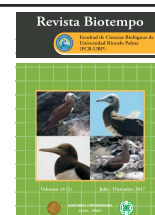




Biotempo (Lima)



ORIGINAL ARTICLE / ARTÍCULO ORIGINAL

COMPARATIVE ANATOMY OF THE BONY LABYRINTH OF THE BATS *PLATALINA GENOVENSIVUM* (PHYLLOSTOMIDAE, LONCHOPHYLLINAE) AND *TOMOPEAS RAVUS* (MOLOSSIDAE, TOMOPEATINAE)

ANATOMÍA COMPARADA DEL LABERINTO ÓSEO DE LOS MURCIÉLAGOS *PLATALINA GENOVENSIVUM* (PHYLLOSTOMIDAE, LONCHOPHYLLINAE) Y *TOMOPEAS RAVUS* (MOLOSSIDAE, TOMOPEATINAE)

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ABSTRACT

The bony labyrinth inside the temporal bone houses the inner ear, sensory organ of hearing and balance. Variations in the three components of the bony labyrinth (cochlea, vestibule, and semicircular canals) give insight into the physiology and evolution of the different groups of mammals. Based on high resolution micro-Computed Tomography (μ CT), we reconstructed the digital endocasts of the bony labyrinths of *Platalina* and *Tomopeas*. We found that both species exhibit unique characteristics among bats, that were mainly located in the cochlea, including the aspect ratio of the cochlear spiral, cochlear width relative to that of the basicranial region, number of cochlear spiral turns, among others. Finally we highlight the need of more morphological comparative studies of the bony labyrinth.

Key words: Cochlea – Chiroptera – Inner ear – Phyllostomidae – Molossidae

RESUMEN

El laberinto óseo dentro del hueso temporal protege el oído interno, órgano sensorial para la audición y balance. La variación en los tres componentes del laberinto óseo (cóclea, vestíbulo y canales semicirculares) ofrece un alcance sobre la fisiología y evolución de los diferentes grupos de mamíferos. Usando la tomografía micro-computarizada de alta resolución (μ CT), reconstruimos los moldes digitales internos de los laberintos óseos de *Platalina* y *Tomopeas*. Encontramos que ambas especies presentan características únicas entre los murciélagos, que están principalmente localizadas en la cóclea, entre ellos la proporción del espiral de la cóclea, ancho de la cóclea con respecto al ancho de la región de la base del cráneo, número de espirales cocleares. Finalmente, resaltamos la necesidad de más estudios de morfología comparada del laberinto óseo.

Palabras clave: Cóclea – Chiroptera – Oído interno – Phyllostomidae – Molossidae

INTRODUCTION

Bats are the only mammals capable of flying and most of them use echolocation to orientate and move in complete darkness. Echolocation is the production of high-pitched sounds, which returning echoes are analyzed by the brain and help these bats detecting obstacles and prey without the use of vision. Most bats produce echolocation signals in the larynx, while a few species echolocate with sounds produced by tongue clicks, and one species may use wing claps (Veselka *et al.*, 2010). Echolocating bats exhibit a unique set of anatomical, neurological, and behavioral characteristics that allow them to send and receive high-frequency sounds. Among the anatomical structures involved in echolocation are three bones in the skull: stylohyal, malleus, and cochlea (Simmons *et al.*, 2008, 2010; but see Veselka *et al.*, 2010). The cochlea, along with the vestibule and the semicircular ducts, form the inner ear, which is surrounded by the bony labyrinth (osseous structure preserved after the desiccation of the soft tissues). Variation in the bony labyrinth shape and dimensions provide insights into the physiology, morphology, and evolution of the different groups of mammals (Ekdale, 2013).

