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# Observations on the scaling relationship between bony labyrinth, skull size and body mass in ruminants

Loïc Costeur<sup>a\*</sup>, Bastien Mennecart<sup>a</sup>, Bert Müller<sup>b</sup> & Georg Schulz<sup>b</sup>

<sup>a</sup>Naturhistorisches Museum Basel, Augustinergasse 2, 4001 Basel, Switzerland;

<sup>b</sup>Biomaterials Science Center, Department of Biomedical Engineering, University of Basel, 4123 Allschwil, Switzerland

## ABSTRACT

The bony labyrinth is the bony capsule of the inner ear, which is the center of hearing and balance in the skull of vertebrates. In mammals this osseous structure ossifies early in the development being fully formed largely before birth. This means that it does not grow after full ossification while the animal continues to grow until full adult size well after birth. At the level of an individual, the bony labyrinth thus shows a negative ontogenetic allometric relationship with the surrounding skull and with the animal's body mass. At the evolutionary level, between species, such a negative allometry has already been evidenced for the middle ear, a component of the ear region made of three tiny bones, the ossicles, in contact with the inner ear. Herein, we test the allometric relationship between the bony labyrinth and skull length as well as body mass on a large sample in the ruminant clade (Mammalia, Ruminantia) using micro computed tomography as the imaging method of choice. We find a strong negative allometry paralleling the ontogenetic allometry described earlier. This evolutionary relationship related to the timing of ossification of the bony labyrinth is probably critical in explaining the large hearing frequency range of mammals as well as their particular ecological adaptations.

**Keywords:** Ruminantia, microCT, evolutionary allometry, bony labyrinth, body mass, evolution, inner ear

## 1. INTRODUCTION

Allometry classically refers to “size-related changes of morphological traits” [1]. In other words, scaling relationships describe differential growth of individual parts in organisms or changes in relative proportions of body parts [2]. These allometries are classically considered as constraints that may channel morphological variation and constrain phenotypic variation, while being also themselves prone to evolve [3, 4]. Scaling relationships between bony structures and body mass in mammals have been thoroughly investigated, see e.g. refs. [5-7], in order to understand various aspects of their development, ecology, adaptations, or evolution [8-10]. Allometry is now seen as one of the major factor of morphological variation tightly related to development and the variation in growth of the body parts considered [11]. The size and growth of sense organs have been shown to be negatively correlated to body mass in mammals (e.g., [12, 13]), often because of an early ossification timing that ensures proper function of the organs themselves around birth time [7]. This developmental heterochrony, particularly well-known for the middle ear bones of placental and marsupial mammals, has induced the formation of the typical mammalian middle ear [6]. The inner ear is composed of two organs controlling hearing and balance. It is enclosed inside the densest bone of the skeleton, the petrosal bone, on the postero-ventral side of the skull behind the pinna. The hollow regions surrounding the inner ear inside the petrosal bone, i.e., the “bony labyrinth” (hereafter “BL”), closely match the anatomy of the organ itself. Dried skeletal specimens from natural history collections can be scanned to access the morphology of the BL, as shown e.g. in refs. [14, 15]. The radius of curvature of the semi-circular canals within the BL, which are responsible for sensing acceleration movements of the head, have been shown to scale with body mass in mammals [7]. However, the scaling relationship of the whole BL with body mass or skull size has never been fully investigated in mammals. In a preliminary approach, Billet *et al.* [16] have shown that BL size in the mammalian clade has a negative allometric relationship with the size of their petrosal bone, i.e., big petrosal bones in larger species have a relatively smaller BL than in smaller petrosal bones in smaller species.

\*[loic.costeur@bs.ch](mailto:loic.costeur@bs.ch); phone: +41 61 266 55 87

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The ruminants are the group of chevrotain, deer, goats, antelopes, cattle, sheep, giraffes, and pronghorns. Extensive works have been recently performed on the ear region of these animals, as, for example, shown in refs. [17-21]. BL has been shown to complete ossification at mid-gestation in ruminants (in the chevrotain *Tragulus kanchil* and in the cow *Bos taurus*; [18, 22]). This means that BL size is set at mid-gestation and will not grow afterwards despite the growth of the skull and more generally of the animal until full adulthood. They thus evidenced a negative ontogenetic allometric growth of the BL relative to the animal skull, paralleling the evolutionary allometry evidenced by Billet *et al.* [16].

