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## Fossil evidence of frequency range of hearing independent of body size in South American Pleistocene ground sloths (Mammalia, Xenarthra)

Preuve fossile de gammes de fréquence d'audition, indépendantes de la taille du corps chez les paresseux géants du Pléistocène d'Amérique du Sud (Mammalia, Xenarthra)

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## ARTICLE INFO

## Article history:

Received 8 March 2012

Accepted after revision 30 July 2012

Available online 15 September 2012

Presented by Philippe Taquet

## Keywords:

Ground sloths

Pleistocene

South America

Hearing

Long-range communication

## Mots clés :

Paresseux géants

Pléistocène

Amérique du Sud

Audition

Communication de longue portée

## ABSTRACT

Recently discovered stapes of Pleistocene South American ground sloths of the genera *Lestodon* and *Glossotherium* are studied. Available body mass estimates are larger for *Lestodon* (4100 kg) than for *Glossotherium* (1500 kg), reflecting the obvious difference in the overall size of the skull and other bones. However, as previously reported, the absolute size of incus and malleus is very similar in both genera. In a previous work, the frequency range of *Glossotherium* (from 44 Hz to 15,489 Hz) was estimated quantitatively from well-preserved tympanic ring dimensions. For the first time the frequency ranges of hearing in both genera are estimated by a method based on the footplate area of the stapes. The obtained frequency ranges are consistent with the previous estimation for *Glossotherium* and are similar in both genera, giving evidence of a frequency range of hearing independent of body size in this group of mammals. Some possible paleobiological implications of the results may include adaptation to some specific sound source, fossoriality, or long-range communication.

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## R É S U M É

Des étriers récemment découverts chez des paresseux géants, des genres *Lestodon* et *Glossotherium*, du Pléistocène d'Amérique du Sud, ont été étudiés. Les estimations disponibles sur la masse corporelle indiquent des valeurs plus élevées chez *Lestodon* (4100 kg) que chez *Glossotherium* (1500 kg), reflétant une différence évidente de la taille d'ensemble du crâne et des autres os. Cependant, comme cela a été rapporté antérieurement, la taille absolue de l'enclume et de l'étrier est similaire dans les deux genres. Dans un précédent travail, la gamme de fréquence de *Glossotherium* (de 44 Hz à 15 489 Hz) a été estimée quantitativement à partir des dimensions d'un anneau tympanique bien conservé. Pour la première fois, la gamme de fréquence d'audition dans les deux genres a été estimée par une méthode basée sur la mesure de la surface de l'extrémité proximale des étriers. Les gammes de fréquence correspondent à l'estimation antérieure réalisée sur *Glossotherium* et sont similaires dans les deux genres, suggérant que les gammes de fréquence d'audition sont indépendantes de la taille corporelle dans ce groupe de mammifères. Différentes implications paléobiologiques possibles, comme l'adaptation à des sources sonores spécifiques, la fossorialité ou la communication de longue portée, sont discutées.

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## 1. Introduction

Sloths are currently represented by the genera *Bradypus* and *Choloepus*, which live in the Amazon forest. Fossil taxa are much more diverse and include very large forms traditionally considered Ground Sloths. This group was very well represented in the Pleistocene South American fauna. In a previous analysis, Blanco and Rinderknecht (2008) studied the middle-ear morphology of the Mylodontidae *Glossotherium* and *Lestodon* (Fig. 1). In a previous work, these authors reported the discovery in the collection of the Museo Nacional de Historia Natural of Montevideo (MNHN) of the malleus and the incus of *Lestodon* and made a comparison with the corresponding ossicles of *Glossotherium*, which were already described in the literature (Patterson et al., 1992). The combined masses of the malleus and incus in *Lestodon* in the specimens MNHN 1637 and MNHN 1638 are around 500 mg. The size of these ossicle bones in *Glossotherium* is almost the same as in *Lestodon*. The combined mass of the malleus, incus, and stapes is about 650 mg for the Indian elephant and the ossicles of other large herbivores are much lighter (Reuter and Nummela, 1998).