The long-snouted bat *Platalina genovensium* Thomas, 1928, is the largest member of the phyllostomid subfamily Lonchophyllinae (Gregorin & Ditchfield, 2005; Cirranello *et al.*, 2016). It occurs in elevations from near sea level up to 2566 m, from localities west of the Andes, from northern Peru to southern Chile and from two localities in central Peru (Griffiths & Gardner, 2008; Ossa *et al.*, 2016; Velazco *et al.*, 2013). *P. genovensium* is a highly specialized bat that feeds primarily on nectar and pollen from five plant families (e.g., Cactaceae, Bromeliaceae, Solanaceae; Sahley & Baraybar, 1996; Baraybar, 2004; Aragón & Aguirre, 2007; Zamora *et al.*, 2013; Maguiña & Amanzo, 2016). The echolocation calls of *Platalina* consist of frequency-modulated (FM), short duration (1.98 ± 0.11 ms) calls with repetitions spaced up to 90.08 ± 13.79 ms. The harmonics range from 42.2 kHz to 111.9 kHz (Ossa *et al.*, 2016).

The enigmatic blunt-eared bat *Tomopeas ravus* Miller, 1900, is an insectivorous bat endemic to the coastal desert of central and northern Peru, with an elevational range from near sea level to near 2300 m (Velazco *et al.*, 2013; Zamora *et al.*, 2014). The phylogenetic affinities of this bat have been a matter of debate

since its description by Miller (1900), where it was placed as a member of Vespertilionidae. Shortly after its description, it was placed under its own subfamily, Tomopeatinae, still under the family Vespertilionidae (Miller, 1907). Many years later, Sudman *et al.* (1994), who used cytochrome-*b* sequences and protein electrophoretic data, demonstrated that *Tomopeas* should be allocated to the family Molossidae instead of the family Vespertilionidae. This placement is currently followed and has been supported by morphological analyses (Gregorin & Cirranello, 2016). The characteristics of the echolocation calls of *Tomopeas* are unknown.

In the present report, we describe and compare the bony labyrinths of *P. genovensium* and *T. ravus*. These are the first descriptions of the bony labyrinths of members of the subfamilies Tomopeatinae (Molossidae) and Lonchophyllinae (Phyllostomidae).

MATERIAL AND METHODS

CT data acquisition

Two adult females were included in this study. Both specimens are housed in the mammal collection of the Department of Mammalogy of the American Museum of Natural History (AMNH) in New York, USA. Skulls of *P. genovensium* (AMNH 278520) and *T. ravus* (AMNH 278525) were scanned using a high-resolution GE Phoenix V|tome|x s240 micro-CT scanner at the Microscopy and Imaging Facility (MIF) of the AMNH. *Platalina* and *Tomopeas* skulls were digitized at a resolution of 37.29 and 19.40 μm (voxel size), respectively. For each bat skull, 1200 slices (X-ray projections) with dimensions of 990×1000 pixels were recorded over the 180° sample rotation. We reconstructed the volume data from those X-ray projections and exported a stack of 2D images corresponding to coronal sections of the volume data in TIFF format using Phoenix datos|x 2 reconstruction version 2.3.2 and VGStudio MAX version 3.0 (Volume Graphics GmbH, Heidelberg, Germany).

3D reconstruction and measurements

After importing the TIFF images in MIMICS 16.0 (Materialise NV, Belgium), we segmented and created a 3D rendering of the right bony labyrinths of *Platalina* and *Tomopeas*. We calculated the volumes of the cochlear and inner ear systems and the proportions of the cochlea and basicranium in MIMICS. Our measurements of cochlear and basicranial widths were

plotted along the measurements of other bats collected by Simmons *et al.* (2008). Cochlear size is known to be correlated with echolocation behavior, where non-echolocating bats tend to have smaller cochlea relative to bats able to echolocate (Simmons *et al.*, 2008).

