Hearing from the ocean and into the river: the evolution of the inner ear of Platanistoidea (Cetacea: Odontoceti)

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Abstract.—The inner ear of the two higher clades of modern cetaceans (Neoceti) is highly adapted for hearing infrasonic (mysticetes) or ultrasonic (odontocetes) frequencies. Within odontocetes, Platanistoidea comprises a single extant riverine representative, Platanista gangetica, and a diversity of mainly extinct marine species from the late Oligocene onward. Recent studies drawing on features including the disparate tympanoperiotic have not yet provided a consensus phylogenetic hypothesis for platanistoids. Further, cochlear morphology and evolutionary patterns have never been reported. Here, we describe for the first time the inner ear morphology of late Oligocene–early Miocene extinct marine platanistoids and their evolutionary patterns. We initially hypothesized that extinct marine platanistoids lacked a specialized inner ear like P. gangetica and thus, their morphology and inferred hearing abilities were more similar to those of pelagic odontocetes. Our results reveal there is no “typical” platanistoid cochlear type, as the group displays a disparate range of cochlear anatomies, but all are consistent with high-frequency hearing. Stem odontocete Prosqualodon australis and platanistoid Otekaikea huata present a tympanal recess in their cochlea, of yet uncertain function in the hearing mechanism in cetaceans. The more basal morphology of Aondelphis talen indicates it had lower high-frequency hearing than other platanistoids. Finally, Platanista has the most derived cochlear morphology, adding to evidence that it is an outlier within the group and consistent with a >9-Myr-long separation from its sister genus Zarhachis. The evolution of a singular sound production morphology within Platanistidae may have facilitated the survival of Platanista to the present day.

Introduction

Living cetaceans primarily use auditory cues to hunt and communicate, because the physical properties of water restrict the use of their other senses (Pihlström 2008). Their ear is highly adapted for underwater hearing at either infrasonic frequencies in mysticetes or ultrasonic frequencies in odontocetes (e.g., Ketten 1997, 2000; Nummela et al. 2007; Churchill et al. 2016; Ekdale 2016a,b; Park et al. 2016). Previous studies of extinct cetaceans show that the first underwater hearing morphologies were acquired in archaeocetes, for example, Remingtonocetidae and Basilosauroidae (Nummela et al. 2004, 2007), and it was proposed that the ancestor of the Neoceti (Mysticeti + Odontoceti) had low-frequency (but likely not infrasonic) hearing (Ekdale and Racicot 2015; Ekdale 2016a,b; Mourlam and Orliac 2017; Park et al. 2017a). Odontocetes have a high-frequency hearing range, and their inner ear is characterized by a short cochlear canal, a stiff basilar membrane with extensive bony support, and a reduced vestibular system, among other characteristics (Oelschläger 1986; Ketten and Wartzok 1990; Ketten 2000; Gutstein et al. 2014; Churchll et al. 2016; Park et al. 2016; Costeur et al. 2018).

Riverine dolphins are a paraphyletic group that includes four extant species: Platanista gangetica (Platanistidae), Lipotes vexillifer...
(Lipotidae), *Inia geoffrensis* (Iniidae), and *Pontoporia blainvillei* (Pontoporiidae; e.g., de Muizon 1988; Cassens et al. 2000; Fordyce and de Muizon 2001; Nikaido et al. 2001). They are a textbook example of convergent evolution (e.g., Geisler et al. 2011), with their long rostrum, small eyes, and unfused cervical vertebrae, among other anatomic characteristics (Page and Cooper 2017; Fordyce 2018; Rommel and Reynolds 2018). Riverine dolphins also share acoustic characteristics, with a high-frequency narrow-banded click structure; high echolocation peak energy (>100 kHz) sounds; and periotic characteristics like a rounded, slender, and high pars cochlearis (Ketten and Wartzok 1990; Gutstein et al. 2014). Generally, their cochleae have a nearly planar spiral in less than 2 full turns, longer outer bony lamina than most other odontocetes, and compressed cochlear ducts. However, some authors have suggested that cochlear morphology does not appear to be convergent (Park et al. 2019; but see Costeur et al. 2018). Riverine species rely on echolocation sounds to sort their complex environment and detect small objects at shorter average distances than pelagic species (Ketten and Wartzok 1990; Jensen et al. 2013).

One living riverine species, *P. gangetica*, warrants special attention. This species is the sole extant representative of an otherwise diverse fossil group, the Platanistoidea (sensu de Muizon 1987), whose contents and phylogenetic relationships are still debated (e.g., Fordyce and de Muizon 2001; Boersma et al. 2017; Tanaka and Fordyce 2017 and references therein; Viglino et al. 2018a,b, 2020; Gaétan et al. 2019; Bianucci et al. 2020). The earliest fossil record of this group comes from the late Oligocene, reaching a peak in diversity by the middle Miocene and a marked decrease by the middle–late Miocene (e.g., de Muizon 1987; Fordyce and de Muizon 2001). Several clades are usually recovered within Platanistoidea: upper Oligocene outcrops from New Zealand record some of the oldest platanistoids, such as *Waipatia* spp., *Otekaieka* spp., and *Awamokoa tokarahi* (Waipatidae; Fordyce 1994; Tanaka and Fordyce 2017 and references therein). Allodelphinids are recorded in lower Miocene outcrops of the eastern and western margins of the North Pacific (Boersma and Pyenson 2016; Kimura and Barnes 2016). In Patagonia, lower Miocene outcrops (Cuitiño et al. 2019) have produced two platanistoid species, the squalodelphinid *Notocetus vanbenedeni* and the platanistoid *Aondelphis talen* (Moreno 1892; Viglino et al. 2018b; Viglino 2019); and two putative members of this group, *Phoberodon arctirostris* and *Prospqualodon australis* (Viglino et al. 2018a; Gaétan et al. 2019). Lower Miocene outcrops in Italy, France, Peru, and the United States hold other squalodelphinid taxa; and Miocene outcrops of mainly Europe and the United States record other extinct Platanistidae species (Paleobiology Database 2020; e.g., Barnes et al. 2010; Lambert et al. 2014; Godfrey et al. 2017). *Platanista gangetica* is a critically endangered (Braulik et al. 2015; Braulik and Smith 2019) species that possesses several unique morphological characteristics, such as pneumatized maxillary crests containing a pterygoid sinus extension, a long mandibular symphysis, and a closed optic foramen, among others (Anderson 1878; Jensen et al. 2013). Curiously, the evolutionary patterns that led to *Platanista*’s bizarre morphology are still unknown, but see Boersma et al. (2017).