The body masses of *Glossotherium* and *Lestodon* were estimated from scale models as 1500 kg and 4100 kg respectively (Bargo et al., 2000) suggesting that the ossicle size, almost the same in both genera, could be related to the detection of a specific range of frequencies and not strictly to body size. Such large ossicles suggest a loss of acuity in hearing at higher frequencies (Heffner and Heffner, 1992) and could imply some advantage; as for example, detecting either infrasound or seismic waves that would be conducted by these bones (Blanco and Rinderknecht, 2008). In elephants it has been suggested (O'Connell-Rodwell

et al., 2000) that such massive ossicles could be adaptations for long-distance airborne sound transmission (15 Hz or lower) or to detect seismic waves in the frequency range of 10 to 40 Hz. The low-frequency limit, high-frequency limit and best frequency have already been estimated for *Glossotherium* from the measurements of the tympanic ring (Blanco and Rinderknecht, 2008). The size of the ossicles in *Lestodon* suggested a very similar size in middle-ear structures and it was suggested that hearing capabilities were probably similar in both genera (Blanco and Rinderknecht, 2008). The present study estimates the frequency range of hearing from the footplate area of *Lestodon* and *Glossotherium*, and provides more direct fossil evidence of size-independent frequency range of hearing in these two mylodontid ground sloths.

## 2. Materials and methods

The materials used for this study consist of a right stapes of *Glossotherium robustum* (MNHN 914) and a left stapes of *Lestodon* sp. (MNHN 2149) deposited in the Palaeontological Collection of the MNHN.

Both stapes are very similar in size (Fig. 2) and do not show much novelty in morphology in comparison with other taxa of Mylodontidae (genera *Myiodon*, *Paramyiodon*, *Scelidotherium* and *Alancitherium*). They are robust with a strong muscular process and are thickened dorsoventrally (Guth, 1956; Woodward, 1900).

As in all Mylodontidae and the genus *Megalonyx* the two stapes described here possess a large stapedia foramen. This foramen does not exist (or is very reduced) in adults of the living genera *Bradypus* and *Choloepus* (Patterson et al., 1992). Like other taxa placed among Mylodontidae, the

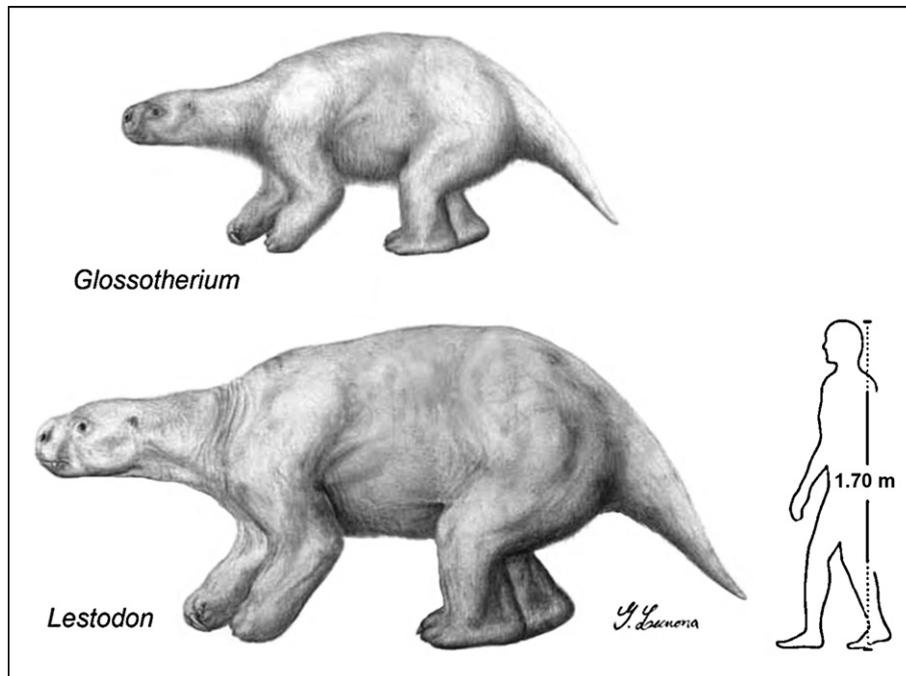


Fig. 1. Hypothetical external appearances of *Glossotherium* and *Lestodon*.

