

Taxonomic background

Moreno (1892) described and illustrated (pl. XI) a new odontocete genus and species, Notocetus Van Benedeni, based on a complete skull with some postcranial remains (MLP 5-5) and an incomplete skull (MLP 5-17). Under Article 32.5.2.2 of the ICZN, the correct name for this species is Notocetus vanbenedeni Moreno, 1892.

Lydekker (1893, pp. 12, 13, pl. VI) noted that the genus name defined by Moreno (1892) was preoccupied by genus Notocetus Ameghino, 1891 based on a mysticete tympanic bulla. Thus, he re-named the genus and species as Argyrodolphis benedeni. He also added a third specimen to the species (MLP 5-10). Ameghino (1894, p. 182) also considered Notocetus Moreno, 1892 and Notocetus Ameghino, 1891 to be homonyms, and gave the new name Diochotichus van Benedeni Ameghino, 1894 to this odontocete taxon. Later, True (1910) also recognized the homonymy of Notocetus Moreno, 1892 and used the name Diochotichus vanbenedeni Ameghino, 1894 to describe a new referred specimen for the species (AMNH 9485). Palmer (1904) and Kellogg (1923) also followed this criterion. However, both Cabrera (1926) and Simpson (1945) consider this pre-occupation invalid. As Cabrera (1926: 391) further explained, the derivations of the name Notocetus Moreno, 1892 and Notocetus Ameghino, 1891 are different, and thus they are not homonyms. Moreover, Article 56.2 of the ICZN states that a one-letter difference does not make two genus names homonyms, and we agree. Therefore, given that the initial homonymy is incorrect and that Moreno’s name has been the most widely used in the scientific literature (over 70 publications; see Supplemental material S1), under the Principle of Priority of Article 23.1 of the ICZN, the valid genus and species name is Notocetus vanbenedeni Moreno, 1892.

Systematic palaeontology

Order Cetacea Brisson, 1762
Unspecified rank Neoceti Fordyce & de Muizon, 2001
Suborder Odontoceti Flower, 1867
Superfamily Platanistoidea (Gray, 1863)
Simpson, 1945
Genus Notocetus Moreno, 1892

1892 Notocetus Moreno: 397, pl. II.
1893 Argyrodolphis Lydekker: 12, pl. VI.
1894 Diochotichus Ameghino: 182; Palmer 1904: 35; True 1910: 19, pls I–V; Kellogg 1923: 35.

Type species. Notocetus vanbenedeni Moreno, 1892.

Diagnosis. As for the type and only species, below.

Notocetus vanbenedeni Moreno, 1892
(Figs 2–12; Tables 1–3)

1892 Notocetus Van Benedeni Moreno: 397, pl. II.
1892 Notocetus vanbenedeni Moreno: 397, pl. II.
1893 Argyrodolphis benedeni Lydekker: 12, pl. VI.
1894 Diochotichus van Benedeni Ameghino: 182.
1894 Diochotichus vanbenedeni Ameghino: 182; True 1910: 19, pls I–V; Kellogg 1923: 35.

Holotype. MLP 5-5: almost complete skull and mandibles, and five vertebrae (atlas, portion of the axis, three other cervicals). The skull is covered with glue from the original preparation and remains of matrix are still attached, so sutures are not visible. The vertebrae were not figured but were described; they are now missing from the collection.

Other referred specimens. MLP 5-10: incomplete skull and almost complete mandibles (mentioned by Lydekker [1893] but not described in detail or figured); MLP 5-
17: incomplete skull, almost complete mandibles, and a fragment of atlas (individual included in original description of the species by Moreno [1892]); AMNH 9485: incomplete skull and mandibles, seven vertebrae (the atlas and six thoracics) and ribs (individual described in True [1910]); AMNH 29026: incomplete skull, several teeth, incomplete vertebrae, incomplete ribs and right scapula (individual described in de Muizon [1987]); MPEF-PV 1660: incomplete skull (undescribed individual); MPEF-PV 1117: incomplete skull and one loose fragment (undescribed individual); MPEF-PV 1118: six fragments of mandibles and two loose fragments, one left periotic and one right tympanic bulla (undescribed individual); MPEF-PV 1119: incomplete skull and seven loose fragments (undescribed individual); MPEF-PV 1120: incomplete skull and two teeth (undescribed individual); MPEF-PV 1375: three loose teeth, two right and one left tympanic bullae, and three right and three left periotics (undescribed individuals); MPEF-PV 1804: incomplete skull, one tooth, incomplete left mandible, 22 almost complete vertebrae (six cervicals, 11 thoracics and six lumbars) and 18 incomplete ribs, still lodged in a jacket (individual described in Uyua [2011]); MPEF-PV 681: incomplete skull (undescribed individual); MPEF-PV 683: incomplete skull, incomplete vertebra and two indeterminate fragments

| Measurements | MLP 5-5 (holotype) | MPEF-PV 1660 | MPEF-PV 1804 | MPEF-PV 2580 |
|--------------|--------------------|--------------|--------------|--------------|
| **Total length**, from most anterior point to posterior margin of condyles | 595+ | 625+ | 421+ | 481.5+ |
| **Length of rostrum** | 384+ | 439+ | 235+ | 283+ |
| **Width of rostrum at base** | 119 | 144.5 | 116 | 149 |
| **Width of rostrum at half its length** | 41 | 55 | – | 70 |
| **Width of premaxillae at rostrum half length** | 24 | 25 | – | 44 |
| **Width of maxilla at rostrum half length** | 17 | 25 | – | 26 |
| **Distance from tip of rostrum to external nares** | 455 | 542+ | – | 371+ |
| **Distance from tip of rostrum to internal nares** | 440 | 515+ | 305+ | 353+ |
| **Anteroposterior length of antorbital notch** (right and left, respectively) | 8 | 10 | 27 | 6 |
| **Lateromedial width of antorbital notch** (right and left, respectively) | 11 | 5.6 | 26 | 9 |
| **Length of premaxillary foramen** (right and left, respectively) | 8 | 16 | – | 8 |
| **Width of premaxillary foramen** (right and left, respectively) | 5 | 19 | – | 12 |
| **Width of premaxillae at a line across posterior limit of antorbital notches** | 3 | 8 | – | 7 |
| **Width of premaxillary sac fossa** (right and left, respectively) | 48 | 35 | – | 35 |
| **Greater preorbital width** | 216 | 231+ | – | 233 |
| **Greater postorbital width** | 247 | 253+ | – | 267 |
| **Length of left orbit**, from apex of preorbital process to apex of postorbital process | 71 | – | 67 (†) | 62 |
| **Greatest anterior width of nasals** | 46 | 43 | – | 54 |
| **Greatest length of nasals** | 20 | 19 | – | 33 |
| **Greatest length of frontal at vertex** | – | – | – | 19 |
| **Greatest width of frontal at vertex** | – | – | – | 35 |
| **Greatest length of left temporal fossa** | 120 | – | – | 116 |
| **Greatest width of left temporal fossa** | 49 | – | – | 60 |
| **Bizygomatic width** | 260 | – | 283 | 286 |
| **Left squamosal length**, from anterior tip of zygomatic process to ventral tip of postglenoid process | 96 | – | 104~ (†) | 100 |
| **Number of teeth, upper row** (right and left, respectively) | 22+ | 20+ | 8+ | 14+ |
| **Number of teeth in mandibles** (right and left, respectively) | 18+ | – | 8+ | 14+ |
| **Greatest length of left ramus** | 225+ | – | – | – |
| **Length of left mandibular fossa** | 133 | – | – | – |
| **Length of mandibular symphysis** | 202+ | – | – | – |
| **Breadth of mandibles at base of symphysis** | 49 | – | – | – |

**Table 1.** List of skull and mandible measurements of the most relevant specimens of *Notocetus vanbenedeni* (in mm). For additional specimens measured, see Supplemental material S2. Symbols: (†), measurement from the opposite side; +, nearly complete; ~, uncertainty in the measurement taken.
**Table 2.** List of periotic and tympanic bulla measurements of the most relevant specimens of *Notocetus vanbenedeni* (in mm). For additional specimens measured, see Supplemental material S2.

| Measurements                                                                 | MPEF-PV 1804 (right) | MPEF-PV 2580 |
|------------------------------------------------------------------------------|-----------------------|--------------|
| Periotic                                                                      |                       |              |
| Maximum anteroposterior length, from anterior apex of anterior process to apex of posterior process | 46                    | 41           |
| Width of periotic across cochlear portion and superior process, at the level of internal acoustic meatus | 17                    | 15           |
| Least distance between the margins of fundus of internal auditory meatus and aperture of vestibular aqueduct | 2                     | 1            |
| Least distance between the margins of fundus of internal auditory meatus and aperture of cochlear aqueduct | 1                     | 1            |
| Length of articular facet of posterior process of the periotic for the posterior process of tympanic bulla | 11                    | 11.5         |
| Antero-posterior length of cochlear portion                                | 14.5                 | 14           |
| Dorsoventral depth at level of fovea epityubiaria                           | 13                   | 12           |
| Transverse width of pars cochlearis from internal edge to fenestra ovalis   | 10                   | 10           |
| Maximum width of anterior process at base                                  | 13                   | 13           |
| Length of anterior process from anterior apex to level of posterior of mallear fossa | 30                   | 25           |
| Length of posterior process                                                | 16                   | 13           |
| Tympanic bulla                                                              |                       |              |
| Standard length of tympanic bulla, distance from anterior tip to posterior end of outer posterior prominence | 53                    | –            |
| Distance from anterior tip to posterior end of inner posterior prominence    | 51                   | –            |
| Distance from postero-ventral tip of outer posterior prominence to tip of sigmoid process | 27                    | –            |
| Distance from postero-ventral tip of outer posterior prominence to tip of conical process | 29                    | –            |
| Width of tympanic bulla at the level of the sigmoid process                 | 29                   | –            |
| Height of tympanic bulla, from tip of sigmoid process to ventral keel       | 44                   | –            |
| Width across inner and outer posterior prominence                           | 29                   | –            |
| Greatest depth of interpromontinal notch                                    | 5                    | –            |
| Width of upper border of sigmoid process                                    | 12                   | –            |

**Table 3.** List of measurements of atlas, axis and scapula of *Notocetus vanbenedeni* (in mm). For additional postcrania measurements, see Supplemental material S2. Symbols: +, nearly complete.

| Measurements                        | MLP 5-5 (holotype) | AMNH 29026 | MPEF-PV 1804 |
|-------------------------------------|--------------------|------------|--------------|
| Atlas                               |                    |            |              |
| Greatest height                     | 75.5+              | –          | 89+          |
| Greatest width                      | 90+                | –          | 110+         |
| Axis                                |                    |            |              |
| Greatest height                     | –                  | –          | 106          |
| Greatest width                      | –                  | –          | 99           |
| Scapula                             |                    |            |              |
| Greatest preserved height           | –                  | 102        | –            |
| Greatest preserved length           | –                  | 103        | –            |
| Length of acromion process          | –                  | 37         | –            |
| Dorsoventral width of acromion process | –                  | 23.5   | –            |
| Length of glenoid fossa            | –                  | 26         | –            |

(undescribed individual); MPEF-PV 2579: incomplete skull (undescribed individual); MPEF-PV 2580: nearly complete skull (undescribed individual); MLP 87-XII-20-1: incomplete left tympanic bulla (undescribed individual); MLP 5-52: seven loose incomplete teeth (undescribed individuals); MLP 76-IX-2-9, 11 and 12: three incomplete right tympanic bullae (undescribed individuals, except MLP 76-IX2-11 and 12 which were mentioned but not described or figured by de Muizon [1987]); MLP 76-VI-1-1: 11 incomplete loose teeth (undescribed individuals); MLP 76-IX-2-5: incomplete right periotic (individual mentioned in de Muizon [1987]); MLP 77-XII-22: 13 incomplete loose teeth (undescribed individuals); MLP 17-XII-22: two rostrum fragments and one incomplete loose tooth (undescribed individual).

**Geographical and stratigraphical occurrence.** The holotype (MLP 5-5) and MLP 5-17 are from the area surrounding the city of Puerto Madryn (Moreno 1892, 37),
Chubut, Argentina. Other specimens are from Cerro Castillo; Bryn Gwyn (= Loma Blanca) on the southern margin of the Chubut River Valley; Playa Santa Isabel; and Estancia La Redonda Chica. All of these localities are in the north-eastern part of Chubut Province, Argentina, and comprise outcrops of the Gaiman Formation. Finally, one specimen comes from near the mouth of the Santa Cruz River, Santa Cruz Province, Argentina, where the Monte Leon Formation crops out (for further details, see Geological setting above).

**Age.** The Gaiman Formation (Chubut Province) and Monte León Formation (Santa Cruz Province) are both lower Miocene (Burdigalian, 20–16 Ma) (for further details, see Geological setting above).

**Emended diagnosis.** For the definition and members of the families and clades mentioned in this diagnosis, we follow the phylogenetic hypothesis obtained under implied weights with $K = 26$. The use of Platanistoidea follows de Muizon (1987) in the sense of comprising the only living genus of the clade, *Platanista*, within the family Platanistidae (see the Phylogenetic analyses section of the results for further details).