There are several hypotheses and much uncertainty surrounding the most important question for Platanistoidea: what are the causes that led diversity to decrease significantly, resulting in a single extant riverine representative today? Some authors have proposed that platanistoids were ecologically replaced by delphinids (e.g., Fordyce and Barnes 1994; Hamilton et al. 2001; Steeman et al. 2009); that the ancestor of platanistids inhabited epicontinental seas and remained in fluvial basins through the sea-level regression during the middle–late Miocene (e.g., Cassens et al. 2000; Hamilton et al. 2001); or that the temperature decline after the middle Miocene climatic optimum negatively affected shallow-water species (e.g., Marx et al. 2016). Similarly, other vertebrate groups also comprise a majority of extinct species and a few extant representatives, for example, the pygmy right whale (e.g., Marx et al. 2018), tuatara (e.g., Meloro and Jones 2012), coelacanth (e.g., Cavin and Guinot 2014), and red panda (e.g., Salesa et al. 2011).
These groups illustrate complex but interesting macroevolutionary patterns which need to be analyzed from different perspectives.

Despite the increasing amount of contemporary information on the phylogenetic relationships of platanistoids, the inner ear morphology and evolutionary pattern associated with this group have never been reported, and it is here described and analyzed for the first time. Thus, the goal of the present contribution is to characterize the inner ear morphology of some late Oligocene–early Miocene extinct marine platanistoids, compare them with their living riverine representative *P. gangetica*, and propose a scenario for the evolution of their morphology. The sample includes, for the first time, platanistoid species from the late Oligocene of New Zealand and early Miocene of Patagonia, a key time in the diversification and ecological expansion of the group. Having representatives of the most frequently recovered families within Platanistoidea allow us to study, on a broader scale, how the inner ear morphology of the group evolved. Our initial hypothesis is that extinct marine platanistoids did not have a derived inner ear like *P. gangetica*, and thus their morphology and inferred hearing abilities were more closely related to pelagic odontocete species. Therefore, *P. gangetica* would represent a unique morphological ecomorphotype specialized for the riverine environment it inhabits.

### Materials and Methods

#### Institutional Abbreviations

AMNH, American Museum of Natural History, New York, USA; MNHN, Museum National d’Histoire Naturelle, Paris, France; MPEF-PV, Colección de Paleovertebrados, Museo Paleontológico “Egidio Feruglio,” Trelew, Argentina; NHMUK, Natural History Museum, London, United Kingdom; NMB, Natuurmuseum Brabant, Tilburg, Holland; NMVC, Museum Victoria Mammalogy Collection, Melbourne, Australia; OU, Geology Museum, University of Otago, Dunedin, New Zealand; USNM, Department of Paleobiology and Department of Vertebrate Zoology (Division of Mammals), National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

#### Sample

To perform this study, we obtained microcomputed tomography (microCT) scans of the periotics (the bone containing the inner ear) of 10 platanistoid genera by imaging osteological and palaeontological specimens from museum collections (total number of specimens = 11) and utilizing data from previous studies (Park et al. 2018, 2019; see Table 1). With these data, we reconstructed 3D models of the inner ears using the segmentation and thresholding editors in Avizo v. 9.0 (Visualization Sciences Group 2016) and then cleaned the resulting 3D models using Geomagic Wrap (3D Systems 2017).

#### Table 1. List of specimens included in the present study, with their corresponding collection numbers and groups as used in statistical analyses.

| Species                   | Specimen number | Group          |
|---------------------------|-----------------|----------------|
| *Awamokoa tokarahi*       | OU 22125        | Platanistoidea |
| *Notocetus vanbenedeni*   | MPEF-PV 1804    | Platanistoidea |
| *Oletkaia huata*          | AMNH-FM 29026   | Platanistoidea |
| *Waipatia macorechenua*   | OU 22306        | Platanistoidea |
| *Zarhachis sp._1*         | NHMUK-M 15789   | Platanistoidea |
| *Platanista gangetica*    | AMNH-FM 145500  | Platanistoidea |
| *Aondelphis talen*        | MPEF-PV 517     | Platanistoidea |
| *Squalodon calvertensis*  | NHMUK-M 15788   | Stem Odontoceti|
| *Prosqualodon australis*  | MPEF-PV 1869    | Stem Odontoceti|
| *Delphinapterus leucas*   | NMB XII 1086    | Delphinida     |
| *Inia geoffrensis*        | NMVC 24976      | Delphinida     |
| *Kogia breviceps*         | AMNH 57333      | Delphinida     |
| *Phocoena phocoena*       | NHMUK-CE 893    | Delphinida     |
| *Physeter macrocephalus*  | NHMUK-CE 893    | Delphinida     |
| *Pontoporia blainvillei*  | MNHN 1934.375   | Delphinida     |
| *Tasmacetus shepherdi*    | NMVC 37967.6    | Physeteroidea  |
| *Tursiops truncatus*      | NHMUK-CE 1866.8.7.1 | Physeteroidea |
| *Ziphiidae*               |                 |                |
| *Lipotes vexillifer*      |                 |                |
| *Physeteroidea*           |                 |                |
| *Zygoryhiza sp.*          | USNM 214433     | Basilosaurida  |
For the purposes of this study, we have defined the clade Platanistoidea as including the genera *Waipatia*, *Otekaikea*, *Avamoko*, *Zarbachis*, *Notocetus*, *Aondelphis*, and *Platanista* (Viglino et al. 2018a,b). These genera represent families that are usually recovered within this clade: Waipatiidae, Squalodelphinidae, and Platanistidae (for details on specimens used, see Table 1) (but note that some authors recovered waipatiids as stem Odontoceti; e.g., Lambert et al. 2018; Bianucci et al. 2020). For further details on the still-debated systematic and phylogenetic aspects of Platanistoidea, see, for example, Fordyce (1994), Lambert et al. (2014), Tanaka and Fordyce (2015, 2017), Boersma and Pyenson (2016), Boersma et al. (2017), Viglino et al. (2018a,b, 2020), Gaetán et al. (2019), and Bianucci et al. (2020), as well as references therein. The sample also included representatives of two putative platanistoids, *Squalodon calvertensis* and *Prosqualodon australis* (for details on the phylogenetic position of these taxa, please see de Muizon [1994] and Gaetán et al. [2019]).

For the statistical analyses (see “3D Geometric Morphometric and Statistical Analyses”), we also included one species as a representative of each of the remaining extant odontocete families (*n* = 9) for comparative purposes, as well as one archaeocete representative (*n* = 1) of the family Basilosauridae (see Table 1). This resulted in a total dataset of 21 specimens.