Fig. 1. Reconstitutions paléobiologiques de *Glossotherium* et *Lestodon*.



**Fig. 2.** Right stapes (A) of *Glossotherium robustum* (Museo Nacional de Historia Natural of Montevideo [MNHN] 914) and left stapes (B) of *Lestodon* sp. (MNHN 2149). Upper: ventrolateral view; lower: stapedial base.

**Fig. 2.** Étrier droit (A) de *Glossotherium robustus* (Museo Nacional de Historia Natural of Montevideo [MNHN] 914) et étrier gauche de *Lestodon* sp. (MNHN 2149). En haut : vue ventrolatérale, en bas vue stapédiale.

general morphology of MNHN 914 and MNHN 2149 resemble the typical stapedial morphology found in the anteaters *Myrmecophaga* and *Tamandua* (Patterson et al., 1992).

The major and minor diameters of the stapedial base of the *Glossotherium robustum* (MNHN 914) and *Lestodon* sp. (MNHN 2149) were measured with a digital vernier caliper. The footplate area was estimated, assuming an elliptical shape.

We found estimates for the low-frequency limit, the best sensitivity frequency and the high-frequency limit by using the corresponding power function fit to audiometric limits and anatomical dimensions from Rosowski (1992). The power function fit equations used here are the following:

- lower-frequency =  $0.40 (\text{Footplate Area})^{-1.1}$ ;
- best frequency =  $6.2 (\text{Footplate Area})^{-0.52}$ ;
- higher-frequency =  $34 (\text{Footplate Area})^{-0.40}$ .

Frequencies are in kHz and areas are in  $\text{mm}^2$ . These predictive equations were obtained from data from specimens with a broad range of body masses from tree shrew (*Tupaia glis*) to horses (*Equus caballus*) and explain 67% of the variance for low-frequency limit, 32% for best frequency, and 68% for high-frequency limit (Rosowski, 1992). The best frequency was defined as the tone frequency at the best threshold (the best threshold is the lowest sound pressure of a tone of any frequency that produced a positive behavioral response). The limits of hearing mentioned by

**Table 1**

Estimates of lower, best and higher hearing frequencies in Mylodontidae ground sloths.

**Tableau 1**

Estimations des fréquences d'audition basses, hautes et moyennes chez les Mylodontidae, paresseux géants.

	Lower-frequency (Hz)	Best frequency (Hz)	Higher-frequency (Hz)
From mean tympanic area of <i>Glossotherium robustum</i> (MNHN 441) and <i>Glossotherium robustum</i> (MNHN 1390) (results from Blanco and Rinderknecht, 2008)	44	1737	15,489
<i>Glossotherium robustum</i> (MNHN 914) from footplate area (present work)	44	2187	15,250
Estimation assumed from similarities in incus and malleus size in <i>Lestodon</i> sp. (MNHN 1637) and <i>Lestodon</i> sp. (MNHN 1638) (from Blanco and Rinderknecht, 2008)	44?	1737?	15,489?
<i>Lestodon</i> (MNHN 2149) from footplate area (present work)	55	2420	16,490

Rosowski (1992) were defined by the intersection of the audiogram, with an isopressure contour defined by the best threshold plus 30 dB. That definition of limits is slightly arbitrary and for *Homo sapiens* the lower-frequency value measured is 150 Hz (other definitions imply much lower values as 20 Hz) with best frequency at 4000 Hz. These values are useful for comparison with the results in sloths and to define infrasound sensitivity. The lower-frequency limit in Rosowski's experimental data is roughly in the infrasound level (90 Hz for *Chinchilla laniger*).

In order to estimate the body size expected differences in tympanum and footplate areas we use the following allometric equations for mammals (Hunt and Korth, 1980):

$$Y = 0.26 X + 1.23,$$

where Y is the base 10 logarithm of the tympanum area in mm<sup>2</sup> and X is the base 10 logarithm of the body mass in kg.  $Y = 0.28 X - 0.07$  where Y is the base 10 logarithm of the stapedial footplate area in mm<sup>2</sup> and X is the base 10 logarithm of the body mass in kg.