*Notocetus vanbenedeni* has a medium-size skull (average CBL: 62 cm) with a long and anteriorly narrow rostrum; teeth with short conical crown anteriorly and lateromedially compressed crown posteriorly, blunt apex, long and curved root, and accessory denticles present on the posterior teeth only. The skull has asymmetrical notches; a distinctly elevated dorsal tubercular supraorbital crest formed mainly by the frontal; temporal fossa has a roof with a frontal window; squamosal with a deep sub-circular fossa and deep and spathulate tympanosquamosal recess; vertex with a squared frontal and a deep sub-circular fossa; wide external auditory meatus; long and smoothly deflected anterior process of periotic; oval fenestra rotunda; periotic with reniform cochlear aqueduct opening and articular rim; long and deep median furrow of tympanic bulla; inner and outer posterior prominence of equal length; unexcavated dorsal margin of involucrum. Differs from *Macrosqualodelphis ukupachai*, *Dilophodelphis fordyceri*, *Medocinia tetragorhina*, *Huaridelphis raimondii*, *Araodelphis natator* and the Peruvian platanistoids (MUSM 1395, 3896, 3897 and 1484) in: widely separated premaxillae at rostrum by mesorostral groove; nasals with point on midline and gap with premaxilla at vertex; narrowly exposed squamosal in posterior view; dorsoven trally thick pars cochlearis of the periotic; larger reniform opening of the cochlear aqueduct of periotic; and shallow grooves on posterior bullar facet of periotic. Differs from the Peruvian platanistoids (MUSM 1395, 3896, 3897 and 1484) and *Araodelphis natator* in: maxilla and lacrimo-jugal forming dorsolateral edge of ventral infraorbital foramina. Further differs from *Dilophodelphis fordyceri*, *Huaridelphis raimondii* and *Araodelphis natator* in: transversely inflated premaxillae at rostrum. Differs from *Macrosqualodelphis ukupachai*, *Medocinia tetragorhina* and *Huaridelphis raimondii* in: deep neck muscle fossa in zygomatic process of squamosal. Further differs from *Macrosqualodelphis ukupachai*, *Dilophodelphis fordyceri* and *Huaridelphis raimondii* in: having nasals at same height as frontals at vertex. Differs from *Medocinia tetragorhina* and *Huaridelphis raimondii* in: nasals and frontals of the same width at vertex. Further differs from the Peruvian platanistoids (MUSM 1395, 3896, 3897 and 1484) in: rostrum narrow at mid-length; premaxillary foramen anterior to antorbital notch; medial facial crest; palatine completely covered by pterygoid in ventral view; smoothly ventrally deflected anterior process of periotic in lateral view; pyramidal process in dorsal surface of periotic; and tubular internal acoustic meatus with a circular outline.

**General description**

All specimens of *Notocetus vanbenedeni* included in the present description, albeit some are incompletely preserved, present no evident diagenetic deformation. Only
MPEF-PV 1117 is significantly deformed by crushing during burial and thus was excluded from the description and comparisons. Finally, in posterior view, MPEF-PV 1804 appears to have some deformation on the left basicranial region (squamosal-parietal-sphenoid). Unless otherwise noted, because too few individuals were available, all specimens listed above (see ‘Holotype’ and ‘Other referred specimens’ section) were considered in the present revised description of *Notocetus vanbenedeni*.

In general, all specimens studied have almost all sutures closed and a distinct nuchal crest, when preserved. Only MLP 5-10 and MPEF-PV 1660 have a closed maxilla-frontal suture at the orbital region. All these features suggest that *Notocetus vanbenedeni* is represented by nearly adult Class V individuals (Perrin 1975). The only specimen with postcranial elements, MPEF-PV 1804, has fully closed epiphyses in all the cervical, thoracic and lumbar vertebrae preserved, and thus it can be classified as an adult Class VI individual (Perrin 1975). Fragments of MPEF-PV 1119 represents the only specimen with open naso-frontal, interfrontal, internasal, frontal-supraoccipital and maxilla-frontal sutures, and thus it would be classified as a subadult Class IV–V? individual (Perrin 1975).

Finally, the average BIZYG of *Notocetus vanbenedeni* is 27 cm (based on well-enough preserved specimens), giving a reconstructed TL of 2.4–2.7 m.

**Premaxilla.** In dorsal view, the rostral portions of the left and right premaxillae (Figs 2–4; Table 1; Supplemental material S2) do not contact each other. The open premaxilla-maxillary suture is grooved (similar to that of *Phoberodon arctirostris* but shallower than that of *Pomatodelphis inaequalis*), but is closed on the anteriormost portion. At the tip of the rostrum, the premaxilla extends farther than the maxilla (MLP 5-10: 52+ mm; MPEF-PV 1660: 40+ mm). The mediolateral compression at the anterior portion of the rostrum results in the premaxilla being dorsal to the maxilla. The lateral margin of the premaxilla is straight in lateral view except in the holotype and AMNH 9485, which display a slightly curved margin. The depth of the mesorostral groove increases posteriorly, and it is only partially closed by sutured premaxillae in MLP 5-10; closed premaxillae are also present in the Peruvian *Notocetus vanbenedeni* MUSM 1395. The porcelanous portion has concave lateral margins anteriorly and narrowers posteriorly, similar to *Zarhachis flagellator* and *Pomatodelphis inaequalis*. It is narrowest at the anterior margin of the external nares and widest at about the premaxillary foramen. In ventral view, the premaxilla has bilateral sutures laterally with the maxilla and medially with the opposite premaxilla, while posteriorly it has a closed suture with the vomer. AMNH 9485, MLP 5-10 and MPEF-PV 1660 have at least two alveoli on the anterior apex of the premaxilla. Given the plesiomorphic mammalian dental formula present in archaeocetes and some stem odontocetes (e.g. Armfield et al. 2013), we infer that *Notocetus vanbenedeni* has at least two, possibly three, teeth. No specimen has the tip of the rostrum completely preserved with teeth in situ, so we cannot ascertain the presence or absence of procumbent upper teeth in the premaxilla. In *Platanista gangetica*, the premaxilla carries four alveoli (the fourth in the suture with the maxilla) and there are no procumbent teeth (Anderson 1878).

On the cranium in dorsal view, the premaxilla laterally contacts the maxilla, and medially the nasals and presphenoid. Posteriorly, it extends up to the anterior margin of the nasals (except in MPEF-PV 1117 where it seems to reach the posterior margin of the nasals) and does not contact the frontal (see True 1910, pl. 1), unlike in, for example, *Pomatodelphis inaequalis*, *Macrodelphis ukupachai*, *Dilophodelphis fordycei*, *Arktocara yakataga*, *Araeodelphis natator*, *Otekaikea marplesi* and *Waipatia maerewhenua*. The maxilla-premaxillary suture describes a sub-circular outline (Moreno 1892; True 1910). The premaxilla forms the lateral margin of the external nares, in disagreement with Moreno’s (1892) drawings. The symmetrical premaxillary foramina are just anterior to the antorbital notch, contrary to observations of Bianucci et al. (2014) in the Peruvian *Notocetus vanbenedeni* MUSM 1395, and are either elongated or circular (AMNH 9485). The anteromedial sulcus is developed in MPEF-PV 1660 and AMNH 9485, extending for up to 67 mm. On the other hand, the postrolateral sulcus is strongly curved with a semicircular path (but straight in MPEF-PV 1660), delimiting almost the entire length of the premaxillary sac fossa. The shallow postrolateral sulcus extends for up to 36 mm and in MPEF-PV 1660 this sulcus is indistinct. Because the resulting prenarial triangle has a rugose surface and striations (as, for example, in *Mesoplodon grayi*), we can infer the presence of the nasal plug muscle in *Notocetus vanbenedeni*. The bilaterally symmetrical oval premaxillary sac fossa dips slightly medially (AMNH 9485, see True 1910), which, together with the supraorbital crest (see below), results in a circumnarial basin. A similar basin is present in *Huaridelphis raimondii*, *Dilophodelphis fordycei*, *Zarhinoctes errabundus* and platanistids. The suture of the premaxilla with the nasal is visible but closed. The premaxilla contributes medially to the medial facial crest (*sensu* Fordyce 1994, p. 149; see below). In MPEF-PV 1660, the premaxillary cleft is anterolateral to this crest, which is longer on the left side. The cleft is shallow and...
descends towards the external nares and premaxillary sac fossa, with a resulting thin and triangular posteromedial splint of the premaxilla. The posterolateral plate of the premaxilla in MPEF-PV 1660 (Fig. 2) is wide and long anteroposteriorly, with a rounded posterior profile in lateral view. It extends farther posteriorly than the porcelanous portion of the premaxilla. This structure could not be identified in the holotype, in AMNH 9485 or in MPEF-PV 681.

Maxilla. In dorsal view at the rostrum, the maxilla (Figs 2–5; Table 1; Supplemental material S2, S5) is narrow anteriorly and widens posteriorly, becoming narrower again near the maxillary flange. A dorsal infraorbital foramen opens at the base of the rostrum, which is larger on the right side. A dorsal infraorbital foramen opens at the base of the rostrum, which is larger on the right side. A posterior dorsal infraorbital foramen is visible on the left in MPEF-PV 1660 and on the right in MPEF-PV 681. The antorbital notches are asymmetrical, being wider and ‘U’-shaped on the left side; this pattern of asymmetry is similar to Waipatia maerewhenua and Huaridelphis raimondii, and was also reported by Bianucci et al. (2014) for the Peruvian Notocetus vanbenedeni MUSM 1395. The posterior wall of the notch is slit-like, as in Prosqualodon australis, and extends posteriorly as a marked fissure; the frontal and maxilla form the dorsal margin (although possibly the lacrimojugal is involved in some specimens, see below), while the lacrimojugal contributes ventrally. Anterior to the antorbital notch and on the lateral margin of the maxilla is the asymmetrical maxillary flange, more developed on the right side as in Waipatia maerewhenua. The dorsal surface of the flange is concave and thins posteriorly.

In ventral view, the maxilla bears 19–23 alveoli on each side, all single-rooted, with the most posterior alveolus 46–97 mm in front of the antorbital notch. The alveolar groove is sub-parallel to the sagittal axis, with

Figure 2. Dorsal view of skull of Notocetus vanbenedeni (MPEF-PV 1660). A, without labels; and B, with labels. Solid lines indicate sutures, and dashed lines indicate important structures.
the most posterior alveoli slightly more medially placed (see also Supplemental material S5). Most alveoli are circular but the most posterior ones are oval, and of variable size (except in MPEF-PV 1117, where all alveoli are of the same size). They have a raised posterior margin, whilst the anterior margin is almost indistinct. The interalveolar septa range from 6 to 16 mm long and decrease posteriorly. At about the last two alveoli, the medially located greater palatine foramina indicate the approximate position of the maxillo-palatine suture. In MPEF-PV 1660, the maxilla presents a palpable elongated concave surface from the last alveoli up to about the antorbital notch. Also, this specimen presents a foramen at the premaxillo-maxillary suture on each side, around 59+ mm from the tip of the rostrum. This foramen is possibly associated with the maxillary labial rami of the infraorbital artery (Costidis & Rommel 2016).

In dorsal view, the cranial portion of maxilla contacts the premaxilla, nasal and frontal, and posteriorly it contacts the supraoccipital. Posterior to the external nares and together with the premaxilla there is an asymmetrical laterally convex median facial crest; in MPEF-PV 1117 it is not easy to distinguish. There is a gap (MPEF-PV 1660: 4 mm; AMNH 9485: 17 mm) between the maxilla at the antorbital notch and the maxilla at the orbital region; so, the maxilla here has a wedge-shaped outline in anterolateral view (Supplemental material S5). At the orbit, the thin maxilla does not completely cover the frontal anteriorly, leaving a narrow exposure of the latter. The characteristic supraorbital crest of Notocetus vanbenedeni is formed by a thin layer of the maxilla and mainly the frontal (see also True 1910 for AMNH 9485), dorsal to the preorbital process of the frontal and posterolateral to the antorbital notch. A similar crest is also present in several platanistoids, for example Dilophodelphis fordycei, Squalodelphis fabianii and Huaridelphis raimondii (Supplemental material S4). Other extant odontocetes that present a non-pneumatized supraorbital crest are Inia geoffrensis and Lipotes vexillifer. The supraorbital crest present in Notocetus vanbenedeni is homologous to the extremely well-developed pneumatic supraorbital crest of Platanista gangetica (albeit mainly formed by the maxilla in the latter species).

In ventral view, the ventral infraorbital foramen is posteromedial to the antorbital notch and anterior to the optic foramen. It is oval to circular in shape and formed dorsolaterally by the maxilla and lacrimojugal, and posteromedially by the maxilla with a possible minor contribution of the frontal. A frontal window exposes the maxilla in ventral view at the roof of the temporal fossa (see Frontal description below).

**Palatines.** In ventral view, each palatine (Figs 3, 5) contacts the maxilla anterolaterally, medially with the vomer and ventrolaterally with the pterygoid. The major and minor palatine foramina indicate the position of the anterior extension of the maxillo-palatine suture, and the two palatines contact anteriorly. The palatine is mediolaterally compressed and remains a thin strip of bone lateral to the vomer, and extending posteriorly to the ventral section of the anterior wall of the nares. Given the weak parallel striations of the medial portion of the palatine and the vomer with the medial lamina of the pterygoid, and the contact surface between the most lateral portion of the maxilla and the lateral lamina of the pterygoid (see below), we infer that the palatine was hidden by the pterygoid. This morphology would be similar to the condition seen in Platanista gangetica (see also Flower 1867; Fraser & Purves 1960), where the palatine has been completely hidden by the long anterior projection of the pterygoid. However, Bianucci et al. (2014) did not agree with this interpretation in the Peruvian Notocetus vanbenedeni MUSM 1395: the authors hypothesized that the palatine extended farther anteriorly than the pterygoid and lateral to the latter, resembling for example Prosqualodon davidis and Kogia breviceps. de Muizon (1994) suggested that either a posterior extension of the maxilla or an anterior extension of the pterygoid resulted in the palatine being overlapped in squalodelphinids, a primitive condition relative to the palatine being laterally displaced in platani- stids. The morphology of the palatine of Notocetus vanbenedeni was also noted by Lambert et al. (2014) as resembling that of the squalodelphinid Huaridelphis raimondii. There is a sinuous sulcus on the right palatine of MPEF-PV 1804, extending from about the antorbital notch to the posterior margin of the ventral infraorbital foramen, possibly a palatine canal. The oral sphenopalatine foramen is posterior to the ventral infraorbital foramina and the orbital lobe of the pterygoid sinus system and medial to the ethmoid foramen.