**Measurements**

We took multiple measurements of internal structures of the cochlea and semicircular canals postulated to be related to hearing physiology (Table 2; e.g., Ketten and Wartzok 1990; Luo and Marsh 1996; Manoussaki et al. 2008; Ekdale and Racicot 2015; Mourlam and Orliac 2017). These were taken using the Measure, Slice, Spline Probe, and Surface Area Volume tools in Avizo, following the protocols of Park et al. (2016). These measurements include: (1) cochlear height; (2) cochlear width; (3) number of turns; (4) cochlear canal length (measured along the midline); (5) extent of the secondary spiral lamina (SSL); (6) cochlear volume; (7) basal radius; (8) apical radius; (9) inter-turn distance (ITD); (10) shorter diameter of the basal turn (W2); (11) diameter of the spiral ganglion canal (GAN); (12) area of the fenestra cochleae (FC); and (13) anteroposterior (AP), (14) antero-lateral (AL), and (15) posterolateral (PL) angles of the semicircular canals. The extension (%) of the SSL was measured by dividing the length of the cochlear canal at the apical-most point of the SSL by the total length of the cochlear canal, then multiplying by 100. The ITD is the thickness of the bony wall separating the first turn from the second turn at the proximal end of the basal turn (Ekdale and Racicot 2015). The GAN was measured in the first quarter turn, following Churchill et al. (2016) and Mourlam and Orliac (2017).

From these measurements, we additionally calculated several previously established ratios, which together form a quantitative description of cochlear morphology (Ketten and Wartzok 1990): (1) axial pitch (height of the cochlea divided by the number of turns); (2) the basal ratio (height of the cochlea divided by its basal diameter), which is negatively proportional to frequency (Ketten and Wartzok 1990); and (3) radii ratio (radius of the cochlea at its base divided by the radius at its apex), which is strongly correlated with low-frequency hearing limits (Manoussaki et al. 2008). However, see Ritsche et al. (2018) for issues with different measurement methods in this metric. Finally, we estimated the low-frequency hearing limit (LFL) for all specimens following Manoussaki et al. (2008):

\[
 f = 1507 \exp(-0.578[p - 1])
\]

where *f* is the low-frequency hearing limit at 60 dB re 20 μPa in air and 120 dB re 1 μPa in water, and *p* is the radii ratio value. However, this equation was derived mainly from terrestrial mammals in air and should therefore be considered tentative (Manoussaki et al. 2008; Ekdale and Racicot 2015).

**3D Geometric Morphometric and Statistical Analyses**

We landmarked the digital models of the inner ear with one fixed landmark and 68 sliding semilandmark curves comprising a total of 625 landmarks (see Supplementary Material), using IDAV Landmark (Wiley 2005).
TABLE 2. Measurements of internal structures of the cochlea of the platanistoid and stem odontocete species included. SSL, secondary spiral lamina; LFL, low-frequency hearing limit; ITD, inter-turn distance; W2, shorter diameter of the basal turn; GAN, diameter of the spiral ganglion canal; FC, area of the fenestra cochleae; AL, anterolateral angle of the semicircular canals; AP, anteroposterior angle of the semicircular canals; PL, posterolateral angle of the semicircular canals.

| Species                  | Number of turns | Canal length (mm) | Radii (%) SSL | Basal ratio (%) | Axial pitch (mm) | Cochlear height (mm) | Cochlear Width (mm) | Volume (mm3) | Estimated LFL (Hz) | ITD (mm) | W2 (mm) | GAN (mm) | FC (mm2) | AL  | AP  | PL |
|--------------------------|-----------------|-------------------|----------------|-----------------|-------------------|----------------------|---------------------|--------------|-------------------|----------|---------|---------|---------|-----|-----|-----|
| *Aondelphis talen*       | 1.75            | 24.65             | 6.85           | 72.28           | 0.62              | 3.27                 | 5.73                | 9.25         | 148.82            | 1.84     | 6.77    | 0.49    | 4.13    | 119.8 | 110.7| 72  |
| *Awamokoa tokarahi*      | 1.75            | 23.78             | 4.00           | 61.00           | 0.57              | 3.01                 | 5.27                | 9.25         | 126.01            | 1.77     | 6.93    | 0.52    | 6.58    | 115.7 | 139.4| 107.6 |
| *Notocetus vanbenedeni* _1_ | 2.00            | 31.99             | 6.36           | 77.18           | 0.52              | 2.95                 | 5.89                | 11.25        | 180.26            | 2.68     | 8.98    | 0.58    | 9.57    | 142.2 | 96.32| 107.6 |
| *Notocetus vanbenedeni* _2_ | 1.75            | 33.07             | 5.74           | 71.57           | 0.50              | 3.20                 | 5.60                | 11.30        | 206.38            | 2.33     | 8.53    | 0.87    | 8.67    | 134.3 | 106.6| 95.3 |
| *Otekaikea huata*        | 2.00            | 21.76             | 5.67           | 64.31           | 0.40              | 1.83                 | 3.65                | 9.18         | 98.63             | 1.59     | 6.26    | 0.57    | 3.95    | 107   | 141.9| 122 |
| *Platanista gangetica*   | 2.00            | 40.69             | 4.23           | 62.98           | 0.42              | 2.71                 | 5.41                | 12.84        | 198.14            | 2.33     | 10.01   | 0.51    | 8.45    | 128.2 | 114.1| 109.59 |
| *Waipatia maerewhenua*    | 2.00            | 22.88             | 5.59           | 66.49           | 0.62              | 2.74                 | 5.47                | 8.76         | 132.80            | 1.59     | 6.01    | 0.62    | 8.86    | 126.1 | –    | 77.71 |
| *Zarhachis sp._1*        | 1.90            | 31.67             | 6.09           | 75.69           | 0.46              | 2.84                 | 5.39                | 11.70        | 157.58            | 2.51     | 8.93    | 0.64    | 7.23    | 128.9 | 106.2| 61.9 |
| *Zarhachis sp._2*        | 2.00            | 34.58             | 6.45           | 68.71           | 0.51              | 2.88                 | 5.75                | 11.23        | 198.16            | 2.25     | 9.19    | -       | 7.94    | 122.7 | 97.8 | 85.42 |
| *Prosqualodon australis* | 2.00            | 28.52             | 6.03           | 73.53           | 0.57              | 3.33                 | 6.66                | 11.65        | 247.73            | 1.74     | 7.01    | 0.80    | 10.04   | 127.5 | 109.83| 87.38 |
| *Squalodon calvertensis* | 1.75            | 25.55             | 8.47           | 69.33           | 0.57              | 2.85                 | 4.98                | 8.72         | 149.69            | 2.05     | 7.44    | 0.69    | 7.44    | 126.9 | 134.7| 82.28 |
The position of these curves followed the protocols of Costeur et al. (2018).

Using these landmarks, we generated and analyzed three different datasets: cochlea and fenestra vestibuli landmark configuration for Platanistoidea only (P_Coch); the complete inner ear landmark configuration for Platanistoidea and comparative Odontoceti and Basilosauridae (P+O_All); cochlea and fenestra vestibuli landmark configuration for Platanistoidea and comparative Odontoceti and Basilosauridae (P+O_Coch). These datasets will facilitate comparisons of the inner ear morphology both among platanistoids and also with other cetacean clades, as well as revealing any potential evolutionary patterns. All of the statistical analyses were conducted for each of these datasets, as described in the following paragraphs.