All these empirical data taken together point to a probable negative evolutionary allometry between BL size and the species size, either represented by skull size or body mass. Within the present tomography study, we test this relationship by investigating the scaling relationship between BL length and body mass and skull length on a large sample of ruminants.

## 2. METHODOLOGY

### 2.1 Micro computed tomography measurements

We measured the BL of 77 species of extant ruminants representing 80% of all known genera and about 36% of the 211 species known, see Table 1. The scans were performed using the advanced microCT-system nanotom<sup>®</sup> m (phoenix x-ray, GE Sensing & Inspection Technologies GmbH, Wunstorf, Germany). This system is equipped with a nanofocus tube, maximal acceleration voltage of 180 kV, which produces a power of up to 15 W. This relatively high acceleration voltage can be employed to scan samples with a maximal diameter of 240 mm and a maximal weight of 3 kg. For the present study, the acceleration voltage (60 to 180 kV), the beam current, the pixel size (5 to 50  $\mu\text{m}$ ) and exposure time were adapted to the sizes and density of the object of interest. 1,440 equiangular radiographs were recorded over the angular range of 360°. The scan times were set to periods between one and five hours. The projections were reconstructed using a cone beam filtered back-projection algorithm using phoenix dato|x 2.0.1 - RTM (GE Sensing & Inspection Technologies GmbH, Wunstorf, Germany). The BLs were segmented using the segmentation editor of AVIZO 7.0 and AVIZO 9.0.

### 2.2 Length measurements

BL length was measured using the “3D Length” measuring tool of AVIZO 9.0 from the top of the common crus between the anterior and posterior semi-circular canals to the apex of the cochlea, see Figure 1c, following the protocol described in ref. [18]. This measurement differs from total length, since the semi-circular canals, especially the anterior semi-circular canal, variably expand beyond the top of the common crus. It gives, however, a reasonable approximation of its overall size. Skull length for each specimen was taken on the scanned skulls, for which the BLs were reconstructed. Some BLs were reconstructed from broken specimens or isolated petrosal bones. In the latter cases, other skulls of the same species were used for skull length determination, see Table 1. Body mass data were taken from the literature [23, 24] and are average body masses for the given species, see Table 1. Sexual dimorphism is common in large ruminants but is unlikely to affect the results, since size and mass are represented on logarithmic scale. The BL is not known to be a dimensionally sexually dimorphic structure, see e.g. ref. [25]. Limited sexual dimorphism restricted to characters of the bony labyrinth was not measured here (radius of curvature of the posterior semi-circular canal); nonetheless seems to have been detected in humans [26].

### 2.3 Allometry investigation

A non-linear growth relationship between two correlated trait measures  $x$  and  $y$  can be expressed by the allometric function:

$$y = b \cdot x^\alpha.$$

Allometry is investigated using a double-logarithmic plot:

$$\log(y) = \alpha \cdot \log(x) + \log(b) = \alpha \cdot \log(x) + b',$$

where  $\alpha$  the coefficient of allometry or slope of the regression line and  $b'$  the intercept of the regression line with the  $y$ -axis. For this calculation the values  $x$  and  $y$  had to become unitless, but one has to consider that the value  $\alpha$  will depend on the choice of the units of  $x$  and  $y$  (e.g. mm, cm, m, ...).