**Pterygoid.** In ventral view, the pterygoid (Figs 3, 5) contacts dorsally with the palatine, and vomer; dorsolaterally with the maxilla; and posteriorly with the vomer, basiocipital and squamosal. This morphology is similar to that of Pomatodelphis inaequalis. MPEF-PV 1660, 1804 and 2580 have sufficient, albeit partial, preservation to allow an understanding of this region. The oral pterygoid sinus fossa is anterior to the internal nares and in MPEF-PV 1804 extends posterolaterally to the internal nares. The medial lamina of the pterygoid is ventral to the palate and vomer and extends posteriorly, contacting the basiocipital crest. The medial lamina is also involved in the lateral and posterior walls of the internal nares. On the other hand, the lateral lamina
of the pterygoid contacts with the maxilla dorsolaterally and posteriorly with the falciform process of the squamosal. There is a continuous lateral lamina of the pterygoid-falciform process also in other platanistoids such as *Huaridelphis raimondii*, *Macrosqualodelphis ukupachai*, *Zarhachis flagellator*, *Pomatodelphis inaequalis*, *Dilophodelphis fordycei* and *Platanista gangetica*.

**Nasal.** The nasal (Figs 2, 4; Table 1; Supplemental material S2) has a raised nodular dorsal surface and trapezoidal profile in dorsal view, with a generally concave and wider anterior margin (but convex in MPEF-PV 1117) and a concave posterior margin. The nasals are asymmetrical; the right is wider. In lateral view, the nasal is in the same plane as the frontal (also noted by Bianucci et al. 2014 for the Peruvian *Notocetus vanbenedeni* MUSM 1395). It contacts the cribiform plate and ectethmoid ventrally, posteriorly with the frontal, laterally with the premaxilla and maxilla, and medially with the opposite nasal. Except for the holotype (MLP 5-5), the internasal suture is distinct and open (e.g. similar to *Otekaikea*). The nasal does not roof over the external nares.

**Ethmoid.** For the identification of the bones at the narial region (Figs 2, 4), we follow Ichishima (2016). Thus, the cribiform plate and ectethmoid are involved in the posterior wall of the narial passages. The nasal septum is formed by the anterior extension of the prephenoid and markedly asymmetrical, being skewed to the left (Moreno 1892; also described for the Peruvian *Notocetus vanbenedeni* MUSM 1395 in Bianucci et al. 2014); a condition even more accentuated in *Platanista*.

Figure 3. Ventral view of skull of *Notocetus vanbenedeni* (MPEF-PV 1660). A, without labels; and B, with labels. Solid lines indicate sutures, and dashed lines indicate important structures.
Figure 4. Other views of the skull of *Notocetus vanbenedeni* (MLP 5-5). A, B, posterodorsal view; C, D, lateral view, left side; E, F, anterior view; without and with labels, respectively. Dashed lines indicate important structures.
gangetica. The cribriform plate and ectethmoid contact the nasal dorsally and the presphenoid contacts the vomer anteriorly. In the holotype (MLP 5-5) and in MPEF-PV 1117 and 1660 there is a medially convex crescentic foramen (see Godfrey 2013) on the posterior wall of the external nares, extending almost the entire length of the wall; this condition is shared with the Peruvian Notocetus vanbenedeni MUSM 1395. There are no traces of terminal nerve foramina, unlike Platanista gangetica.

Lacrimojuga. In ventral view, this bone (Figs 3, 5) contacts the frontal laterally, and the maxilla medially and anteriorly; it forms the ventral portion of the antorbital notch. In MPEF-PV 681, 1660 and 1804 the lacrimojugal also extends dorsally, forming the posterior wall of this notch. In these specimens (except possibly MPEF-PV 1660), the lacrimojugal also contributes to the dorsolateral edge of the ventral infraorbital foramen. It is inferred that this bone contacted the zygomatic process of the squamosal posteriorly (see below).

Vomer. In ventral view, the rostral part of the vomer (Figs 2, 3, 5) appears between the premaxilla and maxilla until 229 mm from the tip of the rostrum (MPEF-PV 1660), forming a long narrow window. In dorsal view, MPEF-PV 1660 shows a faint suture of the vomer with the premaxillae at about 195 mm from the tip of the rostrum on the floor of the mesorostral groove.

In ventral view, the cranial part of the vomer forms the ventral portion of the nasal septum as well as the ventral portion of the medial and posterior walls of the internal nares (horizontal part or wings of the vomer), also covering part of the basisphenoid posteriorly. In the palatal region, the vomer is very thin and plate-like, contacting the palatine laterally. The striations on its surface suggest contact with the medial lamina of the pterygoid (see above). On the rostrum, the vomer is visible in ventral view from the external nares anteriorly up to its mid-length.

Frontal. In dorsal view, at the vertex, the frontal (Figs 2–5; Table 1; Supplemental material S2) contacts the nasal anteriorly, the supraoccipital posteriorly, and the maxilla laterally. It is wider than long, and the anterior and posterior margins are convex (except in MPEF-PV 1660 and 1117 which have straight posterior margins). The interfrontal suture is closed and straight. The holotype has a marked depression at the interfrontal suture, whilst MPEF-PV 1660 and 1117 have a depression at the nasofrontal suture. In lateral view, the temporal fossa extends posteriorly with a teardrop outline as in Squalodelphis fabianii. This outline is also present in the Peruvian Notocetus vanbenedeni MUSM 1395. In ventral view, there is a clear frontal window with exposure of the maxilla at the roof of the temporal fossa, as in Pomatodelphis inaequalis.

In the orbit, in dorsal view the frontal is not completely covered by the thin maxilla anteriorly and its thickened portion is involved in the supraorbital crest (see above). In lateral view, the preorbital and postorbital processes are thickened dorsoventrally and broad based. The preorbital process is anterolaterally oriented (although on the right side of the holotype it is directed anteriorly) and located higher dorsoventrally, whilst the postorbital process is short and ventrally oriented, and has a rounded apex (also found in the Peruvian Notocetus vanbenedeni MUSM 1395). The resulting orbit is widely concave albeit small in lateral view and anterolaterally oriented, although not as small as in Platanista gangetica. In lateral view, the postorbital process is separated by a few millimetres of the zygomatic process of the squamosal, whereas a neomorphic suture is present in Platanista gangetica; balaenopterids also display the same condition (e.g. Marx & Kohno 2016). In ventral view, the postorbital ridge is sharper and higher than the preorbital ridge, meeting with the preorbital and postorbital process, respectively. Between these ridges, the ethmoid foramen opens within the orbital lobe of the pterygoid sinus system (present in MPEF-PV 1804 and 1660, described for the Peruvian Notocetus vanbenedeni MUSM 1395). It seems that this foramen becomes obliterated in adult Platanista gangetica. The suture with the orbitosphenoid is closed and anteriorly the suture with the maxilla is variably distinct.

Parietal. In lateral view, the triangular parietal (Figs 5, 6; Table 1; Supplemental material S2) forms the postero- medial wall of the temporal fossa. It contacts the frontal anteriorly and medially, with the squamosal laterally and with the exoccipital posteriorly. At the vertex, none of the specimens of Notocetus vanbenedeni had an exposed interparietal.

In ventral view at the basioccipital region, there is a quadrangular parietal between the exoccipital and the alisphenoid and medial to the squamosal, usually with a visible suture. As expected, it does not contribute to the foramen ovale or the foramen spinosum but instead forms the postero-lateral margin of the cranial hiatus. Only in MPEF-PV 1804 is the parietal exposed adjacent to rather than within the periotic fossa.

Supraoccipital and exoccipital. The supraoccipital (Figs 4–6) contacts the frontal and maxilla anteriorly and the parietal laterally, and posterovertrally it merges with the exoccipital, with no distinct suture. In posterior view, the supraoccipital has a squared vertical plate (similar to that of the platanistoids Squalodelphis
Figure 5. Ventral view of the skull of *Notocetus vanbenedeni* (MPEF-PV 1804). A, detail of basicranial region with tympanic bulla; B, detail of palatal and orbital area region. Solid lines indicate sutures, and dashed lines indicate important structures. **Abbreviations:** ali, alisphenoid; basiocc, basioccipital; basisph, basisphenoid; exo, exoccipital; fr, frontal; lj, lacrimojugal; md, mandibles; mx, maxilla; orb, orbitosphenoid; pal, palatine; par, parietal; pre, presphenoid; pt(l), lateral lamina of pterygoid; pt(m), medial lamina of pterygoid; sq, squamosal; v, vomer.
fabianii, Dilophodelphis fordycei and Huaridelphis raimondii), with two marked concavities on each side. In the holotype, these concavities are delimited medially by a weak but distinct external occipital crest (similar to *Platanista gangetica*). The supraoccipital forms the posterior wall of the cranium, unlike in *Platanista gangetica* which has contributions of the parietal as well. The bilaterally sigmoidal nuchal crest connects through a dorsoventrally straight border with the parietal at the temporal crest and is different than the narrow, anteriorly pointed semicircular nuchal crest in *Platanista gangetica*.

In lateral view, the temporal crest is more developed posteriorly and the exoccipital (Figs 4–6) projects concavely forward at about the level of the fossa for the sternocephalicus muscle of the squamosal. The robust and ventrally projecting paroccipital process has the posterolateral sinus fossa for the posterior extension of the peribullary sinus in anteroventral view, although this is not clear in the holotype. There is no clear articulation surface for the stylohyoid.

In posterior view, the occipital condyles are robust, higher than wide, thick anteroposteriorly, and with a smooth rounded external surface. They present a short pedicle and ventral and dorsal condyloid fossae, the latter curving over the condyle. The condyles are arranged laterally in a parallel manner, as in *Platanista gangetica*. The oval foramen magnum has no distinct opisthion and the intercondyloid notch is ‘U’-shaped. The jugular notch has a dorsally concave profile, and a deep, dorsoventrally straight border with the parietal at the posteromedial extension of the tympanic process, unlike de Muizon (1987) described (although it is straighter in the holotype and MPEF-PV 1804) and the process is anteromedially oriented, as in *Platanista gangetica*. The short and anteroposteriorly thick postglenoid process is ventral to the ‘C’-shaped deep fossa for the sternocephalicus (Cotten et al. 2008; neck muscle fossa *sensu* Fordyce 1981); however, MPEF-PV 1660 and 1804 have two smaller fossae. There is no distinct surface for insertion of this muscle on the lateral surface of the posttympanic process, unlike de Muizon’s (1987) description for AMNH 29026. Posterior to the postglenoid process, a wide and concave external auditory meatus opens, delimited posteriorly by the posttympanic process of the squamosal. The meatus is narrower than in *Waipatia maerewhenua* but wider than in *Aondelphis talen* and *Platanista gangetica*.

In ventral view, the zygomatic process has a concave surface (more marked in MPEF-PV 1804), with a rounded surface for contact with jugal near its apex. A ridge makes the inner margin of the glenoid surface and the lateral margin of the tympanosquamosal recess. This recess, which houses the middle sinus (Fraser & Purves 1960) is deep and spathulate, with clear lateral, medial and posterior margins. It descends from the subtemporal crest down the medial face of the postglenoid process with no extension farther anteriorly on the zygomatic process. Posteromedially, the recess is deepest towards the external auditory meatus (as in the Peruvian *Notocetus vanbenedeni* MUSM 1395) and the low anterior meatal crest marks its posterior extension. The tympanosquamosal recess of *Notocetus vanbenedeni* has a similar shape to that of *Waipatia maerewhenua*, *Squalodon calvertensis*, *Zarhachis flagellator*, *Pomatodelphis inaequalis* and *Lipotes vexillifer*; and is shallower than that of *Platanista gangetica*.

The thin and anteromedially oriented falciform process marks the posteromedial extension of the tympanosquamosal recess; anteriorly the process extends up to the posterolateral margin of the subtemporal crest. There is a splint of alisphenoid just medial to the falciform process with a closed suture. In MPEF-PV 2580 the external foramen ovale or foramen pseudo-ovale (*sensu* Fordyce 1994) is preserved on the dorsal margin of the continuous falciform process of the squamosal-lateral lamina of pterygoid (Supplemental material S5). Thus, in *Notocetus vanbenedeni* the mandibular nerve exits...
Figure 6. Details of the squamosal of *Notocetus vanbenedeni*. A, C, lateral view; B, D, dorsal view; and G, H, ventral view; without and with labels, respectively (MPEF-PV 1660); E, F, ventral view without and with labels, respectively (MPEF-PV 1117). Solid lines indicate sutures, and dashed lines indicate important structures. *Abbreviations*: ali, alisphenoid; exo, exoccipital; par, parietal; sq, squamosal.
through a bony canal, similar to (for example) *Platanista gangetica* and *Eurhinodelphis longirostris* (Lambert 2004). Although incompletely preserved, we can infer the presence of the spiny process (*sensu* de Muizon 1987); when the periotic is *in situ*, the spiny process would articulate with the lateral surface of the periotic (see below), between the posterior process and the epitympanic hiatus. The ventral surface of the post-tympanic process has parallel-sided sulci. The small and irregular periotic fossa is smaller than in *Waipatia maerewhenua* and has contributions from the parietal and (variably) the alisphenoid, both usually with a closed suture. In MPEF-PV 1117 and 1804, the foramen spinosum is located at about the medial margin of the periotic fossa, usually formed by the alisphenoid and/or parietal.