We followed the protocol of Davies *et al.* (2013a) to measure the length of the basilar membrane. We used ISE-Meshtools 1.3 (Lebrun, 2014; <http://morphomuseum.com/meshtools>) to import the surface files of the 3D bony labyrinths (STL format) and to place 100 equidistant semi-landmarks along the secondary bony lamina, from the outer edge of the round window to the apex of the cochlea (see Davies *et al.*, 2013a: additional file 5, figure S1A-B for illustrations). We exported the 3D landmarks coordinates and calculated the sum of the Euclidean distances between landmarks in Excel to obtain the length of the basilar membrane (see Davies *et al.*, 2013a for the formula). The basilar membrane length of our two specimens were then combined with the measurements of other bats compiled by Davies *et al.* (2013a: table S2), to investigate the relationship between linear measurements of basilar membrane length and body mass. The body mass of the studied specimens of *Platalina* and *Tomopeas* were measured on the field by P.M.V. after the bats were captured (Velazco *et al.*, 2013). To plot the basilar membrane length (mm) versus the cube root of the body mass, all the values were log₁₀ transformed to explore the linear relationship between the two variables.

Finally, we followed West (1985) to measure the number of cochlear spiral turns in both bats. From an apical view of the cochlea, a line was drawn from the round window to the apex. The number of turns was calculated by the number of times the line was crossed by the path of the canal, plus the nearest one quarter of a complete turn. Our measurements were then combined with the bat measurements compiled by Davies *et al.* (2013a: table S2). Cochlear coiling

is correlated with the presence of elongated auditory sensory membranes. We investigated the correlation between the number of turns of our specimens and the relative basilar membrane length. All measurements of *Platalina* and *Tomopeas* are presented in Table 1.

Bony labyrinth 3D models of *Platalina* (AMNH 278520) and *Tomopeas* (AMNH 278525) are available at MorphoMuseum.com (Velazco & Grohé, 2017). The angles between the planes of the semicircular canals were measured using 3D PDF models.

RESULTS

Three distinct components of the bony labyrinth can be distinguished on the digital endocasts of *Platalina* and *Tomopeas* (Figure 1): the cochlea, vestibule, and the three semicircular canals. Selected measurements of *Platalina* and *Tomopeas* bony labyrinths are provided in Table 1. The width of the cochlea relative to the basicranium in *Platalina* is intermediate among other bats (Figures 2A, B), while, in *Tomopeas*, it is grouped among the smallest (Figures 2A, C). The contribution of the cochlear volume to the whole bony labyrinth is similar in both taxa: 69.7% in *Platalina* and 68.6% in *Tomopeas* (Table 1). The coiling of the cochlear canal completes 2.25 turns in *Platalina* and 2 in *Tomopeas* (Figure 1, Table 1). The estimated height of the spiral of the cochlea is 2 mm in *Platalina* and 1.07 mm in *Tomopeas* (Table 1), so that the cochlea is flatter in *Tomopeas*, than in *Platalina* (Figure 1). There is a large apical lacuna at the apex of the cochlear spiral in *Tomopeas*, whereas an apical lacuna is absent in *Platalina* (Figure 1). The basal turn becomes thicker when approaching the vestibule in both *Platalina* and *Tomopeas* (Figure 1). The second turn of the cochlear spiral overlies partially the basal turn in those bats, but the width of the second turn in *Tomopeas* is much narrower than its basal turn while it is only slightly narrower in *Platalina*.