After placing the landmarks as described, we conducted a generalized Procrustes analysis with sliding curves for the semilandmarks using the gpagen function. To test for the effect of size (allometry), we performed regressions of shape on size (log of centroid size) with 10,000 iterations using the procD.lm function. Both analyses used the geomorph package (Adams and Otárola-Castillo 2013) in R software (R Core Team2017). Given that there was no allometric effect (see “Results” section), Procrustes coordinates were used for subsequent statistical analyses.

Then, to explore variation of inner ear shape, we performed a principal component analysis (PCA) using the plotTangentSpace function of the geomorph package (Adams and Otárola-Castillo 2013), and deformation 3D grids were generated to show shape variation among the PC axes. Next, we conducted canonical variate analysis (CVA), which is an ordination method that maximizes between-group variation relative to within-group variation. Deformation 3D grids were generated in these analyses as well. For these analyses, the CVA function of the Morpho package (Schlager 2017) with 10,000 iterations was used. It should be noted that the basilosaurid specimen was excluded from this analysis, as it requires a minimum of two specimens. To evaluate the presence of a phylogenetic signal in shape variation of the inner ear in our sample, we performed the physignal function of the geomorph package (Adams and Otárola-Castillo 2013) with 1000 permutations. This function uses the Kmult-statistic (Adams 2014) that measures similarity of trait values relative to a Brownian motion model of evolution. Finally, we plotted the first two PC axes including a phylogenetic hypothesis using the plotGMPhyloMorphoSpace function of the geomorph package (Adams and Otárola-Castillo 2013) to show a possible evolutionary trajectory for inner ear shape variation. The phylogenetic hypothesis used follows Viglino et al. (2018a,b) and Gaetán et al. (2019), given that it includes all platanistoid species used in our study, and we have thoroughly revised the coding of the matrix used in those publications.

**Results**

**Descriptions of Cochlear Anatomy**

*Aondelphis talen.*—The cochlea of *A. talen* (Table 1) is well preserved, with the exception of minor damage to the basal half of the apical turn. The right cochlea completes approximately 1.75 turns (Fig. 1). The overall shape of the cochlea most closely resembles the spiral shape of ziphiids and differs from delphinids. In anterior view, the cochlear spiral is tall, a feature seen in mysticetes, archaeocetes, and Paleogene odontocetes. The fenestra cochleae is large relative to most extant odontocete taxa. There is no tympanal recess. The cochlear aqueduct is large, similar to *Zygorhiza*. In vestibular view, the first quarter of the basal turn is more loosely coiled than the remaining 1.5 turns. The apical-most half-turn slightly overlaps the basal turn, enclosing a small open space, rather than being fully closed like in stem cetacean taxa (e.g., *Zygorhiza*). The axial pitch is 3.27, and the basal ratio is 0.62 (Table 2). The secondary spiral lamina extends along the radial wall of the cochlear canal for 72% of its total length. The radii ratio is 6.85, a value that is higher than those calculated for the crown odontocetes (except ziphiids) (Park et al. 2016), resulting in an estimated low-frequency hearing limit of 51.15 Hz.

*Notocetus vanbenedeni.*—The left cochlea of *N. vanbenedeni* (Table 1) is well preserved, with only minor damage to the cochlear canal
FIGURE 1. 3D reconstruction of the cochlea of Patagonian stem Odontoceti and platanistoids analyzed in this study. A, anterior; B, lateral; C, dorsal; and D, vestibular views. Scale bars, 5 mm. Abbreviations: ac, anterior canal; ant, anterior; cc, cochlear canal; dor, dorsal; es, endolymphatic sac; fc, fenestra cochleae; fv, fenestra vestibuli; lat, lateral; lc, lateral canal; med, medial; pc, posterior canal; pos, posterior; psl, primary spiral lamina; ssl, secondary spiral lamina; tr, tympanal recess.
and the semicircular canals. The cochlea completes approximately 2 turns (Fig. 1). The overall shape of the cochlea most closely resembles the lower, flatter spiral shape of delphinids (Ekdale and Racicot 2015). The fenestra cochleae is approximately the same size as in most extant odontocete taxa (Table 2). There is no tympanal recess. The cochlear aqueduct is large. In vestibular view, the cochlear canal is loosely coiled, displaying no overlap of the basal and apical turns. This produces a large open space at the apex of the cochlea. The axial pitch is 2.95, and the basal ratio is 0.52 (Table 2). The secondary spiral lamina extends along the radial wall of the cochlear canal for 77% of its total length. The radii ratio is 6.36, a value that is higher than those calculated for crown odontocetes (except ziphiids) (Park et al. 2016), resulting in an estimated low-frequency hearing limit of 67.98 Hz.

Prosqualodon australis.—The left cochlea of P. australis (Table 1) is well preserved. The cochlea completes approximately 2 turns (Fig. 1). The overall shape of the cochlea most closely resembles that of stem odontocetes, being tightly coiled with a tall spire. As in A. talen, the cochlear spiral is tall in anterior view, a feature also seen in mysticetes, archaeocetes, and Paleogene odontocetes. The fenestra cochleae is approximately the same size as in most extant odontocete taxa. Unlike A. talen, the cochlear spiral is tall in anterior view, a feature also seen in mysticetes, archaeocetes, and Paleogene odontocetes. The fenestra cochleae is approximately the same size as that of most extant odontocete taxa. There is no tympanal recess. The cochlear aqueduct is large, similar to Zygorhiza. In vestibular view, the first quarter of the basal turn is more loosely coiled than the remaining 1.5 turns. The apical-most half-turn slightly overlaps the basal turn, enclosing a small open space, rather than being fully closed like in stem cetacean taxa (e.g., Zygorhiza). The axial pitch is 3.01, and the basal ratio is 0.57 (Table 2). The secondary spiral lamina extends along the radial wall of the cochlear canal for 61% of its total length. The radii ratio is 4.00, a value that is similar to those calculated for the crown odontocetes (except ziphiids) (Park et al. 2016), resulting in an estimated low-frequency hearing limit of 266.10 Hz.