The fossa for the articular rim (*sensu* Viglino et al. 2018a) is on the medial surface of the squamosal, postero-dorsal to the external auditory meatus, and at the base of the posttympanic process. Here, the articular rim of the periotic contacts the squamosal (see below). The fossa for the articular rim can also be identified in other platanistoids, such as *Awamokoa tokarahi*, *Zarhachis flagellator* and *Pomatodelphis inaequalis*. The sub-circular fossa (*sensu* de Muizon 1987) is here defined as a fossa within the squamosal, antero-dorsal to the spiny process, postero-medial to the falciform process, and medial to the tympanosquamosal recess (for further details, see Viglino et al. 2018a). When the periotic is *in situ* among the *Notocetus* specimens, it appears that the lateral tuberosity of the periotic might lie in this fossa on the squamosal; otherwise, it is of unknown function. The sub-circular fossa has variable depth (deep in the holotype, MPEF-PV 1117 and AMNH 29026; shallow in MPEF-PV 1660; and almost indistinct in MPEF-PV 1804), and usually has a rounded outline. There is also some variation among platanistoids; it is shallow in *Squalodelphis fabianii*, *Zarhachis flagellator* and *Pomatodelphis inaequalis*, and deep in the Peruvian *Notocetus vanbenedeni* MUSM 1395. It is not visible in *Zarhinchetus errabundus*. As for *Otekaikea* and *Waipatia*, the sub-circular fossa would be homologous to the anterior portion of the periotic fossa.

**Sphenoid.** The alisphenoid (Figs 3, 5, 6) sutures laterally with the squamosal at the base of the falciform process, and posteriorly with the parietal. It forms the anterolateral margin of the cranial hiatus, as well as the posteromedial margin of the subtemporal crest. In dorsal view, a small portion of the alisphenoid is visible at the floor of the temporal fossa. In MPEF-PV 1117, the outer margin of the foramen ovale is preserved on the left side of the basicranium, marking the origin of the groove for the mandibular nerve. It is not clear what other bones formed the foramen ovale. In MPEF-PV 1804, the foramen ovale was more of a notch at the cranial hiatus and only formed by the alisphenoid. The groove for the mandibular nerve extends forward and dorsally, remaining on the alisphenoid and reaching the subtemporal crest at the external foramen ovale. There is a deep circular fossa for the pterygoid sinus system on the anterior portion of the alisphenoid, medial to the falciform process and lateral to the basioccipital crest.

In MPEF-PV 1804, the optic canal, dorsoventrally long optic foramen, and ethmoid foramen mark the presence of the presphenoid and orbitosphenoid (Figs 3, 5, *Platanista gangetica*), on the contrary, has a minute optic foramen, almost obliterated in adults (Anderson 1878; Pilleri 1974). The long and narrow optic canal ends ventrally in a rounded and large foramen, probably the orbital fissure, dorsal to the lateral lamina of the pterygoid and medial to the alisphenoid. In addition, this specimen presents a groove for the maxillary nerve on the posterolateral margin of the optic canal, extending posteriorly towards the possible foramen rotundum, a condition similar to that in *Papahu taitapu*.

In ventral view, the basisphenoid (Fig. 5) contacts the basioccipital posteriorly and the vomer anteriorly. In MPEF-PV 1804, in lateral view, the ventral carotid foramen is on the lateral side of the basioccipital crest, slightly anterior to the foramen ovale; the latter probably marks the anteroposterior level of the synchondrosis with the basioccipital.

**Periotic.** For the purpose of description, the isolated periotic is placed sitting in a stable position on a flat surface with the fenestra ovalis facing ventrolaterally, to produce a ventral view. The periotic (Fig. 7; Table 2; *Supplemental material* S2) presents a somewhat rounded to squared pars cochlearis; an anteriorly oriented and short anterior process; and a long, robust and posteroventrally oriented posterior process.

The anterior process is short, dorsoventrally thick in lateral view, and laterally compressed most obviously in dorsolateral view. It has a variably developed medial tubercle in medial view. In lateral view, the anterior process is oriented anteromedially with a sharp apex at the anteroventral angle, indicating the distal extension of the anterior bullar facet. In ventral view, the oval, deep, grooved and smooth anterior bullar facet is bounded by variably raised parallel-sided margins; it is narrower and shorter than the posterior bullar facet. A ‘C’-shaped parabullary sulcus (*sensu* Tanaka & Fordyce 2014) extends laterally to the anterior bullar facet, on the lateral side of the anterior process. It is similar to that of *Otekaikea* but deeper than that of *Waipatia maerewhenua*. The parabullary sulcus generally merges posteriorly with the narrow and shallow anteroexternal sulcus (*sensu* Tanaka & Fordyce 2014) and presents an associated foramen in
MPEF-PV 1375 and 1804 (Fig. 7F, foramen). The anterointernal sulcus, when distinct, extends from anterior to the lateral tuberosity to the anterior end of the dorso-medial surface of the anterior process. Both sulci are also present in the Peruvian *Notocetus vanbenedeni* MUSM 1395, but only the anteroexternal sulcus was described (Bianucci *et al.* 2014). The fovea epitubaria is anteroposteriorly long, and saddle-shaped but shallow, with distinct anterior and medial margins. There is a variably shaped anterointernal sulcus, medial to the fovea epitubaria, anterior to the medial tubercle and at the base of the anterior process (Supplemental material S5). Similarly, an anterointernal sulcus was described for *Waipatia maerewhenua*, and it was identified in *Squalodon calvertensis* (although very shallow and groove-like) and *Squalodelphis fabianii* (although more anteriorly placed). An anterointernal foramen could only be recognized in MPEV-PV 1375-6 and 1375-7.

There is a variably developed vestigial dorsal crest – which de Muizon (1987) described and labelled as a

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**Figure 7.** Left periotic of *Notocetus vanbenedeni* (MPEF-PV 1804). A, dorsal view; B, medial view; C, ventromedial view; D, ventral view; E, lateral view; F, dorsolateral view; G, posterior view; H, anterior view. Dashed lines indicate important structures.
superior process on AMNH 29026 – lateral to the internal acoustic meatus, and on the anterior process. It is uncertain whether a variable tubercle at the anterior process here is the anterodorsal angle; it is bounded medially by a deep and triangular concave surface (Fig. 7H, concave surface?), similarly to Waipatia maerewhenua. Anteriorly, a rough-surfaced flattened anterior keel descends from the prominent tubercle to the tip of the anterior process; the keel has a rounded lateral margin and a creased medial margin. When the periotic is in situ, the anterior keel contacts the falciform process of the squamosal, as in Platanista gangetica. In dorsal view, a distinct dorsal tuberosity is separated from the rest of the posterior process by a distinct narrowing, a feature noted by de Muizon (1987) for AMNH 29026. Usually, a crest follows this tuberosity posteriorly to the apex of the posterior process. Lateral to the internal acoustic meatus is a rudimentary and short pyramidal process, similar to the condition in an unnamed squalodontid (Luo & Eastman 1995) and Papahu taitapu.

The somewhat rounded to squared pars cochlearis is moderately inflated, longer than wide, with no visible median promontorial groove. It has a convex medial margin, and a marked anterointernal and more-rounded posterointernal angles (sensu Fordyce 1994). In medial view, the anterior incisure has a few visible ridges. The anteriormost pars cochlearis at the anterior incisure has a variably smooth tear-shaped area of raised bone (Fig. 7D, anterior incisure and concave surface) facing forward and slightly ventrally. The raised bone may be a contact for the accessory ossicle or, less likely because of its orientation, an origin for tensor tympani muscle. This feature was also observed in Squalodon calvertensis and it is less developed in Platanista gangetica, Phocagenus venustus and Squalodelphis fabianii. The raised feature was illustrated by de Muizon (1987) for AMNH 29026 without comment. Variably, the anterointernal angle presents a small nodule.

The sub-circular fenestra rotunda has a shallow and short slit on the posterior margin. The larger aperture for the cochlear aqueduct is reniform with distinct ridges, located near the posterointernal angle of the pars cochlearis (circular in AMNH 29026 and in the Peruvian Notocetus vanbenedeni MUSM 1395). It differs from Platanista gangetica, which has a minute aperture for the cochlear aqueduct. The deep and transversely elongated oval to sub-circular aperture for the vestibular aqueduct is located lateroposteriorly to the internal acoustic meatus, level with the aperture for the cochlear aqueduct. The two apertures are widely separated, more than in Waipatia maerewhenua and Otekaikea but similarly to Squalodelphis fabianii.

The tubular internal acoustic meatus is sub-oval to sub-circular, as de Muizon (1987) described for AMNH 29026, opening about mid-length on the pars cochlearis; there are no thick ridges around the meatus, unlike in Platanista gangetica. The Peruvian Notocetus vanbenedeni MUSM 1395 has a tear-shaped internal acoustic meatus (Bianucci et al. 2014). The meatus contains four key features: the proximal opening of the facial canal; the foramen singulare; the spiral cribriform tract; and the area cribrosa media. Anteriorly to the meatus, a small canal or slit opens forward at the small hiatus Fallopian, with the slit passing into the anterior incisure. The proximal opening of the facial canal is oval; the minute foramen singulare is circular as in Squalodelphis fabianii, and is smaller than that of Zarhinocetus errabundus, whilst slightly larger than that of Platanista gangetica, Zarhachis flagellator and Phocagenus venustus. However, Ichishima et al. (2021) questioned the identification of this foramen as defined by Mead & Fordyce (2009). Future projects including the cochlea reconstruction should aid in the correct identification of the foramina present in the internal acoustic meatus of Notocetus vanbenedeni. A distinct thick transverse crest separates these foramina from the spiral cribriform tract and area cribrosa media; it is variably low or high and similar to the condition found in Platanista gangetica. de Muizon (1987) illustrated the transverse crest of AMNH 29026 but did not describe it. The rounded spiral cribriform tract widens ventrally so that its margins are not all visible.

On the body of the periotic in ventral view, the mallear fossa is shallow, anteroposteriorly longer than wide; it is smaller than in Platanista gangetica. The mallear fossa has thick anterior and posterolateral ridges, and sometimes is slightly elevated with respect to the anterior process. Medially, the apex of the mallear fossa is bounded by the posterior end of the anterior incisure, similar to the condition found in Platanista gangetica. The variably developed lateral tuberosity may project beyond the lateral border of the periotic; its posterior face is variably grooved, but whether this is for the spiny process or for another feature is uncertain. When the periotic is articulated, the lateral tuberosity is anteromedial to the spiny process and probably ventral to the foramen spinosum. The circular distal opening of the facial canal is small compared with that of Waipatia maerewhenua, and it is slightly anterior to the fenestra ovalis, as in Otekaikea. Posteriorly, the narrow facial sulcus extends along the medial and posterior edge of the posterior process, immediately dorsal to the facial crest; the sulcus widens and shallows posteriorly. A small, sub-oval, shallow fossa incudis is located lateral to the facial crest and level with the fenestra ovalis;
From the fenestra ovalis by a narrow ridge. It is stapedial muscle is anteroposteriorly long, separated fabianii and condition found in elliptical (sharper edge anteromedially), similar to the fossa in AMNH 29026. The fenestra ovalis is small and in, for example,ior process. Homologous structures appear to be present just anterior to the concave lateral surface of the poster-

PV 1804, 1375, MLP 76-IX-2-5 and AMNH 29026), AMNH 29026. There is a concave surface (Fig. 7F) on
groove on the medial edge of the posterior process.  

The long posterior process is posteroventrally ori-

ated. In ventral view, the posterior bullar facet is obliquely elongated and sub-rectangular (sub-parallel-
sided), blunt-ended and widest anteriorly, similar to what de Muizon (1987) described for AMNH 29026. It is smooth to variably ridged, and slightly concave along the long and transverse axes. Only the right periotic of MPEF-PV 1804 has thickened lateral and medial mar-
gins delimiting the posterior bullar facet, apparently similar to what de Muizon (1987) illustrated for AMNH 29026. There is a concave surface (Fig. 7F) on the lateral side of the posterior process, offunction or homology. MLP 76-IX-2-5 and MPEF-PV 1375 have a tiny posteroexternal foramen on the lateral view, anteriorly, AMNH 29026 presents a thin antero-
dorsal crest extending posteriorly to about the broken base of the anterior pedicle of the malleus. The posterior process was described and figured by de Muizon (1987) and by True (1910) as follows (AMNH 29026 and 9485). The rectangular posterior process is long and dorsoventrally thick and oriented obliquely posterolaterally. It extends farther posteriorly than the bulla, unlike in Platanista gangetica. We have identified three facets of articulation on the posterior process of the tympanic bulla. The facet for articulation with the posterior meatal crest of the squamosal is deep, with marked ridges on both sides, and extends the entire length of the anterior margin of the process, like the condition in Waipatia maerewhenua. This would be an interpretation different from that of de Muizon (1987), who identified it as the area of contact with the spiny process of the squamosal; we do not agree because the spiny process of the squamosal is located more anteriorly than the posterior process of the tympanic bulla. Medially, the facet for articulation with the posterior process of the periotic has a tear-shaped to quadrangular outline, a smooth surface, and marked ridges on both sides. Finally, the longitudinally grooved facet of articu-
lation with the postotympanic process of the squamosal is at the posterolateral margin, almost perpendicular to the rest of the posterior process; the same feature is present in Waipatia maerewhenua. de Muizon (1987) interpreted this facet in AMNH 29026 as a possible contact with the paroccipital process; we do not concur as such a bony contact has not been reported for odontocetes (Fraser & Purves 1960; Kasuya 1973; Mead & Fordyce 2009). The posterior process of the tympanic bulla dor-
sally roofs the sub-oval elliptical foramen, as described by de Muizon (1987) and True (1910) (AMNH 29026 and 9485). In MPEF-PV 1804 and 1117, remnants of the outer posterior pedicle below the oblique posterior face of the conical process are also consistent with an open elliptical foramen.