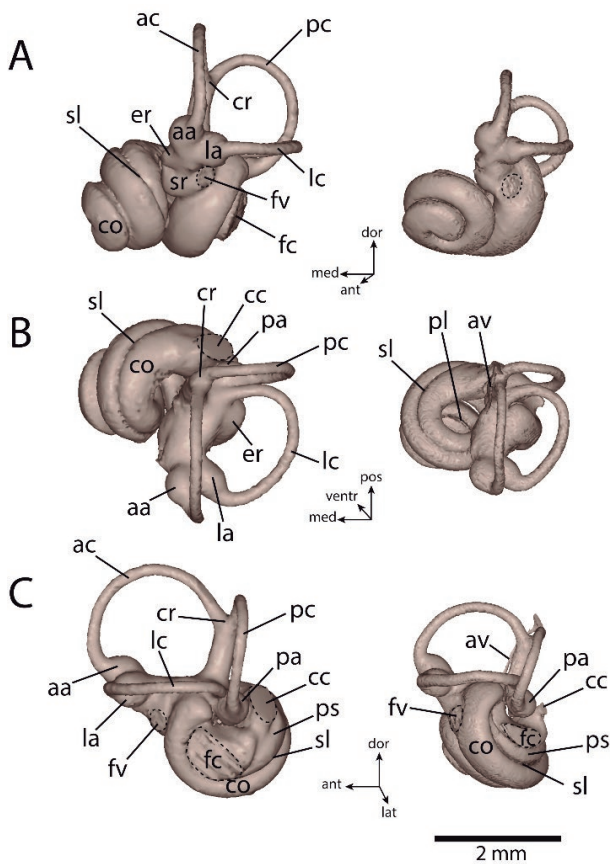


Figure 1. Right (mirrored) bony labyrinths of *Platalina genovensium* (AMNH 278520; left) and *Tomopeas ravis* (AMNH 278525; right). **A**, labeled digital endocast in anterolateral view; **B**, labeled digital endocast in dorsal view; **C**, labeled digital endocast in posterolateral view. **Abbreviations:** **aa**, anterior ampulla; **ac**, anterior semicircular canal; **ant**, anterior direction; **av**, bony channel for vestibular aqueduct; **cc**, canaliculus cochleae for cochlear aqueduct; **co**, cochlea; **cr**, common crus; **dor**, dorsal direction; **er**, elliptical recess of vestibule; **fc**, fenestra cochleae; **fv**, fenestra vestibuli; **la**, lateral ampulla; **lat**, lateral direction; **lc**, lateral semicircular canal; **med**, medial direction; **pa**, posterior ampulla; **pc**, posterior semicircular canal; **pl**, primary bony lamina; **pos**, posterior direction; **ps**, outpocketing for perilymphatic sac; **sl**, secondary bony lamina; **sr**, spherical recess of vestibule; **ventr**, ventral direction.

Table 1. Body mass and dimension of the skull and bony labyrinth of *Platalina* and *Tomopeas*.

| | <i>Platalina</i> | <i>Tomopeas</i> |
|------------------------|------------------|-----------------|
| BLV (mm ³) | 5.37 | 2.71 |
| CV (mm ³) | 3.74 | 1.86 |
| CV % | 69.65 | 68.63 |
| CH (mm) | 2.00 | 1.07 |
| WBT (mm) | 2.21 | 1.90 |
| SICS (index) | 0.90 | 0.56 |
| CST (N°) | 2.25 | 2.00 |
| WB (mm) | 11.02 | 6.91 |
| BML (mm) | 12.61 | 9.40 |
| BM (g) | 14.50 | 3.00 |

Abbreviations: **BLV**, bony labyrinth volume; **BM**, body mass; **BML**, basilar membrane length; **CH**, height of spiral of the cochlea; **CV**, cochlear volume; **CV %**, cochlear volume percentage of bony labyrinth; **CST**, number of cochlear spiral turns; **SICS**, shape index of cochlear spiral (**CH/WBT**); **WB**, width basicranium; **WBT**, width of the basal turn of the cochlea.

A secondary bony lamina is present in both species (Figure 1; Ekdale, 2013). The secondary bony lamina is visible on the outer edge of the first turn in *Tomopeas* and on the two first turns in *Platalina* (sl in Figure 1). In *Platalina*, the aspect ratio of the cochlear spiral (height of the spiral divided by width of the basal turn) is the greatest in bats and the second largest among placental mammals, after the rodent *Cavia* (Table 1; Ekdale, 2013: table 2). The aspect ratio for *Tomopeas* is average among bats (Table 1; Ekdale, 2013: table 2). A canaliculus cochleae is observed in both *Platalina* and *Tomopeas* posterodorsally to the wide fenestra cochleae (cc in Figure 1). The canaliculus in *Tomopeas* is located and oriented similarly to the one in *Tadarida* (cc in Figure 1; Ekdale, 2013: figure 48C). The plane of the basal turn of the cochlea of *Platalina* forms an angle with the plane of the lateral semicircular canal (lc in Figure 1) that is similar to the one exhibited by other phyllostomids (e.g., *Trachops*; Davies *et al.*,