Otekaieka huata.—The cochlea of O. huata (Table 1) is well preserved, although the cochlear canal has been slightly damaged by sediment, resulting in a more textured endocast, as opposed to a smooth one. The left cochlea completes approximately 1.75 turns (Fig. 2). The overall shape of the cochlea is similar to that of crown odontocetes, having a lower spiral than Zygorhiza and Waipatia, most closely resembling Otekaieka huata in its spiral shape. In anterior view, the cochlear spiral is tall, a feature seen in mysticetes, archaeocetes, and Paleogene odontocetes. The fenestra cochleae is approximately the same size as that of most extant odontocete taxa. There is no tympanal recess. The cochlear aqueduct is large, similar to Zygorhiza. In vestibular view, the first quarter of the basal turn is more loosely coiled than the remaining 1.5 turns. The apical-most half-turn slightly overlaps the basal turn, enclosing a small open space, rather than being fully closed like in stem cetacean taxa. Unlike A. tokarahi, there is a tympanal recess present (sensu Park et al. 2017c), with the scala tympani being inflated radially along almost the entire first half turn. The cochlear aqueduct is small. In vestibular view, the first quarter of the basal turn is more loosely coiled than the remaining 1.5 turns. The apical-most half-turn slightly overlaps the basal turn, enclosing a small open space, rather than being fully closed like in stem cetacean taxa.
FIGURE 2. 3D reconstruction of the cochlea of New Zealand platanistoids analyzed in this study. A, anterior; B, lateral; C, dorsal; and D, vestibular views. Scale bars, 5 mm. Abbreviations: ac, anterior canal; ant, anterior; cc, cochlear canal; dor, dorsal; es, endolymphatic sac; fc, fenestra cochleae; fv, fenestra vestibuli; lat, lateral; lc, lateral canal; med, medial; pc, posterior canal; pos, posterior; psl, primary spiral lamina; ssl, secondary spiral lamina; tr, tympanal recess.
(e.g., *Zygorhiza*). The axial pitch is 1.83, and the basal ratio is 0.40 (Table 2). The secondary spiral lamina extends along the radial wall of the cochlear canal for 64% of its total length. The radii ratio is 5.67, a value that is similar to those calculated for the crown odontocetes (except ziphiids) (Park et al. 2016), resulting in an estimated low-frequency hearing limit of 101.4 Hz.

*Waipatia maerewhenua.*—The cochlea of *W. maerewhenua* (Table 1) is quite well preserved, although the cochlear canal has been damaged by sediment, as were the other New Zealand species included in this study, resulting in a textured endocast, as opposed to a smooth one. The left cochlea completes approximately 2 turns (Fig. 2). The overall shape of the cochlea is similar to that of *Zygorhiza*. In anterior view, the cochlear spiral is tall, a feature seen in mysticetes, archaeocetes, and Paleogene odontocetes. The fenestra cochlea is approximately the same size as that of *P. australis* and *Squalodon calvertensis*. There is no tympanal recess. The cochlear aqueduct is small. In vestibular view, the first quarter of the basal turn is more loosely coiled than the remaining 1.5 turns, but not as loose as in *Otekaikea* or *Awamokoa*. The apical-most three-quarter turn slightly overlaps the basal turn, enclosing a very small open space, which is almost fully closed like in stem cetacean taxa (e.g., *Zygorhiza*). The axial pitch is 2.74, and the basal ratio is 0.62 (Table 2). The secondary spiral lamina extends along the radial wall of the cochlear canal for 66% of its total length. The radii ratio is 5.59, a value that is similar to those calculated for crown odontocetes (except ziphiids) (Park et al. 2016), resulting in an estimated low-frequency hearing limit of 106.1 Hz.

### 3D Geometric Morphometric Analyses

We initially analyzed the allometric effect on shape variation in each dataset, to test whether size had a significant effect. For all datasets, the effect of size was not significant (P+O_All $p = 0.68$; P+O_Coch $p = 0.80$; P_Coch $p = 0.90$), so all subsequent statistical analyses were performed on the Procrustes coordinates. We will focus our analyses and discussion on the results from the P+O_All dataset only; for the remaining dataset results, please see Supplementary Material.

### Principal Component Analysis

The PCA for the P+O_All dataset showed the highest variation in the first 12 PCs (95% total variance), but we will focus on the first two (58.7% total variance) (Fig. 3). When plotting PC 1 vs. PC 2, there is a slight overlap between Platanistoidea (*Platanista gangetica*) and Delphinida in both axes (for species included in each taxonomic group, see Table 1). The stem Odontoceti representatives overlap with the Platanistoidea morphospace in PC 1, while *Zygorhiza* sp. is on the extreme positive side of PC 1. Curiously, *Physeter macrocephalus* and *Tasmacetus shepherdi* overlap with platanistoids, while *Kogia breviceps* is on the negative extreme of PC 1. The morphospace occupied by the Platanistoidea is the largest of any of the groups included in this study. The main variables in PC 1 are the width of the cochlea, especially the basal turn, and the position and area of the fenestra vestibuli; on PC 2, the main shape variation includes the tightness of the cochlear spiral, the width of the basal turn, and the height of the cochlea.

### Canonical Variate Analysis

The CVA (excluding *Zygorhiza* sp.), on the other hand, further supports a clear separation between Platanistoidea and Delphinida, with an overlap between stem Odontoceti and Platanistoidea on CV 1 (Fig. 5). The Physeteridae and Ziphiidae species overlap on CV 1 with Platanistoidea as well. The first two CV axes account for 95% of the variation on the sample, so it has higher explanatory power than the PCA. The Mahalanobis distance between Delphinida and the remaining groups are statistically different (Table 3).
Phylogenetic Signal

Both the complete inner ear as well as the cochlea datasets presented a statistically significant phylogenetic signal (P+O_All p = 0.01, K = 0.81; P+O_Coch p = 0.03, K = 0.65).

Comparisons

Among platanistoids, there is a wide morphological diversity recorded, and we could not identify a typical “platanistoid” inner ear (Figs. 3, 6). However, some common patterns were observed. All of the platanistoids studied have 1.75–2 number of turns, >60% extent of the secondary bony lamina, and 0.40–0.62 basal ratio. All of these measurements fall within the ranges reported for extant odontocete cochleae (Ketten and Wartzok 1990; Ketten 1992; Park et al. 2016). The radii ratio for platanistoids (4.00–6.45) is within ranges reported for most odontocetes, except for A. talen and stem Odontoceti S. calvertensis, which are more similar to ziphiids, as well as archaeocete
and mysticete values (Ekdale and Racicot 2015; Park et al. 2016). The fenestra cochleae is widest in stem odontocete P. australis and narrowest in A. talen, and all of the platanistoids have smaller fenestra cochleae than those reported for extant mysticetes (Park et al. 2017a). The cochlea is higher in stem odontocete Prosqualodon, and platanistoids Waipatia, Zarhachis, and Otekaika, while it is wider in Notocetus, Platanista, Awamokoa, and Aondelphis. Cochlear volumes for platanistoids are within those reported for odontocetes (Ekdale and Racicot 2015; Park et al. 2016) and mammalodontid mysticetes (Park et al. 2017a), and again stem odontocete P. australis showed the highest value. The diameter of the spiral ganglion canal in platanistoids is higher than in toothed mysticetes but lower than in extant baleen whales (Park et al. 2016), and their values are similar to the Type I morphology of Ketten and Wartzok (1990). The estimated low-frequency limit for all fossil platanistoids is distinctly lower than in P. gangetica but higher than those of mysticetes (Park et al. 2016, 2017a).