Tympanic bulla. For the purpose of description, the dorsal view is defined as when the bulla’s ventral face is sitting on a flat surface. The tympanic bulla (Fig. 8; Table 2; Supplemental material S2, S5) has a generally heart-shaped profile, long and prominent anterior spine, distinct anterolateral convexity and anterolateral notch (sensu de Muizon 1987), and prominent median furrow.

The tympanic bulla has an elongated anterior spine, as in Platanista gangetica, but in Notocetus vanbenedeni it is more laterally placed. The deep anterolateral notch, just posterior to the spine, is followed by a marked anterolateral convexity. In dorsal view, the involucrum is gently sigmoideal anteroposteriorly and has a steep face into the tympanic cavity. Level with the sigmoideal process and in anterior view, a tubercle projects from the lateral side of the involucrum, as in Otekaikea mar-

plesi. In medial view, three transverse grooves on the involucrum descend onto the medial face, probably marking the position of the peribullary sinus. Here, the smooth presumed sinus surface extends far ventrally, succeeded by rough bone perhaps indicating a tendinous connection to the adjacent basioccipital crest. In dorsal view, anteriorly, AMNH 29026 presents a thin antero-
dorsal crest extending posteriorly to about the broken base of the anterior pedicle of the malleus.

Notocetus vanbenedeni from the early Miocene of Patagonia (Argentina)
In well-preserved specimens, such as MPEF-PV 1117, the high vertical sigmoid process is at the posterior third of the outer lip, with the posterior margin (dorsal or lateral view) immediately anterior to the apex of the conical process. However, the sigmoid process of *Notocetus vanbenedeni* is not as high as in *Platanista gangetica*. In anterior view, the profile of the sigmoid process is semi-circular; the dorsal margin is generally rounded, with a slightly oblique posterior surface in posterior view. It has a posteroventrally curved profile at the sigmoid cleft (Fordyce & Marx 2016) as it merges into the outer lip. The sigmoid process is shorter than in *Platanista gangetica*. There is no obvious surface to indicate the original proximity to the lateral tuberosity. de Muizon (1987) identified a lateral furrow in AMNH 29026, but this feature could not be confirmed in the other studied specimens. The oblique and laterally descending malleal ridge is prominent and elevated, but thin medially at the position for the malleus, similar to *Squalodelphis fabianii*. The malleus is detached in all specimens studied. Remnants of the anterior pedicle may be fused to the anterior malleal ridge. Fine grooves are usually present between the malleal ridge and the sigmoid process. The outer lip is generally damaged anterior to the malleal ridge; the accessory ossicle was not preserved in any studied specimen.

The conical process has a triangular profile in medial view, with a rounded lateral face and steep medial face in posterior view, and a sub-planar oblique posterior

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**Figure 8.** Right tympanic bulla of *Notocetus vanbenedeni* (MPEF-PV 1804). A, dorsal view; B, ventral view; C, medial view; D, lateral view; E, anterior view; F, posterior view. Dashed lines indicate important structures and filled-in areas represent broken surfaces.
surface bounded laterally by a marked crest, as described by de Muizon (1987) on AMNH 29026. Anteriorly, the conical process passes into the base of the sigmoid process at the lower tympanic notch. The tympanic sulcus is apparent in posterior to medial and dorsomedial views, associated with the crest at the lower margin that rises forward into the posterior face of the sigmoid process (Supplemental material S5). A ridge marking the sulcus can be traced forward from the oblique posterior surface of the conical process onto the medial wall, where the sulcus has a biconcave profile, before passing onto the sigmoid process.

In ventral view, the main feature is the deep, straight and long median furrow, extending almost the entire length of the tympanic bulla, as in Squalodelphis fabianii. However, it does not extend onto the anterior spine as Bianucci et al. (2020) reported in Peruvian Notocetus vanbenedeni MUSM 3896. Platanista gangetica and Zarhinocetus errabundus have a medially convex furrow. In Notocetus vanbenedeni, the median furrow has a moderately rugose surface; the anterior portion is especially deep and slightly nodular. The width of the furrow remains constant along its length and it lacks spikes or spines, as described by de Muizon (1987) for AMNH 29026, and posteriorly it merges with the interprominent notch with no visible horizontal shelf. The lateral margin of the tympanic bulla is markedly wider at about the sigmoid process, although not as much as in Platanista gangetica or Zarhinocetus errabundus. The outer posterior prominence is longer and more rounded than the wider inner prominence, resulting in a bilobed posterior profile of the bulla. In anterior view, the oblique and rounded ‘V’-shaped musculotubal canal leads to the anteriorly wider tympanic cavity.

Anderson (1878) described for the earbones (periotic and tympanic bulla) of Platanista gangetica a more thoroughly wedged and interlocked connection with the bones of the basicranium, resulting in the observation ‘that the bones never separate from the skull except by fracture’ (Anderson 1878: 519; see also e.g. Fraser & Purves 1960; Kasuya 1973; Oelschläger 1986). This is an unusual condition compared to the remaining extant odontocete species (except ziphioids and physeteroids), in which the earbones are loosely attached and easy to remove from the skull (e.g. Fraser & Purves 1960; Kasuya 1973; Oelschläger 1986). Thus, the Platanista-like condition was yet not developed in Notocetus vanbenedeni.

Auditory ossicles. All three auditory ossicles (Fig. 9) were preserved among MPEF-PV 1804 (malleus and incus) and AMNH 29026 (malleus and stapes; de Muizon 1987). The malleus has a prominent head and crest-like tubercule, whilst the manubrium is poorly developed; it is similar to that of Pomatodelphis inaequalis (see also de Muizon 1985, 1987). The tubercule is more elongated than in Platanista gangetica. In lateral view, the anterior process is broken but appears to be reduced – although de Muizon (1987) did not describe this structure in AMNH 29026 – opposite to the condition of Platanista gangetica or Lipotes vexillifer, and the sulcus for the chorda tympani is elongate and narrow. A circular fossa marks the insertion for the m. tensor tympani on the muscular process, on the anteroventral surface of the tubercule. It is not as deep as in Platanista gangetica or Lipotes vexillifer. In medial
view, the small lateral incudal facet and large anterior incudal facet are oval and asymmetrical, slightly larger than in *Platanista gangetica*, next to a deep and triangular depression. Ventral to these facets is the elongated, deep groove that separates the tubercule from the head; it is shallower and shorter in *Platanista gangetica*.

This is the first description of the incus of *Notocetus vanbenedeni*. It has saddle-shaped anterior and lateral articular surfaces for the malleus in ventral and anterior view, with a very short crus breve (it does not appear to be broken) and a skewed conical body that is slightly higher than wide, and lacking any constriction. The incus of MUSM 603 (Squalodelphinidae indet; Lambert et al. 2014) has a shorter body than that of *Notocetus vanbenedeni*. In dorsal view, the posterior apex of the body has a small and rounded lenticular process. According to Anderson’s (1878) drawings and description, the incus of *Notocetus vanbenedeni* is morphologically quite similar to that of *Platanista gangetica*.

As for the stapes of *Notocetus vanbenedeni*, de Muizon (1987, p. 11) described it as partially preserved and still in situ on the periotic in AMNH 29026. He mentioned only that the basal part does not have a stapedial foramen, as in *Platanista gangetica* and other extant Odontoceti (Mead & Fordyce 2009).

**Teeth.** *Notocetus vanbenedeni* is polydont and nearly homodont (Fig. 10; Table 1; Supplemental material S2). For the upper tooth row, the premaxilla has at least two alveoli. We infer there were three alveoli in this bone, a condition similar to that of, for example, stem Odontoceti *Phoberodon arctirostris*, *Prosqualodon* and *Inticetus vertizi*. Then, the maxilla has 19–23+ alveoli and there are 18+ alveoli for the lower tooth row. Moreno (1892) estimated a total of 23 upper teeth on the maxilla and 19 lower teeth for *Notocetus vanbenedeni* (MLP 5-5 and 5-17). We infer that *Notocetus vanbenedeni* had 22–26+ upper teeth and 18+ lower teeth.

For the purpose of description, we consider the crown to be the portion of teeth formed by enamel, whereas the root comprises the portion inserted in the bone. All teeth have a long and posteriorly curved single root (a few loose teeth have a straight root); posterior teeth present a thickening at the most dorsal portion of the root. Crown size appears to decrease posteriorly, although slightly; the transition zone between the crown and the root is characterized by a smooth surface with a variable anteroposterior constriction and was exposed above the gum.

Anteriorly, teeth have a conical crown with an acute apex. Upper teeth are linguually curved and ventrally oriented, whilst lower teeth are lingually curved and dorsally oriented. Only MLP 5-10 appears to have the anteriormost preserved lower teeth slightly procumbent.

The enamel has vertical striations and no accessory denticles, and usually has a visible anterior keel. It may sometimes present a nearly indistinct entocingulum on the anterolingual aspect of the crown. Posteriorly, all teeth have a shorter and triangular (lateromedially compressed) crown, with a distinct entocingulum, in agreement with de Muizon (1987) (but an ectocingulum was reported by Bianucci et al. [2020] for the Peruvian *Notocetus vanbenedeni* MUSM 1484). The enamel also presents vertical striations. Posterior upper teeth are posteriorly curved and ventrally oriented, whilst lower teeth are posteriorly curved and more dorsally oriented. Teeth present anterior and posterior keels; the latter sometimes bears one accessory denticle. The posteriormost two upper teeth in MLP 5-10 are laterally oriented. The crown apex of MPEF-PV 1120 presents a wear facet.
Mandibles. The description of the mandibles is based on specimens MLP 5-5 (holotype), MLP 5-10, 5-17 and AMNH 9485; MPEF-PV 1118 and 1804 were excluded due to their fragmentary and incomplete condition. The ‘Y’-shaped mandibles (Fig. 11; Table 1; Supplemental material S2) have a fused symphysis that occupies almost half their length. The dorsal surface of the symphysis is slightly depressed, more so on the posterior-most section (a long and deeply curved mandibular symphysis is present in *Platanista gangetica*). There is no groove on the ventral side of the symphysis. In lateral view, the body of the mandible is dorsoventrally low, with a convex lateral surface and a convex ventral margin. The last alveolus is located posterior to the mandibular symphysis, whereas in *Platanista gangetica* it is at about the same level as, or just anterior, to it. Bianucci *et al.* (2020) reported embrasure pits on the mandibles of the Peruvian *Notocetus vanbenedeni* MUSM 3897; no pits were identified in *Notocetus vanbenedeni*. There are 1–4 mental foramina on each side, similar to *Platanista gangetica* and *Phoberodon arcticostris*. A marked depression in dorsal view (Fig. 11D, concave surface) is located just posterior to the anterior limit of the ramus. The ‘pan bone’ (MLP 5-5: 5 mm) is laterally inflated in posterior view, more than in *Waipatia maerewhenua*. *Platanista gangetica*, the mandibular fossa is shallow (dorsoventrally low) and anteroposteriorly short. The alveolar groove is followed posteriorly by a marked coronoid crest, including a short dorsal bulge or precoronoid crest. The mandible has a low coronoid process (it is high in *Platanista gangetica*) and a reduced angular process, unlike the prominent process in the Peruvian *Notocetus vanbenedeni* MUSM 3896 and 3897 (Bianucci *et al.* 2020). The mandibular notch appears to be indistinct. The mandibular condyle protrudes slightly beyond the lateral surface of the mandible’s body and is excavated on its medial side, similar to *Waipatia maerewhenua*. *Platanista gangetica*, on the other hand, has an oval but unexcavated mandibular condyle.

Postcranial skeleton. The vertebrae from three specimens (holotype MLP 5-5, AMNH 9485 and MPEF-PV 1804), some ribs from MPEF-PV 1804 and the scapula of AMNH 29026 allow the description of some portions of the postcranial skeleton of *Notocetus vanbenedeni*. General vertebral features are: unfused cervical vertebrae; thoracic and anterior lumbar regions have a discooidal morphology of the vertebral body anteriorly (vertebral body length < vertebral body height and width) whilst posteriorly vertebrae are spool-shaped (vertebral body length > vertebral body height and width) (Buchholtz & Schur 2004).