2013a: figure 2). This angle in *Tomopeas* is similar to the angle measured in the molossid *Tadarida* (Figure 1; Ekdale, 2013: figure 48). The fenestra vestibuli is elliptical in both *Platalina* and *Tomopeas* (fv in Figure 1). The elliptical and spherical recesses are separated in *Platalina* and *Tomopeas* (er and sr in Figure 1). The vestibule of both *Platalina* and *Tomopeas* exhibit an anterior excavation for the anterior and lateral ampullae and a posterior excavation for the posterior ampulla and common crus (aa, la, pa, and cr in Figure 1). The ampullae in both *Platalina* and *Tomopeas* are well differentiated (aa, la, and pa in Figure 1). In *Platalina*, the spherical recess and the elliptical recess are separated by a shallow furrow, whereas in *Tomopeas* they are separated by an almost imperceptible furrow (er and sr in Figure 1A).

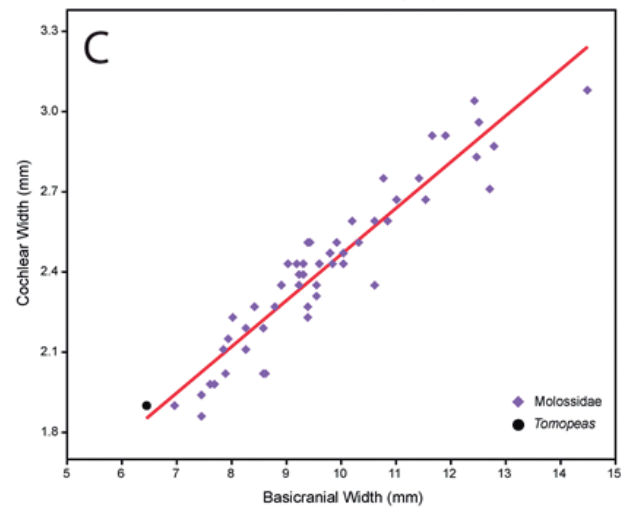
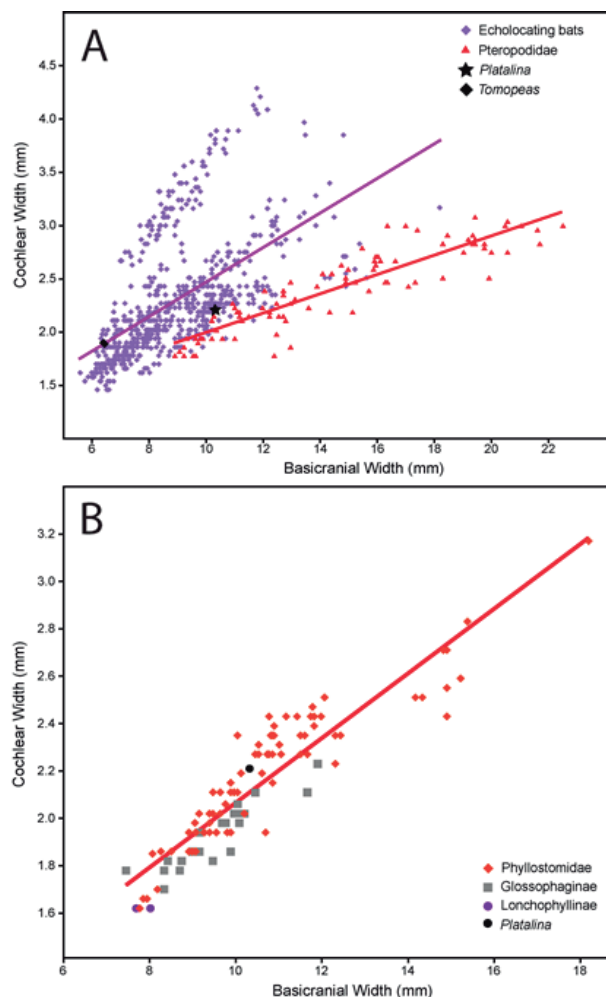