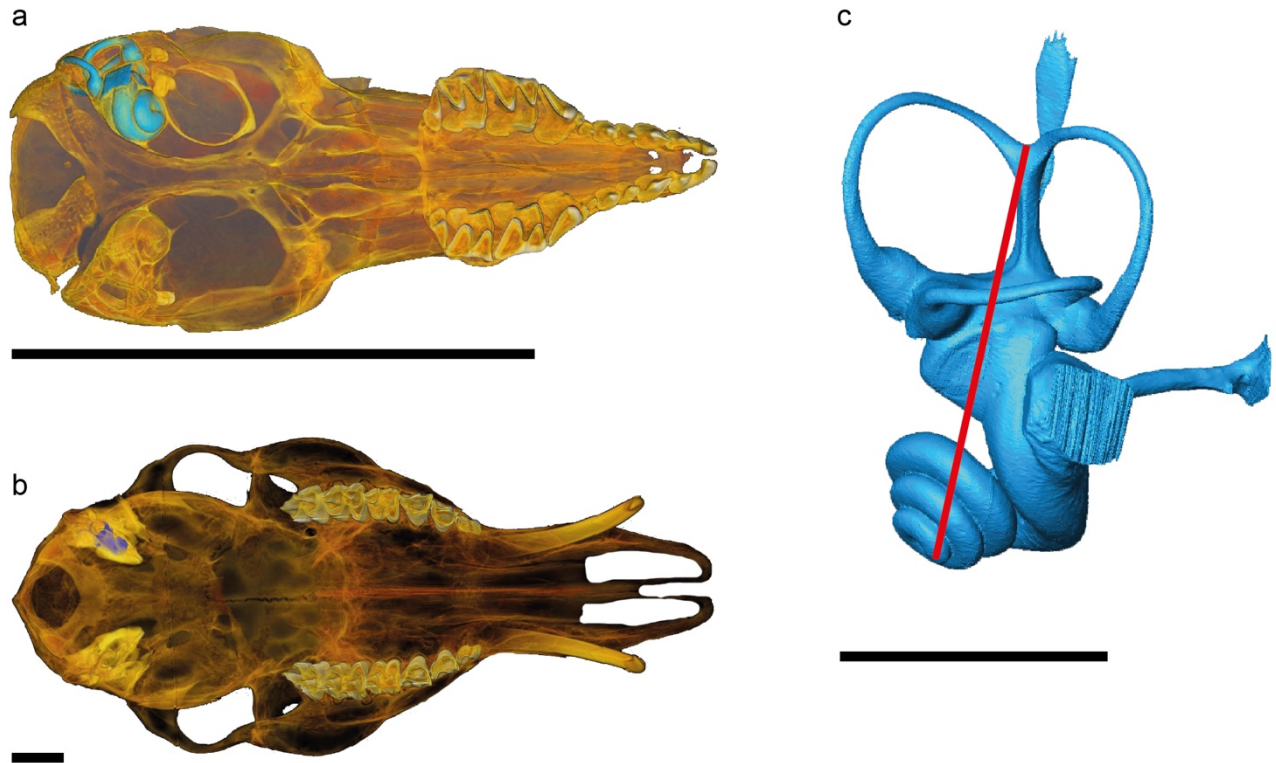


Figure 1. a: Semi-transparent view of the skull of the tiny Etruscan Shrew *Suncus etruscus* (NMB 6053) showing the large bony labyrinth (blue) in the brain cavity. b: Semi-transparent view of the skull of the ruminant Siberian musk deer *Moschus moschiferus* (NMB 8874), note the small bony labyrinth (purple) in comparison to that in a. c: Bony labyrinth length measurement (postero-lateral view of the bony labyrinth of the cow *Bos taurus*, specimen NMB 1034) given by the red-colored distance. The length of the bars corresponds to 1 cm.

In our case, the allometric relationship (equation of the regression line between the two investigated parameters) is as follows:

$$\log(l_i) = \alpha \cdot \log(l_s) + b'$$

or

$$\log(l_i) = \alpha \cdot \log(m) + b',$$

where  $l_i$  is the BL length,  $l_s$  the skull length and  $m$  the body mass.

A slope of the regression line of the two parameters (BL length and skull size, or BL length and body mass), which equals unity, is associated with the isometric relationship, i.e. the BL, the skull or body mass grows at the same rate. A value larger than unity means positive allometry, i.e. the BL grows faster than the skull or the body mass, or larger animals possess relatively large. A value below unity relates to a negative allometry, i.e. the BL grows slower than the skull or the body mass.