Cervical vertebrae. All cervical vertebrae are unfused (Fig. 12; Table 3; Supplemental material S2), as in *Platanista gangetica*. The atlas is anteroposteriorly long, with deeply concave anterior condyloid facets and shallow facets for the articulation with the axis. Upper and lower transverse processes are separate and the latter are

**Figure 11.** Mandibles of *Notocetus vanbenedeni* (MLP 5-10). A, D, dorsal view; B, E, ventral view; C, F, lateral view; without and with labels, respectively. Dashed lines indicate important structures and filled-in areas represent broken surfaces.
poorly developed. The hypapophysis is short and wide, with a blunt apex. Medial to the facet for the axis is the tubercle for the transverse ligament. No transverse foramina or neural spine were preserved; True (1910) indicated the presence of transverse foramina in AMNH 9485 but did not figure these.

The axis has long and posteriorly oriented transverse processes. In ventral view, a thick ridge with a concave surface on each side continues the odontoid process along the entire length of the vertebra. The neural spine is short and posteriorly oriented; because of poor preservation, no posterior zygapophysis was identified. The remaining cervical vertebrae have progressively smaller vertebrarterial canals and longer transverse processes. The neural canal is taller than wide. The anterior and posterior zygapophyses are oriented dorsally and ventrally, respectively. The vertebral body is short, high and transversely narrow. Moreno (1892) identified the preserved cervicalsof the holotype as atlas and the fourth through sixth cervicals. The morphology of the cervical vertebrae of the Peruvian Notocetus vanbenedeni MUSM 1395 (Bianucci et al. 2014) resembles that of the holotype.

**Thoracic vertebrae.** The body of these vertebrae (Fig. 12; Supplemental material S2) becomes progressively longer and taller posteriorly and has a concave ventral surface. Vertebrae are short and high (discoidal) anteriorly, whilst posteriorly they are longer than tall (spool-shaped). However, Platanista gangetica has a predominant discoidal morphology (short and high; Buchholtz & Schur 2004). The articular facet for the capitulum of the atlas and the fourth through sixth cervicals. The morphology of the cervical vertebrae of the Peruvian Notocetus vanbenedeni MUSM 1395 (Bianucci et al. 2014) resembles that of the holotype.

**Lumbar vertebrae.** The vertebral bodies of lumbar vertebrae as preserved (Fig. 12; Supplemental material S2) are increasingly longer posteriorly, but the skeleton is too incomplete to further ascertain any morphological trends. It appears the body is mainly spool-shaped (longer than tall or wide; Buchholtz & Schur 2004), unlike the morphology of Platanista gangetica (see above). Neural spines are anteroposteriorly wider than in the thoracic region. The synclinal point (i.e. neural spine with 90° orientation; Slijper 1946) appears to be between the first two lumbar vertebrae preserved (Supplemental material S2), whilst in Platanista gangetica it is around the sixth thoracic. Transverse processes, although poorly preserved, indicate that they become longer posteriorly and maintain approximately the same height. Metapophyses are anterodorsally oriented and robust as in Platanista gangetica.

**Ribs.** MPEF-PV 1804 has a total of 18 ribs preserved (11 right and seven left), and among them seven are double-headed. Ribs are ventrolaterally curved, wider at the head and thinner at their distal end (Fig. 12).

**Scapula.** The fan-shaped scapula (Fig. 12; Table 3) is very thin, with an estimated angle between the anterior and posterior borders (with respect to the glenoid cavity) of ~92°, resulting in almost a quadrangular profile of the scapula. In lateral view, the suprascapular border is not as long as in Platanista gangetica. It is assumed that in life, the glenoid cavity was ventrally oriented like in extant odontocetes (Rommel 1990). The supraspinous fossa is absent as in Platanista gangetica, and a vestigial scapular spine almost forms the anterior border of the scapula. The large infraspinous fossa, on the other hand, is smooth and shallow, with a superficial teres minor fossa on the posterior region. The anteriorly oriented acromion is elongated, anteroposteriorly longer than dorsoventrally wide; it projects from the anterior margin of the scapula, as in Platanista gangetica, Squalodon calvertensis and Prosqualodon davidis. The coracoid process is absent, as in Platanista gangetica and Prosqualodon davidis. Finally, a slight depression in medial view could correspond to the fossa for the subscapularis.

**Phylogenetic analyses**

We performed two cladistic analyses to test the phylogenetic position of Notocetus vanbenedeni: one with equal weights and the other with implied weights. With the analyses under equal weights, we obtained 16 MPTs of 2194 steps (Consistency Index = 0.2, Retention Index = 0.6). With the analyses under implied weights, topology changes within the ingroup were observed with K = 4 (two MPTs of fit = 81.69), K = 12 (two MPTs of fit = 81.69), K = 16 (one MPT of fit = 68.43), K = 18 (one MPT of fit = 63.31) and K = 26 (one MPT of fit = 48.67) (for the full topologies, see Supplemental material S5). Grids derived from sensitivity analyses at key nodes and clades indicate how frequently they were recovered in each of the phylogenetic hypotheses analysed (Fig. 13). Below, we will mention
Figure 12. Postcranial elements of *Notocetus vanbenedeni*. A, lateral view; and B, medial view of left scapula (AMNH 29026); C, anterior view; and D, posterior view of atlas (MLP 5-5); E, G, anterior view; and F, H, posterior view of cervical vertebrae of unknown position (MLP 5-5); I–L, dorsolateral view of postcranial skeleton (MPEF-PV 1804). **Abbreviations:** cv, cervical; L, lumbar; T, thoracic; TTL, tubercle for transverse ligament.
some important topology changes among the trees and relevant synapomorphies.

We recovered a monophyletic Platanistoidea in the analyses under equal and all implied weights (Fig. 13). Under equal weights and all implied weights (except $K = 4–5, 12, 14$ and $15$) the clade is supported by eight ambiguous synapomorphies: longitudinal groove on underside of mandibles (ch. 33); premaxillary foramen anterior to antorbital notch (ch. 55) and medially located (ch. 56); lateral lamina of pterygoid articulated with alisphenoid (ch. 130); pterygoid fossa extending beyond the antorbital notch (ch. 135); long anterior spine of tympanic bulla (ch. 211); and shallow or absent coracoid process of the scapula (ch. 245). Under equal weights and $K = 1–5, 8$ and $24–100$, the premaxillary foramen anterior to antorbital notch (ch. 55) and anteroposterior ridge on dorsal side of periotic (ch. 175) were also recovered as synapomorphies for this clade. Under equal weights and implied weights with $K = 1–3, 6–11, 13$ and $25–100$, we recovered a ninth synapomorphy: presence of an anteroposterior ridge on the dorsal side of the periotic (ch. 175). Under implied weights with $K = 12$ and $14–15$, the clade Platanistoidea is supported by seven synapomorphies (ch. 20, 56, 120, 135, 206, 211 and 245) and it is included in a polytomy together with Waipatia, Otekaika, Papahu taitapu, Phoberodon arcticrisus and Inticetus vertizi (Fig. 13; Supplemental material S5).

Finally, under implied weights with $K = 4–5$ (Fig. 13), Platanistoidea includes other species (i.e. Squalodon calvertensis) and internal phylogenetic relationships are unlike previous phylogenetic hypotheses (Supplemental material S5). Here, the clade is supported by seven synapomorphies (ch. 26, 86, 95, 168, 185, 203 and 249).

Squalodelphinidae, defined here as including only Squalodelphis fabiani (Fig. 13), is supported by two apomorphies (ch. 101 and 111) under equal weights and implied weights with $K = 1–3, 6–11, 13$ and $16–100$; in these analyses, Squalodelphis fabiani is closely related to OU 22670 (but note that OU 22670 is currently under review by Ewan Fordyce, and thus is excluded from further discussion). Under implied weights with $K = 4–5$, Squalodelphis fabiani’s position is defined by one apomorphy (ch. 101); and under implied weights with $K = 12$ and $14–15$ (Fig. 13) it is defined by nine apomorphies (ch. 8, 29, 30, 53, 101, 111, 160, 162 and 197). Then, the family Alloodelphinidae is recovered under equal weights and all implied weights (except with $K = 4–5$). The phylogenetic relationships within alloodelphinids vary under implied weights with $K = 12$ and $14–24$ (see Supplemental material S5).

Under equal weights and all implied weights (except with $K = 4–5$), a monophyletic family Platanistidae including Phocageneus venustus, Zarhachis flagellator, Pomatodelphis inaequalis and Platanista gangetica (Fig. 13) is supported by two ambiguous synapomorphies (ch. 172 and 194) and one unambiguous synapomorphy (ch. 204). Under implied weights with $K = 4–5$, Phocageneus venustus is not recovered in this clade, and Platanistidae is supported by 13 synapomorphies (ch. 19, 24, 36, 65, 114, 116, 148, 155, 191, 194, 201, 211 and 220). Moreover, species recorded in New Zealand (Papahu taitapu, Waipatia spp., Awamokoa tokarahi and Otekaika spp.), hereafter called Group B (Fig. 13), are stemward to Platanistoidea + other crown Odontoceti and not included in the former clade. Under equal and implied weights $K = 1–3, 6–11, 13$ and $25–100$, Group B is supported by four ambiguous synapomorphies (ch. 62, 86, 114 and 190); with $K = 16–17$ only two of these synapomorphies are recovered (ch. 62 and 114); and with $K = 18–24$ only three synapomorphies (ch. 62, 86 and 114). Under implied weights with $K = 4–5, 12$ and $14–15$, Group B is not recovered.

Under equal weights and all implied weights (except with $K = 4–5$), Patagonian Notocetus vanbenedeni, Peruvian platanistoids (MUSM 1395, 3896, 3897 and 1484), Macrosqualodelphis ukupachai, Dilophodelphis fordycei, Medocinia tetratorghina, Huaridelphis raimondii and Araedelphis natator are included in a clade here called Group A (Fig. 13), always closely related to the family Platanistidae. Group A is supported by four ambiguous synapomorphies: medium width of premaxilla at mid-rostrum (ch. 11); one anterior dorsal infraorbital foramen (ch. 51); short humerus (ch. 250); and apex of deltopectoral tuberosity within distal portion of the humerus (ch. 251). Then, Notocetus vanbenedeni is defined by seven apomorphies: 17–23 teeth in mandibles (ch. 30); absence of a longitudinal groove on the mandibles (ch. 33); nasals with point on midline and gap with premaxilla (ch. 90); narrowly exposed squamosal in posterior view (ch. 115); short anterior process of periotic with respect to pars cochlearis length (ch. 171); reniform cochlear aqueduct opening of periotic (ch. 195); and shallow grooves on posterior bullar facet of periotic (ch. 203). In all the analyses, Patagonian Notocetus vanbenedeni and the Peruvian platanistoids (MUSM 1395, 3896, 3897 and 1484) do not form a clade. Finally, the IterPCR analysis did not detect any unstable taxa.

**Time-calibrated phylogenetic hypothesis**

We chose the phylogenetic hypothesis obtained under implied weights with $K = 26$ for calibration because it is the most frequently recovered topology in the implied weights phylogenetic analyses and the most congruent with the majority of previous phylogenetic hypotheses in the literature. The calibrated phylogenetic hypothesis shows an early
Oligocene (late Rupelian) origin for the Platanistoidea clade (Fig. 14). Then, during the late Oligocene (Chattian) both Group B and Allodelphinidae are first recorded, followed during the early Miocene (Aquitanian–Burdigalian) by the stem odontocetes Prosqualodon, Phoberodon arctirostris, Intictetus vertizi and Papahu taitapu (the latter belonging to Group B), as well as platanistoids from the Group A, Squalodelphinidae and Platanistidae families. Both Aondelphis talen and ZMT-73 (considered in the literature to be putative platanistoids) are also recorded during this time.

**Figure 13.** Results of the cladistic phylogenetic analyses using the hypothesis under implied weights with $K = 26$. Numbers above branches indicate Bremer support, whilst numbers below are GC jackknife support. Grids derived from sensitivity analyses indicate the presence (filled square) or absence (unfilled square) of the corresponding node/clade under equal and implied weights ($K = 1–100$) (for further details, see Material and methods).
Thus, the greater diversity of platanistoids appeared during the late Oligocene–early Miocene ( Chattian–Burdigalian) interval, supporting the previously suggested hypothesis of an initial radiation during this time period (e.g. Fordyce 1994; Lambert et al. 2014; Tanaka & Fordyce 2014, 2015a, b; Boersma & Pyenson 2016; Viglino et al. 2018a, b). Then, from the middle Miocene (Langhian) onward, only the family Platanistidae (except Phocageneus venustus) is recorded. It should be noted that there is a long ghost lineage leading to the origin and diversification of the Group A + OU 22670 + Squalodelphinidae + Platanistidae; another ghost lineage occurs within Platanistidae and Allodelphinidae. These ghost lineages mainly occur between the late Oligocene ( Chattian) and early Miocene (Aquitanian–Burdigalian) (Fig. 14), in only partial accordance with the Aquitanian fossil record gap for cetaceans (e.g. Marx & Fordyce 2015; Marx et al. 2019).

Discussion

Platanistoidea evolutionary history
Initially, Platanistoidea included the extant genera Platanista, Inia, Lipotes and Pontoporia, all of which are considered ‘river dolphins’ (Gray 1863; Simpson 1945). Only recently did de Muizon (1987) redefine the clade including just the genus Platanista and its closely related extinct taxa (for further systematic details, see e.g. Fordyce & de Muizon 2001; Barnes et al. 2010; Lambert et al. 2014; Tanaka & Fordyce 2015a; Boersma & Pyenson 2016; Bianucci et al. 2020). With its highly variable taxonomic history, Platanistoidea has been the focus of palaeontological studies for many years. Here, our results propose new phylogenetic hypotheses and evolutionary scenarios for the clade.