Figure 2. Relationship between the cochlear width (mm) vs. basicranial width (mm) in **A**, echolocating ($y = 0.16393x + 0.82697$, $r^2 = 0.3402$) versus non-echolocating bats ($y = 0.091462x + 1.0756$, $r^2 = 0.8193$ [Pteropodidae]); **B**, *Platalina genovensium* and other species of the family Phyllostomidae ($y = 0.13661x + 0.69954$, $r^2 = 0.844$); and **C**, *Tomopeas ravus* and other species of the family Molossidae ($y = 0.17273x + 0.73879$, $r^2 = 0.891$).

The common crura of *Platalina* and *Tomopeas* are shorter and wider compared to other bats (cr in Figure 1; tall and slender in *Nycteris*, *Rhinolophus*, *Tadarida*: Ekdale, 2013). The bony channel for the vestibular aqueduct in *Tomopeas* leaves the inner ear medial and anterior to the vestibular aperture of the common crus similar to the condition observed in *Tadarida* (av in Figure 1; Ekdale, 2013: figure 48B, C). The channel gently curves and opens on the surface of the petrosal near the dorsal end of the common crus (av in Figure 1C). The bony channel for the vestibular aqueduct in *Platalina* could not be determined because the resolution of the volume was not appropriate to reconstruct the structure.

The posterior limb of the lateral semicircular canal opens directly into the vestibule between the posterior ampulla and the base of the common crus in both *Platalina* and *Tomopeas* (lc and pa in Figure 1). It is

located more dorsally than the ventral limb of the posterior semicircular canal, the dorsoventral separation between the lateral and posterior semicircular canals being greater in *Tomopeas* than in *Platalina* (lc and pc in Figure 1). The angle between the planes of the posterior and anterior semicircular canals is 95° in both *Platalina* and *Tomopeas* (Figure 1B). The angle between the anterior and lateral semicircular canals is perpendicular (90°) in *Platalina*, where it is smaller (75°) in *Tomopeas* (Figure 1A). The angle between the posterior and lateral semicircular canals is perpendicular (90°) in *Platalina*, where it is larger (107°) in *Tomopeas* (Figure 1C). The semicircular canals are slightly narrower in *Platalina* than in *Tomopeas* (Figure 1).

The semicircular canals of *Platalina* are mostly planar, whereas in *Tomopeas* the anterior and lateral canals deviate substantially from their planes (out-of-plane curvature) and the posterior canal is mostly planar (Figure 1). The anterior semicircular canal is more extended dorsally than the posterior semicircular canal in both species, but the anterior and posterior semicircular canals are more compressed dorsoventrally in *Tomopeas* than in *Platalina* (ac and pc in Figure 1). The lateral semicircular canal has an oval shape in dorsal view that is similar in both species (lc in Figure 1). The anterior semicircular canal extends more anteriorly than the lateral semicircular canal in *Platalina*, while the anterior and lateral semicircular canals extend at the same level anteriorly in *Tomopeas* (ac and lc in Figure 1).

In comparison with other extant bats, the basicranial region of *Platalina* indicates that it has a relatively small cochlea that falls into the zone of overlap of echolocating and non-echolocating bats (Figure 2A), while it is known that *Platalina* is an echolocating bat (Malo de Molina *et al.*, 2011). The cochlear width of *Platalina* (compared to that of the basicranium) is of medium size when compared with other species of phyllostomids, but it is one the largest when compared to other phyllostomid bats with similar feeding behavior (Glossophaginae and Lonchophyllinae; Figure 2B). The lonchophylline sample size is small ($n = 3$) but it shows that the other two species (*Lionycteris spurrelli* Thomas, 1913 and *Hsunnycteris thomasi* (Allen, 1904)) have the smallest relative cochlear widths in the family, clearly distinguishing them from *Platalina* (Figure 2B).