Regarding the remaining odontocetes included in our sample, some brief comparisons are made here. In agreement with Park et al. (2014) and Costeur et al. (2018), we found that Platanista, Inia, Lipotes, and Pontoporia do not fall into the same position in the morphospace (Figs. 3, 4). Moreover, like Costeur et al. (2018), we found no morphological similarity between Lipotes and Inia, although our sample is limited in extant representatives and might therefore be masking such characteristics, though a single specimen should be indicative of morphology (Martins et al. 2020). Therefore, although numerous common adaptations are reported in the skull and postcranial skeleton of riverine dolphins (Page and Cooper 2017; Fordyce 2018; Rommel and Reynolds 2018), in agreement with Park et al. (2019), we found no “river dolphin” convergent morphology for the inner ear. The pygmy sperm whale (K. breviceps) was consistently recovered in the morphospace as distantly positioned with respect to Physeter and the ziphiids included in our analyses (Figs. 3, 4). These results would support the different cochlear morphological regimes recently proposed by Park et al. (2019), the relationship between cochlear morphology and deep-diving capabilities suggested for the group, and the unique echolocation system of Kogia (Thornton et al. 2015).
Finally, the position of *Zygorhiza* sp. (Basilosauridae) on the extreme positive end of PC 1 and PC 2 (Fig. 3) on our analyses suggests that the cochlea was higher, more tightly coiled, and wider compared with the odontocete species included in our sample, characteristics that have been related to a low-frequency hearing capability (Ketten 1992; Ekdale and Racicot 2015). Current knowledge suggests that the common ancestor of Neoceti had low-frequency hearing (Ekdale and Racicot 2015), which was retained by stem mysticetes and even potentially some stem odontocetes (Park et al. 2017a; Racicot et al. 2019).

**Discussion**

The scope and position of Platanistoidea remain controversial, but recent anatomic and phylogenetic analyses have increased our understanding of the group (e.g., Lambert et al. 2014; Boersma et al. 2017; Tanaka and Fordyce 2017; Viglino et al. 2018a,b; Gaetán et al. 2019; Bianucci et al. 2020). We present, for the first time, qualitative and quantitative descriptions, comparisons, and analyses of the inner ear of fossil and extant platanistoids, allowing us to better understand how the hearing abilities (and by extension, echolocation abilities)
of this group have evolved. This, in turn, has broadened our understanding of cochlear evolution in odontocetes as a whole.

Cochlear Evolution in Platanistoidea

Both descriptions and measurements taken indicate that all extinct platanistoids had high-frequency hearing broadly similar to that of extant odontocetes (Ketten and Wartzok 1990; Ketten 1992; Park et al. 2016). Like all cetaceans, except for pakicetids, the semicircular canals are smaller than the cochlea, which is thought to be related to a reduced sensitivity to rotational movements (Spoor et al. 2002; Ketten and Wartzok 1990; Ketten 1992, 2000; Costeur et al. 2018). Despite having characteristically odontocete cochleae, there are some intra- and interclade differences between platanistoids and other extant odontocetes.

PCA describing the cochlear shape variation revealed that Platanistoidea has the largest area of morphospace in the first two PC axes of all groups, indicating a higher diversity in inner ear morphology than the other groups in our sample (Fig. 3). In accordance with the Type I morphology of high-frequency hearing by Ketten and Wartzok (1990), all platanistoids included in our study have 2 or fewer turns, as well as >60% extension of the secondary bony lamina. This morphological type was associated with nearshore or freshwater odontocetes of narrower frequency range (Ketten and Wartzok 1990; Ketten 1992). Conversely, the basal ratio of platanistoids (except O. huata, Z. sp._1, and P. gangetica) is within the range defined for the Type II cochlear morphology (Ketten 1997); it is higher than for xenorophids (Churchill et al. 2016; Park et al. 2016) but lower than the value reported for an undescribed squalodontid (Luo and Eastman 1995). Therefore, marine extinct platanistoids inner ear morphology was not clearly associated with any known cochlear type (sensu Ketten and Wartzok 1990) and suggests that this clade might have its own pattern.

The presence of a long secondary bony lamina and reduced number of turns in platanistoids, key characteristics of odontocete cochlear morphology (Ketten and Wartzok 1990; Ketten 1992; Ritsche et al. 2018), supports the hypothesis that high-frequency hearing capabilities were acquired early in the evolution of toothed whales (Churchill et al. 2016; Park et al. 2016). However, these morphological characteristics are already far more specialized than those seen in older and earlier-diverging odontocetes (Churchill et al. 2016; Park et al. 2016; Racicot et al. 2019). These adaptations likely represent an improved ability to navigate complex acoustic environments, which could be related to occupying more nearshore habitats, as has been hypothesized for several

### Table 3

*p*-value of Mahalanobis distance of CVA analyses with the different datasets. Note that asterisks indicate a statistically significant distance (*p* < 0.05). Datasets: P_Coch, cochlea and fenestra vestibuli landmark configuration for Platanistoidea only; P+O_All, the complete inner ear landmark configuration for Platanistoidea and comparative Odontoceti and Basilosauridae; P+O_Coch, cochlea and fenestra vestibuli landmark configuration for Platanistoidea and comparative Odontoceti and Basilosauridae. The Basilosauridae specimen was excluded from these analyses, please see “Materials and Methods.”

| P_Coch                  | Platanistidae | Stem Odontoceti | Stem Platanistoidea |
|-------------------------|---------------|-----------------|---------------------|
| Stem Odontoceti         | 0.996         | –               | –                   |
| Stem Platanistoidea     | 0.789         | 0.965           | –                   |
| Waipatiidae             | 0.864         | 0.916           | 0.131               |

| P+O_All                 | Delphinida    | Physeteroidea+Ziphiiida | Platanistoidea |
|-------------------------|---------------|-------------------------|----------------|
| Physeteroidea+Ziphiiida | 0.048*        | –                       | –              |
| Platanistoidea          | 0.003*        | 0.278                   | –              |
| Stem Odontoceti         | 0.010*        | 0.804                   | 1.000          |