### 3. Results

The major and minor diameters of the stapedial base of *Glossotherium robustum* (MNHN 914) were 3.84 mm and 2.46 mm, respectively, and those of *Lestodon* (MNHN 2149) were 3.24 mm and 2.40 mm. These values give footplate areas of 7.42 mm<sup>2</sup> and 6.11 mm<sup>2</sup> respectively. The footplate area is slightly larger in the smaller *Glossotherium*. However, the expected values of the footplate area from allometric equations are 6.60 mm<sup>2</sup> and 8.74 mm<sup>2</sup> respectively. The tympanum areas expected from allometric equations are 113.7 mm<sup>2</sup> and 147.7 mm<sup>2</sup>. In a previous work it was determined that in *Glossotherium* the tympanum area was much larger than expected, that is in the range 180 to 208 mm<sup>2</sup> (Blanco and Rinderknecht, 2008).

Using the corresponding power function fit to audiometric limits and anatomical dimensions from the literature (Rosowski, 1992), we found that the low-frequency limits are in the infrasound region and the best sensitivity frequencies and the high-frequency limits are relatively low values (Table 1). The results for *Glossotherium* are very close to those obtained by Blanco and Rinderknecht (2008) and for *Lestodon* the results are very close to the expected results mentioned above.

### 4. Discussion

The body mass of *Glossotherium* was estimated at 1500 kg, clearly smaller than the body mass of 4100 kg estimated for *Lestodon*, suggesting that the ossicle's size, almost the same in both genera, is probably related to the detection of a specific range of frequencies and not strictly dependent on body size. The results show that for a mammal with the same body mass the expected tympanum areas are roughly 60% of the value previously measured in *Glossotherium* (Blanco and Rinderknecht, 2008). Also, the results show that for mammals with those body masses the expected difference in stapedial footplate areas is larger than the measured values (see results section). Thus, the similarities in frequency ranges are not related to differences in body mass.

In both genera, the ossicles are very large and in a previous work Blanco and Rinderknecht (2008) suggested that they were probably designed to detect airborne sound transmission or low-frequency seismic waves. The main argument proposed was that these large ossicles, which imply loss of acuity for hearing high frequencies, were useful for better localization of the sound source (Heffner and Heffner, 1992) and could imply some advantage. Mammals with small heads need to hear higher frequencies than larger mammals in order to use binaural and monaural spectral clues for sound localization. That is reflected in the correlation ( $r = -0.84$ ) between maximum interaural distance and the high-frequency limit (Heffner and Heffner, 1992). If it is assumed that 15,000 Hz corresponds to the high-frequency limit for the studied ground sloths, the observed correlation between functional head size and high-frequency hearing limit (Fig. 34,7 in Heffner and Heffner, 1992) gives a rough estimation of the expected interaural distance for good sound localization. In that case the expected interaural distance is around 3000  $\mu$ s (from data in Heffner and Heffner, 1992). Assuming a sound speed of 340 m/s the interaural distance is 1 m. The anatomical interaural distances measured in the fossil skulls with a digital caliper are 114 mm in *Glossotherium* MNHN 441, 93.5 mm in *Glossotherium* MNHN 914, 147.6 mm in *Lestodon* MNHN 1637, and 144.5 mm in *Lestodon* MNHN 1638. In both genera, the interaural distances are low for mammals of such body size. Elongated and thin skulls are characteristic of mylodontid ground sloths (Pascual, 1967; Paula Couto, 1979). Even in the larger skull of *Lestodon*, the interaural distance in time units (that means the

interaural distance divided by sound speed) is around 440  $\mu$ s and in the larger skull of *Glossotherium* is around 320  $\mu$ s. For these values of interaural distance, the general tendency in Figure 34,7 in Heffner and Heffner (1992) implies a higher-frequency limit for good sound localization around 40 kHz. In the most extreme case Heffner's figure 34,7 shows extant animals with head sizes similar to the two extinct sloths with high-frequency limits of 20 kHz. Even in that case the value is larger than the high-frequency limits obtained here.