The basicranial region of *Tomopeas* in turn indicates that it has a small cochlear width and falls on the

regression line of echolocating bats (Figure 2A). When compared with other molossids, *Tomopeas* has one the smallest cochlear widths in the family (Figure 2C).

The plot of the log basilar membrane length versus the log body mass^{0.33} showed that *Platalina* and *Tomopeas* grouped within the different families of echolocating bats (Figure 3A). *Platalina* falls in the middle of the variation for its family (Phyllostomidae), whereas *Tomopeas* falls on the lower end for both variables when compared to its family (Molossidae) and all the bats (Figure 3A).

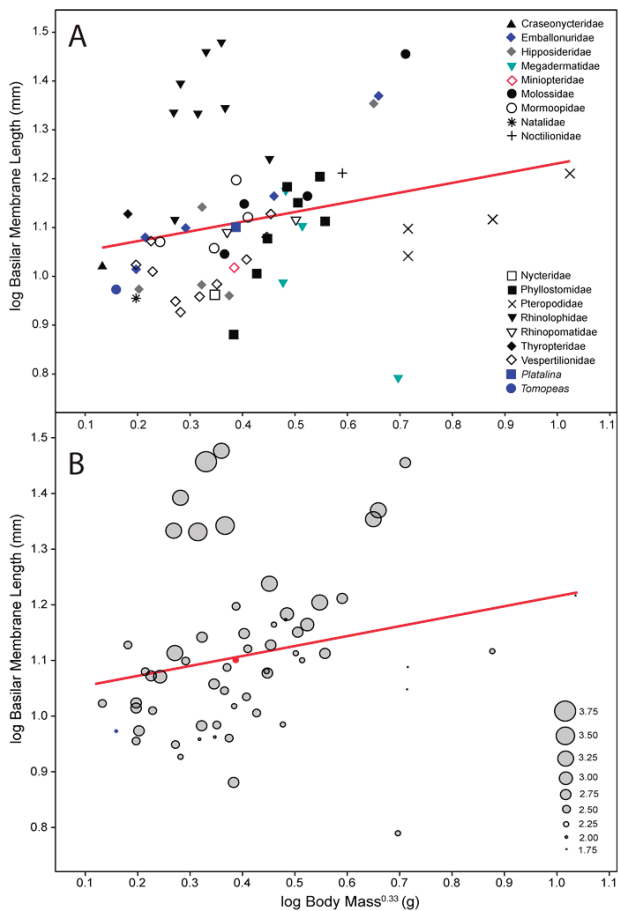


Figure 3. Log basilar membrane length (mm) vs. log of the cube root of body mass (g) plotted across 16 families of bats. **A**, overall dispersal of the different families ($y = 0.1988x + 1.0324$, $r^2 = 0.05849$): Craseonycteridae (filled black triangle), Emballonuridae (filled blue diamond), Hipposideridae (filled gray diamond), Megadermatidae (filled green inverted triangle), Miniopteridae (red diamond), Molossidae (filled black circle), Mormoopidae (empty black circle), Natalidae (asterisk), Noctilionidae (plus), Nycteridae (empty square), Phyllostomidae (filled black square), Pteropodidae (cross), Rhinolophidae (inverted triangle), Rhinopomatidae (open inverted triangle), Thyropteridae (open diamond), Vespertilionidae (open diamond), *Platalina* (filled blue diamond), and *Tomopeas* (filled blue circle).

black square), Phyllostomidae (filled black square), Pteropodidae (x), Rhinolophidae (filled black inverted triangle), Rhinopomatidae (empty black inverted triangle), Thyropteridae (filled black diamond), Vespertilionidae (empty black diamond), *Platalina genovensium* (filled blue square), *Tomopeas ravus* (filled blue circle); and **B**, with circles sized according to the number of cochlear spiral turns.