Phylogenetic analyses under equal and implied weights recover a monophyletic Platanistoidea (Fig. 13) as the most basal lineage within crown Odontoceti. It should be noted that recent molecular studies suggest the earliest diverging crown Odontoceti lineage is Physeteroidea (e.g. McGowen et al. 2009, 2020; Steeman et al. 2009; Geisler et al. 2011), so a molecular backbone might be considered in future phylogenetic analyses. The time-calibrated phylogenetic hypothesis indicates an early Oligocene origin for Platanistoidea (~28.5 Ma, Rupelian), which is older than other proposed origins of the group in the literature (Hamilton 2014).
et al. 2001; Geisler et al. 2011; Boersma & Pyenson 2016; Boersma et al. 2017). Note that no exact dating is available yet for Arktocara yakataga (Boersma & Pyenson 2016), which might pull the clade’s origin further back. Nearly all platanistoids are recorded between the Chattian (late Oligocene) and the Burdigalian (early Miocene; Fig. 14) across almost all the oceanic basins. The origin and high initial diversification of platanistoids during the Oligocene–early Miocene would be related to the opening of the Antarctic Circumpolar Current and the new ecological niches made accordingly available (Fordyce 1980; McGowen et al. 2009; Steeman et al. 2009; Marx & Uhen 2010). Then, by the middle Miocene (Langhian–Serravallian), platanistoids are only recorded in the Northwest Atlantic and Northeast Pacific, followed by a long gap until the extant representative, Platanista gangetica (Fig. 14) occurs in the Ganges–Brahmaputra–Meghna and Indus river systems of southern Asia (Braulik et al. 2021). The rapid decline in platanistoid diversity has been related to three main hypotheses: (1) that the delphinoid clade originated and radiated, thus ecologically replacing platanistoids (Fordyce & Barnes 1994; Hamilton et al. 2001; Steeman et al. 2009; McGowen et al. 2009; Bianucci et al. 2018); (2) that a platanistid ancestor remained in fluvial basins after the reduction of epicontinental seas formed during the middle Miocene (Cassens et al. 2000; Hamilton et al. 2001); or (3) that global temperature declined after the Middle Miocene Climatic Optimum, thus affecting more coastal-freshwater species (Zachos et al. 2008; Marx et al. 2016). At present, these hypotheses are equally plausible, and future anatomical, sedimentological and isotopic analyses on fossil platanistoids should further elucidate which is the most suitable scenario.

Unlike in many previous analyses (e.g. Fordyce 1994; Tanaka & Fordyce 2014, 2015a, b, 2017; Boersma & Pyenson 2016; Viglino et al. 2018a, b; Gaetán et al. 2019), here Waipattia, Awamokoa tokarahi, Papahu tai-tapu and Otekaikea (Group B) were most frequently recovered outside of Platanistoidea (Fig. 13). Except for Papahu tai-tapu, these are heterodont odontocete genera from late Oligocene–early Miocene ( Chattian–Aquitanian) New Zealand deposits; they were considered representatives of the earliest diverging platanistoids (Fordyce 1994; Tanaka & Fordyce 2014, 2015a, b, 2016, 2017). The most basal platanistoid lineages in our preferred phylogenetic hypothesis are the late Oligocene–middle Miocene allodelphinids ( Chattian through Langhian) from North Pacific outcrops (Fig. 14; Kimura & Barnes 2016; Boersma & Pyenson 2016). So, species of Group B are possibly older than and/or coeval with some allodelphinids, have more primitive morphologies, and share some morphological characteristics with Platanistoidea (e.g. Fordyce 1994; Tanaka & Fordyce 2017 and references therein). Given the variable phylogenetic position of Group B, we propose two hypotheses: (1) Group B represents the first lineage within Platanistoidea and there is an as yet undiscovered most recent common ancestor that, when included in future phylogenetic analyses, will lead to the recovery of Group B within Platanistoidea; or (2) one of the species from Group B is more closely related to the most recent common ancestor of Platanistoidea than any other extinct odontocete, from which the latter group arose.

Within Platanistoidea, we consistently recovered clades Alloodelphinidae, Squalodelphinidae, Group A and Platanistidae (Fig. 13), in accordance with previous phylogenetic analyses (Fordyce 1994; Tanaka & Fordyce 2017 and references therein; Lambert et al. 2014; Boersma & Pyenson 2016; Boersma et al. 2017; Viglino et al. 2018a, b; Bianucci et al. 2018, 2020; Gaetán et al. 2019). The close relationships among clades Squalodelphinidae, Group A and Platanistidae support the clade Platanidelphidi (Bianucci et al. 2020). However, the species included in each clade vary. For example, we did not recover Araeodelphis natator or Dilophodelphis fordyc ei as platanists, unlike other phylogenetic analyses (Boersma et al. 2017; Godfrey et al. 2017). Comparable to previous authors, Macrosqualodelphis ukupachai, Medocinia tetrarorrhina, Huaridelphis raimondii, Phocageneus venustus and Notocetus vanbenedeni (e.g. Bianucci et al. 2018) were recovered within Platanistoidea but – surprisingly – outside Squalodelphinidae. All these results highlight the volatility of the phylogenetic relationships among platanistoids. Therefore, we will not venture new taxonomical propositions other than some specific comments regarding Notocetus vanbenedeni. Nonetheless, we believe it is necessary to continue revising historical taxa and describing new platanistoids, as this will bring us closer to a more consensual phylogenetic hypothesis and unravel the still poorly understood evolutionary history of this group.

Some of the synapomorphies recovered that support Platanistoidea are in accordance with previous studies (de Muizon 1987, 1991; Fordyce 1994; Tanaka & Fordyce 2014, 2015a, b, 2017; Lambert et al. 2014; Boersma & Pyenson 2016; Boersma et al. 2017; Viglino et al. 2018a, b) – in particular, the reduced or absent coracoid process of the scapula (ch. 245), as de Muizon (1987, 1991) and Kimura & Barnes (2016) suggested. However, we caution that it has been coded in only a few species, and even in non-platanistoid taxa like squa- lodontids (de Muizon 1991), and the evolution of this character could thus vary if more species are coded. We
acknowledge that this particular scapular morphology (i.e. absence of coracoid process and acromion located on the anterior edge) would have biomechanical consequences for swimming that should be further analysed.

Squalodelphinidae

Regarding the Squalodelphinidae, we consistently recovered it as comprising only the type genus and species *Squalodelphis fabianii* (Fig. 13). None of the synapomorphies proposed for the family Squalodelphinidae by Lambert et al. (2014), de Muizon (1987) or Bianucci et al. (2020) were recovered. We would suggest then that the concept of the family Squalodelphinidae should be redefined as monotypic, including only *Squalodelphis fabianii*. Our results (Fig. 13) support a close relationship among Squalodelphinidae, Group A and Platanistidae, in agreement with de Muizon (1987). Previous studies agree with these results (e.g. Fordyce 1994; Barnes et al. 2010; Lambert et al. 2014; Tanaka & Fordyce 2017 and references therein; Boersma et al. 2017; Godfrey et al. 2017; Bianucci et al. 2018, 2020; Viglino et al. 2018a, b). Finally, given that the time-calibrated phylogenetic hypothesis indicates an Aquitanian origin for Squalodelphinidae + Group A + Platanistidae (Fig. 14), more sampling of suitable sedimentary units of this age may clarify the phylogenetic relationships and possible palaeobiogeographical patterns of these clades.

Notocetus vanbenedeni

Our anatomical description, palaeobiological inferences and taxonomic background confirm *Notocetus vanbenedeni* as a distinct and valid species. Unlike in previous studies (e.g. Dal Piaz 1917; de Muizon 1987; Barnes et al. 2010; Bianucci et al. 2014; Lambert et al. 2014; Tanaka & Fordyce 2017 and references therein; Boersma et al. 2017; Viglino et al. 2018a, b; Gaétán et al. 2019), *Notocetus vanbenedeni* is not recovered within Squalodelphinidae here.

Dal Piaz (1917) indicated that the number of upper and lower teeth could differentiate squalodelphinids *Notocetus vanbenedeni* from the type species *Squalodelphis fabianii*, being both greater and unequal in the former. Bianucci et al. (2014) supported this differentiation (based on the holotype, AMNH 9485, AMNH 29026, and MUSM 1395) and the apomorphies recovered for *Notocetus vanbenedeni* in our present study partially concur (Supplemental material S4). Dal Piaz (1917) and Bianucci et al. (2014) also mentioned the presence of accessory denticles on the most posterior teeth (ch. 19) as a distinguishing feature of *Notocetus vanbenedeni* (whilst in *Squalodelphis fabianii* the enamel is denticulate), although it was not recovered as such. Finally, Dal Piaz (1917) proposed single-rooted conical upper and lower teeth as a shared characteristic between the species; however, such characteristics can also be found in other platanistoids, and thus lack diagnostic value to identify squalodelphinids. Other skull characteristics that tentatively distinguish *Notocetus vanbenedeni* from *Squalodelphis fabianii*, for example cranium wider than long and greater development of the supraorbital crest (Dal Piaz 1917), were also not recovered as apomorphies for either species. Bianucci et al. (2020) indicated, as a diagnostic squalodelphinid characteristic, a deep ‘V’-shaped left antorbital notch and a left-side torsion of the rostrum, which were not observed in the present sample of *Notocetus vanbenedeni*. The authors also described a square pars cochlealis of the periotic, but it is squared to rounded in *Notocetus vanbenedeni*; a large and thin-edged aperture for the cochlear aqueduct, but this is also observed in odontocete *Aondelphis talen*; and a median furrow extending over the anterior spine, which we did not observe. Moreover, a long median furrow can also be observed in the odontocete specimen ZMT-73 and platanistids *Platanista gangetica* and *Zarhachis flagellator*. Bianucci et al. (2020) also indicated an apical extension of the manubrium of the malleus, but it is poorly developed in *Notocetus vanbenedeni*; and a strongly developed dorsal transverse processes and reduced ventral processes of the atlas, a condition that also occurs in *Otekaikea huata*. None of these diagnostic characteristics were recovered as synapomorphies of either the Squalodelphinidae or Group A. Other skull characteristics that further support the distant phylogenetic position of *Squalodelphis fabianii* from Group A + Platanistidae (and thus of *Notocetus vanbenedeni* from Squalodelphinidae) are the following: *Squalodelphis fabianii* has enlarged anterior teeth on the mandible and a very low coronoid process, whereas teeth are of the same size along the mandible in *Notocetus vanbenedeni* and the coronoid process is higher for this taxon and *Platanista*. The postorbital process of the frontal is ventrally oriented in Group A (except *Medocinia tetragrhina*) and absent in Platanistidae (signaling the progressive loss of vision in the extant representative); this process is posterolaterally oriented in Squalodelphinidae. The premaxillary cleft is present and shallow in Platanistidae and most of Group A, whereas it is absent in Squalodelphinidae. The nuchal crest is below the nasals/frontals in *Squalodelphis fabianii*, but at the same level for Group A and Platanistidae, suggesting possible different cervical and facial muscle arrangements on the skull in each group (Marx et al. 2016). The posterior portion of the periotic fossa is large and deep in *Notocetus vanbenedeni* and *Platanista*, but
shallow in Squalodelphinidae. Finally, the internal acoustic meatus of the periotic is pyriform and has a funnel-like fundus in *Squalodelphis fabianii*, whereas it is circular and has a tubular fundus in *Notocetus vanbenedeni* and *Platanista*. In summary, all these anatomical differences reinforce the phylogenetic position of *Notocetus vanbenedeni* outside of Squalodelphinidae as proposed here and suggest the need to re-evaluate the membership and definition of this family.

*Notocetus vanbenedeni* represents a mosaic of plesiomorphic and derived features that suggest an intermediate morphotype in the evolutionary history of Platanistoidea. The species shares with *Platanista* plesiomorphic skull characteristics such as the pterygoid completely covering the palatine, a pyramidal process on the periotic, and the reduced or absent coracoid process of the scapula. *Notocetus vanbenedeni* also presents derived characteristics similar to *Platanista*, like the presence of a supraorbital crest, an articular rim of the periotic and corresponding fossa on the squamosal, an enlarged tympanosquamosal recess of the squamosal, and an anterior spine and long and deep median furrow of the tympanic bulla. Thus, *Notocetus vanbenedeni* shows that by the early Miocene key characteristics of the Platanistidae clade had already been acquired.

Surprisingly, we rarely observed intraspecific variation among the 26 *Notocetus vanbenedeni* specimens studied here. Nonetheless, throughout the description and in the matrix codings we have included observed minor differences. For example, the premaxilla at the base of the rostrum can be narrow (holotype and MPEF-PV 1660) or moderately wide (AMNH 9485, MLP 5-10 and MPEF-PV 2580); the posterolateral sulcus of the premaxilla is straight only in MPEF-PV 1660; and the lacrimomajugal extends dorsally at the antorbital notch in MPEF-PV 681, 1660 and 1804. In the basicranium, the sub-circular fossa can be deep (in the holotype, MPEF-PV 1117 and AMNH 29026), shallow (in MPEF-PV 1660) or almost indistinct (in MPEF-PV 1804). For the earbones, we observed variation in the presence of an anterointernal foramen (MPEV-PV 1375-6 and 1375-7) and posteroexternal foramen (MLP 76-IX-2-5 and MPEF-PV 1375) on the anterior and posterior processes of the periotic, respectively. There is also some intraspecific variation on the articular rim of the periotic, from a short bulge (MPEF-PV 1118) to an elevated rim (MPEF-PV 1804 and 1375, MLP 76-IX-2-5, and AMNH 29026). Although rare, other examples of low intraspecific variation in cetaceans (e.g. Martins et al. 2020) have been reported.