The combination of frequency range shifted toward low tones and the small interaural distances of the ground sloths studied here suggests a very poor performance in sound localization. Generally, sound localization is used to enable an animal to direct its gaze to the source for further scrutiny. In a case where this function is not relevant for fitness, low-frequency sensitivity can be selected for. As Heffner and Heffner (1992) pointed out, it would be expected that any species of mammals that could not localize sound would lose its ability to hear high frequencies and this seems to be the case of fossorial mammals such as pocket gophers and blind mole rats that detect low-frequency seismic signals.

In a previous biomechanical study (Bargo et al., 2000), it was suggested that *Lestodon*, *Glossotherium*, and *Scelidotherium* (body mass estimated of around 800 kg) were well adapted to perform strenuous activities with their forelimbs, in which force is enhanced over velocity, useful for functions such as digging. Large Pleistocene caves are known in the Pampean region with a size consistent with the size of *Glossotherium* and *Scelidotherium* scratches found on the walls and roofs of some caves agree well with the manus morphology of both genera (Vizcaíno et al., 2001; Zárate et al., 1998). Fossorial habits are a possible explanation for the utility of low-frequency sensitivity in this group.

In the case of some desert rodents an increased low-frequency sensitivity can also be related to hearing low-frequency sounds produced by some nocturnal predators such as snakes and owls just prior to striking Webster and Plassmann, 1992 and references therein). The detection of sound clues from specific predators of ground sloths, perhaps the larger ones as *Smilodon* or *Arctotherium*, is another possibility. However, this hypothesis has no support at present because there is not enough knowledge about the predator-prey relationships of ground sloths (Spencer et al., 2003).

Another possibility is related to an adaptation for semi-aquatic habits. Large ossicles in some living mammals with semi-aquatic habits appear to be an adaptation for underwater hearing (Reuter and Nummela, 1998 and references therein; Shipley et al., 1992). A semi-aquatic sloth (*Thalassocnus* spp.) was discovered in the Miocene-Pliocene of Perú and Chile (Muizon and de McDonald, 1995; Muizon et al., 2004) but it was not closely related with Mylodontidae (Gaudin, 2004) and all the paleontological evidence shows that Mylodontidae were completely terrestrial animals (Bargo and Vizcaíno, 2008; Paula Couto, 1979).

As previously suggested by Blanco and Rinderknecht (2008), low-frequency sensitivity could be an adaptation for long-range communication as observed in living

elephants. Low-frequency sound is useful for long-range communication because it is less affected by scattering from vegetation, and atmospheric absorption is essentially nonexistent (Garstang et al., 1995 and references therein). It was claimed that infrasound with frequencies from 14 Hz to 35 Hz is used for communication at ranges up to 4 km (Garstang et al., 1995). However, recent analyses (McComb et al., 2003) suggest that the most important frequency components for long-distance communication of social identity may be well above the infrasonic range and the authors have doubts about the use of airborne sound much below 100 Hz for long-distance hearing. The present result implies that ground sloths have good sensitivity at such low frequencies (the lower-frequency limit is close to 50 Hz in both *Glossotherium* and *Lestodon*). Present results and the use of low-frequency sounds for long-range communication in living large mammals such as elephants suggest the possibility that ground sloths could also have used low-frequency sounds for long-range communication.

## 5. Conclusion

The new results seem to support previous speculations that both genera have similar frequency ranges. From all the previous discussion it is possible to conclude that there probably existed in some ground sloths an adaptive selection for some specific low-frequency window. The selective pressure for such adaptation is unknown, but detection of specific predators, fossoriality, long-range communication, and seismic wave detection, must be considered. The long-range communication hypothesis is probably the best suited at present to explain the size-independent low-frequency sensitivity in some ground sloths.

## Acknowledgments

J.J. Rosowski made several useful comments. Gustavo Lecuona made the reconstructions in Fig. 1 and provided help with the photographs for Fig. 2.

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