Both, *Platalina* and *Tomopeas*, present the shortest number of cochlear spiral turns in their respective families (Figure 3B). *Platalina* has 2.25 cochlear spiral turns while the other 7 phyllostomid species in the sample range from 2.5 to 3.25 turns (Figure 3B). With 2 cochlear spiral turns, *Tomopeas* has the smallest number of turns among the echolocating bats, along with *Cardioderma cor* (Peters, 1872), *Nycteris thebaica* É. Geoffroy St.-Hilaire, 1818, and *Plecotus auritus* (Linnaeus, 1758). The only other bats with a shorter number of cochlear spiral turns are members of the non-echolocating family Pteropodidae with 1.75 cochlear spiral turns (Figure 3B). The other molossid presented in the sample ($n = 5$) have a cochlear spiral turns range from 2.5 to 3.0 (Figure 3B).

DISCUSSION

The morphological description of the bony labyrinths of *Platalina* and *Tomopeas* presented here represents the first study of inner ear bats of the subfamilies Lonchophyllinae and Tomopeatinae. The cochlear attributes of both species demonstrated unique characteristics. *Platalina* presents the greatest aspect ratio of the cochlear spiral in bats, and among placental mammals it is second only to rodents of the genus *Cavia*. Also, it has a medium-size cochlear width when compared with other phyllostomids, but it is one the largest when compared to other phyllostomid bats with similar feeding behavior (Glossophaginae and Lonchophyllinae). Additionally, both *Platalina* and *Tomopeas* have the shortest number of cochlear spiral turns in their respective families and among echolocating bats. *Tomopeas* is also characterized by having one the smallest cochlear width relative to that of the basicranial region among the Molossidae. From

the four bats described by Ekdale (2013), *Tomopeas* is morphologically closer to *Tadarida*, both are members of the same family.

The study of the different aspects of the bony labyrinth in bats is mainly based on histological cross sections, x-ray images, and fossilized petrosals (e.g., Pye, 1966a, b, 1967, 1970; Hinchcliffe & Pye, 1968; Habersetzer & Storch 1992; Simmons *et al.*, 2008; Odendaal & Jacobs, 2011; Carter & Adams, 2015; Czaplewski, 2017). However, the recent availability to researchers of new technology like Computed Tomography (CT) to study the internal morphology of biological structures without damaging the specimens allows the reconstruction of structures that were impossible to observe on their entirety before. One of these structures is the bony labyrinth, but most studies using 3D models of inner ears in bats are focused on using measurements from these models to explore the evolution of flight, echolocation, etc. (e.g., Davies *et al.*, 2013a, b; Pfaff *et al.*, 2015). Only one study provides detailed descriptions of the bony labyrinth morphology of bats (non-echolocating *Pteropus hylei* Andersen, 1908 and echolocating *Nycteris grandis* Peters, 1865, *Rhinolophus ferrumequinum* (Schreber, 1774), and *Tadarida brasiliensis* (I. Geoffroy St.-Hilaire, 1824)) using 3D models (Ekdale, 2013). There is a clear need for more comparative data on the bony labyrinth morphology of bats and more effort should be devoted to the use of the 3D data available from repositories of digital data (e.g., DigiMorph <http://www.digimorph.org/>; MorphoSource <http://morphosource.org/>; MorphoMuseum.com; www.phenome10k.org etc.).

ACKNOWLEDGEMENTS

We would like to thank Morgan Hill and Henry Towbin of the Microscopy and Imaging Facility at AMNH for assistance with instrumentation; Carlos Tello for providing bibliography; Kerry Kline, Ricardo Moratelli, and one anonymous reviewer for comments on an early version of the manuscript; Gregg F. Gunnell, Jörg Habersetzer, and Nancy B. Simmons for sharing the data used in figure 2.

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Received July 7, 2017.

Accepted August 16, 2017.