The present extensive anatomical and phylogenetic analyses of the holotype and other *Notocetus vanbenedeni* specimens from Patagonia do not suggest a close phylogenetic relationship with Peruvian platanistoids (MUSM 1395, 3896, 3897 and 1484) (Fig. 13). Thus, the latter group might represent a different taxonomic unit. There are some skull differences to take into consideration, as outlined above in the diagnosis: for example, *Notocetus vanbenedeni* has the premaxillary foramen anterior to the antorbital notch, whereas in the Peruvian platanistoids (MUSM 1395, 3896, 3897 and 1484) it is at the level of the notch. *Notocetus vanbenedeni* premaxillae are separated by the mesorostral groove and the palatine is completely covered by the pterygoid; however, the mesorostral groove is closed and the palatine extends anteriorly and laterally to the pterygoid in the Peruvian platanistoids (MUSM 1395, 3896, 3897 and 1484). Also, the anterior process of the periotic is smoothly ventrally deflected and there is a pyramidal process on the dorsal surface in *Notocetus vanbenedeni*, but in the Peruvian platanistoids (MUSM 1395, 3896, 3897 and 1484) the anterior process is abruptly deflected. A final example is the shape of the opening of the cochlear aqueduct of the periotic: which is reniform in *Notocetus vanbenedeni*, and rounded in the Peruvian platanistoids (MUSM 1395, 3896, 3897 and 1484). However, until a first-hand revision of these Peruvian platanistoids is conducted considering the present updated anatomical description of *Notocetus vanbenedeni*, we will not venture any more conclusions. Nonetheless, we acknowledge a close relationship between the Patagonian and Peruvian odontocete faunas (Figs 13, 14) as Bianucci et al. (2014) proposed, as a result of a possible connection during the early Miocene through the open Panama seaway. Thus, increasing efforts for fieldwork in lower Miocene outcrops both in the south-western Atlantic and south-eastern Pacific will help elucidate palaeobiographical patterns during a time of rapid diversification for platanistoids.

**Palaeobiological inferences about Notocetus vanbenedeni**

Below is a brief account of some palaeobiological aspects of *Notocetus vanbenedeni*, emphasizing soft-tissue inferences related to the echolocation system and hearing (facial region, pterygoid sinus system and earbone morphology). These results, together with the updated description provided above, resulted in a palaeobiological reconstruction of the species that we present here for the first time (Fig. 15).

**Supraorbital crest.** The first and most outstanding feature of the facial region of *Platanista gangetica* is the presence of the pneumatized supraorbital crest invaded by a lobe of the pterygoid sinus system medially and, thus, possibly related to its echolocation abilities.
(Anderson 1878; Fraser & Purves 1960; Purves & Pilleri 1973; Pilleri 1974; Jensen et al. 2013). *Notocetus vanbenedeni* has a supraorbital crest in the form of an elevated dorsal tubercle formed mainly by the frontal, whereas in *Platanista gangetica* it is a pneumatized crest formed by the maxilla. The supraorbital crest has also been identified in other odontocetes, such as *Waipatia maerewhenua*, *Zarhinocetus errabundus*, *Squalodelphis fabianii*, Group A and Platanistidae (Supplemental material S4, S5). Platanistidae (except *Phocageneus venustus*) is the only clade presenting pneumatized supraorbital crests. The supraorbital crest is mainly formed by the maxilla in the extinct platanistoids *Zarhinocetus errabundus*, * Macrosqualodelphis ukupachai*, *Medocinia tetraroghina* and *Huaridelphis raimondii* (Supplemental material S4, S5). It should also be noted that there are many issues with the identification of and terminology for this crest (Mead & Fordyce 2009, diagram 2). Boersma et al. (2017) proposed that the supraorbital crest was initially formed by equal parts of maxilla and frontal, involving only the maxilla in *Platanista gangetica*. Based on our time-calibrated phylogenetic hypothesis and optimization of the character (Supplemental material S5), we propose an early (i.e. Chattian) origin of the supraorbital crest, initially involving only the maxilla in some stem Odontoceti (e.g. *Waipatia maerewhenua*). Then, a supraorbital crest involving either mainly the maxilla (*Zarhinocetus errabundus*, * Macrosqualodelphis ukupachai*, *Medocinia tetraroghina*, *Huaridelphis raimondii* and *Platanista*), mainly the frontal (*Notocetus vanbenedeni*, Peruvian platanistoids (MUSM 1395, 3896, 3897 and 1484), *Araeodelphis natator* and *Squalodelphis fabianii*) or both (*Dilophodelphis fordyceti*, *Zarhachis flagellator* and *Pomatodelphis inaequalis*) evolved convergently during the Miocene in platanistoids. A change in the relative pneumatization of the supraorbital crest is also observed during the evolutionary history of platanistoids.
(Boersma et al. 2017). Initially, the crest is only slightly developed (Zarhinocetus errabundus) or with a tubercular morphology of varying height (Notocetus vanbenedeni, Squalodelphis fabianii, Dilophodelphis fordycei, Macrosqualodelphis ukupachai and Huaridelphis rai-mondii) but with no air cavities. Then, in the Platanistidae this crest shows some degree of pneumatization (Zarhachis flagellator and Pomatodelphis inaequalis), with the derived, extensively pneumatized supraorbital crest morphology, as in the extant representative Platanista gangetica (Boersma et al. 2017).

**Echolocation and underwater hearing.** In *Notocetus vanbenedeni*, the presence of the premaxillary sac fossa (the only osteological correlate of the nasal sac system), prenarial triangle and premaxillary foramen suggests a naso-sac system of a similar level of development to that of most extant odontocetes (e.g. Lawrence & Schervill 1956; Costidis & Rommel 2012, 2016). The ascending process of the maxilla, infraorbital foramina and antorbital notch indicate the presence of nasofacial muscles and associated innervation related to the nasal sac system and melon, a condition also similar to that of extant odontocetes (e.g. Lawrence & Schervill 1956; Costidis & Rommel 2012, 2016). For the pterygoid sinus system, derived from the Eustachian tube and associated with the middle ear cavity (Fraser & Purves 1960; Costidis & Rommel 2012, 2016), *Notocetus vanbenedeni* has osteological correlates that indicate the presence of the orbital, pterygoid, peribullary, posterior, and middle sinuses (Fraser & Purves 1960).

The contact between the lateral lamina of the pterygoid and the falcial form process of the squamosal (ch. 147), with the associated presence of an external foramen ovale in *Notocetus vanbenedeni*, is a plesiomorphic characteristic also present in basilosaurids (e.g. Luo & Gingerich 1999; Martínez-Cáceres et al. 2017), some eurhinodelphinids (e.g. Lambert 2004, 2005), platanistoids Huaridelphis raimondii, Macrosqualodelphis ukupachai, Zarhachis flagellator, Pomatodelphis inaequalis, Dilophodelphis fordycei, Platanista gangetica and Pontoporia blainvillei (Anderson 1878; Fraser & Purves 1960; de Muizon 1988). In other extant odontocetes, the external foramen ovale might be variably present and a tendinous sheet (Fraser & Purves 1960) replaces the bony lateral wall around the pterygoid sinus.

As part of the underwater hearing adaptations, odontocetes developed an uncoupled tympanoperiotic complex with tendinous connections to the skull, although a bony contact is present in some extant species (Fraser & Purves 1960). If we optimize the character articular rim of the periotic (ch. 197), the derived hook-like morphology was convergently acquired in both *Squalodelphis fabianii* and Platanistidae (except *Phocageneus venustus*) already in the early Miocene (Burdigalian; *Supplementary material* 5). Thus, *Notocetus vanbenedeni* would have the plesiomorphic condition of a slightly developed articular rim. Together with the contact surface between the posterior process of the tympanic bulla and the posttympanic process of the squamosal, these characteristics suggest that *Notocetus vanbenedeni* had a plesiomorphic, somewhat developed, bony connection between the earbones and the squamosal, probably not as tight as in *Platanista* (Anderson 1878). The functional consequences of this morphology for underwater hearing capabilities remain unknown. The periotic of *Notocetus vanbenedeni* also presents a moderately inflated squared pars cochlearis, a morphological characteristic present among extant river dolphins (Gutstein et al. 2014). Recent analyses of the inner ear morphology of *Notocetus vanbenedeni* showed that this species has a derived cochlear morphology amongst platanistoids, adapted for high-frequency hearing. Unlike what we observed for the skull, cochlear morphology shows high intraspecific variation for this species (Viglino et al. 2021).

Finally, the articulation surfaces of the auditory ossicles in *Notocetus vanbenedeni* with the tympanic bulla and periotic and the stapedial muscle fossa suggest a vibrational mechanism for these ossicles, similar to that of extant odontocetes (e.g. Cranford et al. 2010).

**Palaeoecological role of the odontocetes in the early Miocene of Patagonia**

In the early Miocene Patagonian seas, the platanistoid *Notocetus vanbenedeni* co-existed with other odontocetes, such as Aondelphis talen, Phoberodon arctirostris and Prosqualodon australis (Viglino et al. 2018a, b; Gaetán et al. 2019; Cuitiño et al. 2019). *Notocetus vanbenedeni* is the only early Miocene Patagonian odontocete species with a nearly homodont and single-rooted condition. Together with the characteristics of the rostrum and temporal fossa, the feeding apparatus morphology of *Notocetus vanbenedeni* suggests this species was a combination suction-feeder, whereas Phoberodon arctirostris and Prosqualodon australis had a plesiomorphic raptorial feeding method (Viglino et al. 2020). Underwater hearing and echolocalization abilities have been inferred for all Patagonian odontocete species (except for Phoberodon arctirostris); in addition, *Notocetus vanbenedeni* shares derived periartic (e.g. articular rim) and cochlear morphological characteristics with *Platanista gangetica* (Viglino et al. 2021). In terms of body size, *Notocetus vanbenedeni* falls within the small morphotype category together with Aondelphis talen (TL 2–2.7 m), similar in terms of TL to *Platanista gangetica* (Anderson 1878; Viglino et al. 2018a). The
TL in these extinct species differs from the longer TL of >3 m inferred for Phoberodon arctirostris and Prosqualodon australis (Viglino et al. 2018b; Gaetán et al. 2019), suggesting the coexistence of diverse body sizes. On the other hand, sedimentological analyses of the Gaiman Formation indicate that all these species lived in a protected and shallow inner shelf environment with occasional freshwater influence (Cutillo et al. 2019). Notocetus vanbenedeni is strikingly the most abundant species in these outcrops, suggesting that it already preferred shallow habitats with fluvial influence, similar to Platanista. Therefore, considering these anatomical and habitat differences, we suggest distinct palaeoecological roles for Notocetus vanbenedeni, Aondelphis talen, Phoberodon arctirostris and Prosqualodon australis. These species probably differed in their prey type, foraging methods and/or habitat use (e.g. Kiszka et al. 2011). A similar ecological trophic partitioning has been proposed, for example, for the early Miocene odontocete fauna of the Chilcatay Formation (Bianucci et al. 2018, 2020). Future comprehensive palaeoecological studies may help to better understand the ecological role of odontocetes in the early Miocene seas of Patagonia.

Conclusions

The anatomical, palaeobiological and phylogenetic analyses presented here support Notocetus vanbenedeni as a valid platanistoid species that inhabited the early Miocene Patagonian seas. Unlike in previous studies, this species is not recovered as a Squalodelphinidae but as a member of a new clade (i.e. Group A) and as a taxon distinct from Peruvian platanistoids (MUSM 1395, 3896, 3897 and 1484).

Notocetus vanbenedeni presents a combination of plesiomorphic and derived features that allows us to interpret it as an intermediate platanistoid morphotype. The elevated dorsal tubercular supraorbital crest of this species, together with the diverse tubercular morphotypes recorded in other species from Group A and Squalodelphinidae, indicates that a supraorbital crest had already been acquired in platanistoids since the early Miocene. Only Platanista shows a highly pneumatized supraorbital crest condition. Notocetus vanbenedeni also shows initial stages of a plesiomorphic bony connection between the earbones and skull, although functional implications for hearing remain elusive. The nasal sac system, pterygoid sinus system and earbone morphology suggest that Notocetus vanbenedeni was able to hear high-frequency sounds and echolocate underwater, similarly to extant odontocetes.

For the early Miocene seas of Patagonia, Notocetus vanbenedeni represents a highly derived odontocete morphotype. The feeding apparatus of Notocetus vanbenedeni makes it the only combination suction-feeder recorded and among the smallest odontocete in this cetacean community as well. The species shares earbone and cochlear morphological characteristics with the extant representative Platanista. Finally, the abundant records of Notocetus vanbenedeni in an inner shelf environment with freshwater influence suggest a possible preference for such protected habitats already in the early Miocene. Therefore, considering all the anatomical and habitat differences, we propose different palaeoecological roles for the various early Miocene odontocetes of Patagonia.

The revised palaeobiological and phylogenetic analyses of Notocetus vanbenedeni presented here now lead to even more questions: was it more of a prey or a predator in Patagonia? Why was Notocetus vanbenedeni the only abundant platanistoid recorded there? Why did Notocetus vanbenedeni have low intraspecific variation in terms of skull morphology? What palaeobiogeographical pattern explains the evolutionary connection of the platanistoid fauna from the Southern and Northern Hemisphere during the early Miocene? Notocetus vanbenedeni can certainly offer more information to help us elucidate the evolutionary history of Platanistoidea.

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