| P+O_Coch                | Delphinida    | Physeteroidea+Ziphiiida | Platanistoidea |
|-------------------------|---------------|-------------------------|----------------|
| Physeteroidea+Ziphiiida | 0.227         | –                       | –              |
| Platanistoidea          | 0.936         | 0.219                   | –              |
| Stem Odontoceti         | 0.984         | 1.000                   | 0.990          |
Figure 6. 3D models representing stem Odontoceti and Platanistoidea species used in our study in a reduced phylogenetic hypothesis (see “Materials and Methods” for details) in: A, anterior; B, lateral; C, dorsal; and D, vestibular views. The phylogenetic hypothesis used follows Viglino et al. (2018a,b) and Gaetán et al. (2019). Silhouettes are from PhyloPic, by Chris Huh, used under a Creative Commons Attribution-ShareAlike 3.0 Unported License (http://creativecommons.org/licenses/by-sa/3.0). Scale bars, 5 mm.
platanistoids (Dowsett and Wiggs 1992; Fordyce 1994; Gottfried et al. 1994; Tanaka and Fordyce 2015, 2017; Cuitiño et al. 2019), producing shorter-range echolocation signals (Madsen et al. 2004; Johnson et al. 2008; Jensen et al. 2013), or potentially feeding on smaller prey items. The latter has already been found to be correlated with skull shape (McCurry and Pyenson 2018), and we suggest that paleoecology is the primary driving factor here. It is also noteworthy that during the late Oligocene–early Miocene, a variety of rostra and associated tooth morphologies among platanistoids coexisted (Tanaka and Fordyce 2017; Viglino et al. 2018a, 2020; Bianucci et al. 2020), implying a range of feeding strategies existed within Platanistoidea, similar to extant odontocetes (Werth 2006; Hocking et al. 2017a,b). Together with the more-derived inner ear morphology found here, it might indicate that feeding and ecological niches were powerful factors acting on the evolution of echolocating abilities and diverse skull morphologies in early odontocetes (Gutstein et al. 2014; Mourt- lam and Orliac 2017; Costeur et al. 2018).

Some peculiarities are also worth discussing from our results. Consistently among all analyses, Zarhachis sp._1 is distantly located in a unique region of morphospace with respect to the remaining platanistoids (Figs. 3–5). It is unclear what separates this specimen from the others, as its overall morphology appears to be similar and measurements fall within the range observed for the group, or even for odontocetes (Ketten and Wartzok 1990; Ketten 1992; Churchill et al. 2016; Park et al. 2016). Stem odontocete Squalodon calvertensis and platanistoid Aondelphis talen possess the lowest limit of hearing frequency among our sample (Table 2), higher than Zygorhiza and closely related to the values reported for some mysticetes (Park et al. 2017a). For both species, basal ratio and extent of secondary bony lamina fall within odontocete ranges reported (Ketten and Wartzok 1990; Ketten 1992; Park et al. 2016). In the phylomorphospace, these species do not cluster together and are actually on opposite sides of the PC and CV axes (Figs. 3–5). Therefore, S. calvertensis and A. talen seem to have had a unique morphology either related to a wider range of frequencies heard or to a shorter and lower total frequency range than the remaining platanistoids compared. Future analyses including a wider sample of stem Neoceti or other measurements related to hearing frequency might help explain the pattern observed.

Finally, it is worth mentioning that Physeter and Tasmacetus overlapped within the Platanistoidea morphospace (Fig. 3). As outlined by Park et al. (2019), these extant species share an open bony contact (i.e., not closed or fused) between the tympanoperiotic and the skull, unique middle-ear morphology, and the presence of a tympanal recess on the cochlea. On the other hand, Platanista is also characterized by having an open bony suture between the periotic and the skull (Anderson 1878). It could be possible to hypothesize then, that the shared plesiomorphic characteristic of an open bony suture between the tympanoperiotic and the skull in all these taxa is reflected in the cochlear morphology and thus results in the observed overlap on the morphospace. A thorough understanding of the consequences of an open bony contact between the tympanoperiotic and the skull in the underwater hearing capabilities in extant odontocetes is needed to fully comprehend and estimate them in extinct species.

Odontocetes from the Lower Miocene of Patagonia

Among the Patagonian specimens, inner ear morphology varied, indicating differential hearing abilities. The platanistoid Notocetus vanbenedeni shows the most derived cochlear shape (Figs. 4, 6), in accordance with its phylogenetic position as more closely related to P. gangetica (e.g., Lambert et al. 2014, 2018; Viglino et al. 2018a,b; Bianucci et al. 2020). Notocetus and Platanista share a loosely coiled and wide cochlea, a low number of widely separated turns, and >60% extension of the secondary bony lamina. They additionally have a relatively high cochlear volume compared with most other odontocetes in our sample (Table 2; Figs. 1, 6). It is also worth noting that both Notocetus specimens included in our study were not clustered together in the morphospace (Figs. 3–4; see also Supplementary Material), possibly indicating a wider disparity in cochlear morphology for the species.
than previously thought or potentially even separate taxa, given that intraspecific variation is thought to be low in odontocetes (Martins et al. 2020). Ontogenetic effects on the shape of the cochlea can be discarded, as the cochlea in odontocetes attains adult proportions in early gestation stages (Thean et al. 2017).

*Prosqualodon australis* is the first Patagonian stem odontocete known to possess a tympanal recess (sensu Park et al. 2017c; Figs. 1, 6). This structure has been speculatively suggested as a specialization for lower-frequency sound reception via a vibroacoustic duct mechanism (March et al. 2016; Park et al. 2017b). However, its function is currently unclear, and its widespread and apparently stochastic distribution across multiple mysticete and odontocete lineages (Ekdale 2016b; Park et al. 2017b,c, 2019) makes it uncertain whether there is a single function for the structure. Therefore, we cannot hypothesize on the effects of the tympanal recess in underwater hearing capabilities, and a thorough understanding of this structure and function in living cetaceans is decidedly needed. Nonetheless, the cochlear morphology of *P. australis* indicates that this species had high-frequency hearing, similar to extant odontocetes.

As for the platanistoid *A. talen*, the spiral and tightly coiled cochlea most closely resembles that of ziphiids and stem cetaceans (see “Descriptions of Cochlear Anatomy”; Figs. 2, 3, 5). The tighter coiling is also a feature shared with the New Zealand taxa *Awamookoa* and *Waipatia*, both of which are very close to *A. talen* in the morphospace. Morphologically, the periotics of all three genera share some characteristics; for example: a vestigial dorsal crest (plesiomorphic characteristic), an elongated anterior bullar facet and a larger and squared posterior bullar facet, and an anterointernal sulcus on the dorsal surface of the anterior process (Fordyce 1994; Tanaka and Fordyce 2017; Viglino et al. 2018b). Curiously, the inferred low-frequency limit is similar to that of stem mysticetes, *Eschrichtius robustus*, and balaenopterids (Ketten 1997; Ekdale and Racicot 2015; Park et al. 2017a); significantly lower than the frequency range for extant odontocetes, except ziphiids (e.g., Ketten and Wartzok 1990; Ketten 1997, 2000; Park et al. 2016); and even lower than in *P. gangetica* (Kelkar et al. 2018). Therefore, the inferred low-frequency limit for *A. talen* would be in agreement with its more basal inner ear morphology (Fig. 6), and we could then hypothesize that either this species had a wider frequency range, or it was uniquely less specialized in high-frequency hearing than its coeval Patagonian platanistoids and stem Odontoceti species.

Anatomic and phylogenetic studies have suggested that Patagonian platanistoids and stem odontocete species employed niche separation to maximize resource use (Viglino et al. 2018a,b, 2020; Gaetán et al. 2019). The morphological differences among Patagonian platanistoid cochleae would support this hypothesis. Diverse feeding apparatuses and hearing abilities could have resulted in avoidance of direct ecological competition between species (Madsen et al. 2004; Johnson et al. 2008; Jensen et al. 2013). Future studies integrating other feeding and auditory anatomic structures of Patagonian species, as well as paleoenvironmental information (e.g., Galatius et al. 2018), might help in analyzing and proposing paleoecological interactions between them more clearly.

Late Oligocene Platanistoids from New Zealand

Similar to the Patagonian platanistoids studied, species included here from New Zealand also show some variation in their inner ear morphology. *Awamookoa tokarahi*, *Waipatia maerewhenua*, and *O. huata* shared an endocast slightly damaged by sediment or diagenetic mineral precipitation, possibly related to their depositional environment in the upper Oligocene Otekaike Limestone Fm. (Fordyce 1994; Tanaka and Fordyce 2015, 2017). Also, the three species share a tall cochlear spiral, similar to stem cetaceans, mysticetes, and stem odontocetes (e.g., Ekdale and Racicot 2015; Park et al. 2016, 2017a; Ritsche et al. 2018), as well as a long secondary spiral lamina similar to that of extant odontocetes (e.g., Ketten and Wartzok 1990; Ketten 1992; Costeur et al. 2018; Ritsche et al. 2018).

When comparing the inner ear morphology of all New Zealand platanistoids, *W.*
maerewhenua represents a more basal morphology (e.g., size of fenestra cochleae, high overlap of apical turn, less loosely coiled basal turn, narrow cochlea; Fig. 6), and O. huata is the only species that presents a tympanal recess, like the Patagonian stem Odontoceti P. australis (Fig. 2). On the other hand, A. tokarahi shares an estimated low-frequency hearing similar to that of the extant representative P. gangetica, while the limit in W. maerewhenua and O. huata is lower (Table 2). Nonetheless, all species are within the estimated ranges for odontocetes (e.g., Ketten and Wartzok 1990; Ketten 1997, 2000; Park et al. 2016).

In summary, platanistoids from the late Oligocene of New Zealand present inner ear morphological characteristics that indicate they had high-frequency hearing, such as a short cochlear canal length, 2 or fewer turns, long secondary bony lamina, and low radii ratio (Fig. 6; Table 2). This inference is also supported by their skull morphology, where osteological correlates of the nasal sac and pterygoid sinus system were described (Fordyce 1994; Tanaka and Fordyce 2015, 2017). Even though these species were probably less specialized than marine odontocetes (Figs. 2, 6), they could hear high-frequency sounds, supporting an early-acquired ability for odontocetes during their evolutionary history (e.g., Churchill et al. 2016; Park et al. 2016; Mourlam and Orliac 2017). Continuing efforts to study hearing abilities in fossil odontocetes are key to understanding how and when early odontocetes diversified and expanded in marine and riverine habitats, as modern forms do today.

Survival of Platanista

The combination of Type I and Type II features observed in the fossil platanistoid cochlea in this study only partially supports our initial hypothesis that they would have a cochlear morphology dissimilar to extant Platanista. However, the cochlea of Platanista was consistently overlapping with delphinoid odontocetes in the morphospace (Figs. 3–6), indicating it has the most derived morphology among platanistoids. It was also always distant in the morphospace from its sister taxon Zarhachis sp., particularly from Zarhachis sp._1 (Figs. 3–5; also see Supplementary Material), consistent with a >9 Myr separation between these genera (Paleobiology Database 2020). Platanista gangetica is characterized by loosely coiled turns in a wide and short cochlea (Fig. 6). The echolocation signals of this species were reported to be adapted to search for prey at short distances and in lower-frequency levels than marine delphins (Jensen et al. 2013).

Cochlear morphology, in addition to their highly autapomorphic maxillary crests that might aid in sound directionality during echolocation (Jensen et al. 2013), overall skull morphology (Anderson 1878; Purves and Pilleri 1973; Pilleri et al. 1976), and pterygoid sinus system (Fraser and Purves 1960), demonstrates that Platanista still represents a unique and bizarre morphological type among platanistoids, and indeed even Cetacea, reflecting a disparate and highly specialized echolocation system. Interestingly, Boersma et al. (2017) found that crest enlargement first evolved in platanistoids in the Oligocene, but only the latest-surviving platanistids (including Platanista) possessed highly pneumatized crests, thought to function in sound production (Purves and Pilleri 1973; Jensen et al. 2013; Boersma et al. 2017). Here, we propose that the evolution of these anatomic adaptations would have allowed platanistids to survive during the course of the late Neogene when other platanistoid taxa went extinct, resulting in the unique morphotype of P. gangetica. Moreover, the significant reorganization of the major tributaries of the Ganges and Indus Rivers around 0.5 Myr ago affected these species populations’ distribution and represented a strong ecological factor of adaptation (Braulik et al. 2015). New findings of fossil platanistoids, particularly from the middle–late Miocene, will help test these hypotheses.

Conclusions

The inner ear anatomy of fossil Platanistoida is described for the first time. Our comparisons reveal there is no “typical” platanistoid cochlear type, as the group displays a disparate range of cochlear anatomies that possess a combination of basal and derived features. Nonetheless, we found that early-diverging platanistoid cochleae have morphological
characteristics that are clearly better adapted for high-frequency hearing than the coeval earliest stem Odontoceti, thus indicating a rapid evolution of this functional complex. *Notocetus* and *Platanista* share a loosely coiled and wide cochlea, a low number of widely separated turns, and >60% extension of the secondary bony lamina. Stem odontocete *Prospaclodon australis* and platanistoid *Otekaiken huata* are the only species in our sample that present a tympanal recess in their cochleae, of yet unknown specific function in the underwater hearing mechanism in cetaceans. Also, *Aonodelphis talen*’s basal inner ear morphology and inferred frequency range indicate it had lower high-frequency hearing than other odontocetes. Finally, *Platanista* has the most-derived cochlear morphology, a finding in accordance with its unique skull anatomy, adding to evidence that it is an outlier within the group. The cochlear morphology of *Platanista* is also in accordance with its distant position in the morphospace from its sister genus *Zarhachis*. The evolution of this singular sound production system within Platanistidae may have facilitated the survival of *Platanista* to the present day.

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**Data Availability Statement**

Data available from the Dryad Digital Repository: [https://doi.org/10.5061/dryad.g4f4qrpfm](https://doi.org/10.5061/dryad.g4f4qrpfm).

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