### 3. RESULTS AND DISCUSSION

A first glance, the raw data listed in Table 1 show that the longest BLs with a length above 15 mm are found in the largest species (16.82 mm in the okapi specimen *Okapia johnstoni*; 15.95 mm in the giraffe specimen *Giraffa Camelopardalis*; 15.67 mm in the cow specimen *Bos taurus*. On the other side of the size spectrum, the smallest BLs reach about half the length of the longest BLs in the smallest species, i.e. from 6.91 mm for the spotted chevrotain *Moschiola meminna*, 7.01 to 7.70 mm in the Lesser Oriental Chevrotain *Tragulus kanchil*, or 8.09 mm in Bates's pygmy antelope *Neotragus batesi*).

Table 1. Specimen data and measurements (NMB: Naturhistorisches Museum Basel; \* [27])

| Family         | Genus               | Species                           | Accession number | BL length (mm) | Skull length (mm) | Average body mass (kg) | Remarks                        |
|----------------|---------------------|-----------------------------------|------------------|----------------|-------------------|------------------------|--------------------------------|
| Antilocapridae | <i>Antilocapra</i>  | <i>americana</i>                  | NMB 1618         | 9.74           | 268               | 53                     |                                |
| Bovidae        | <i>Aepyceros</i>    | <i>melampus</i>                   | NMB 9017         | 11.56          | 261               | 52                     |                                |
| Bovidae        | <i>Ammotragus</i>   | <i>lervia</i>                     | NMB 2084         | 10.6           | 193               | 90                     |                                |
| Bovidae        | <i>Antidorcas</i>   | <i>marsupialis</i>                | NMB 10853        | 10.85          | 231               | 39                     | skull L: NMB 16394             |
| Bovidae        | <i>Antilope</i>     | <i>cervicapra</i>                 | NMB 3251         | 11.07          | 221               | 37.5                   |                                |
| Bovidae        | <i>Bos</i>          | <i>taurus</i>                     | NMB 1034         | 15.67          | 495               | 900                    |                                |
| Bovidae        | <i>Boselaphus</i>   | <i>tragocamelus</i>               | NMB 10258        | 12.55          | 410               | 200                    | skull L: NMB 10257             |
| Bovidae        | <i>Bubalus</i>      | <i>depressicornis</i>             | NMB 3269         | 11.52          | 261               | 225                    |                                |
| Bovidae        | <i>Capra</i>        | <i>hircus</i>                     | NMB 6920         | 10.42          | 172               | 50                     |                                |
| Bovidae        | <i>Capra</i>        | <i>ibex</i>                       | NMB 5837         | 11.21          | 264               | 90                     |                                |
| Bovidae        | <i>Capra</i>        | <i>sibirica</i>                   | NMB 4219         | 11.05          | 210               | 80                     |                                |
| Bovidae        | <i>Capricornis</i>  | <i>sumatrensis</i>                | NMB 4987         | 11.67          | 237               | 90                     | skull L: NMB 4987              |
| Bovidae        | <i>Cephalophus</i>  | <i>callipygus</i>                 | NMB 15591        | 9.85           | 197               | 21.9                   |                                |
| Bovidae        | <i>Cephalophus</i>  | <i>natalensis</i>                 | NMB 3572         | 9.49           | 156               | 11.8                   |                                |
| Bovidae        | <i>Cephalophus</i>  | <i>rufilatus</i>                  | NMB 16169        | 9.01           | 152.8             | 10                     |                                |
| Bovidae        | <i>Cephalophus</i>  | <i>sylvicultor</i>                | NMB 16226        | 12.44          | 310               | 70                     | skull L: NMB 16223             |
| Bovidae        | <i>Connochaetes</i> | <i>gnou</i>                       | NMB 7591         | 12.48          | 440               | 160                    |                                |
| Bovidae        | <i>Damaliscus</i>   | <i>pygargus</i>                   | NMB 1948         | 11.56          | 300               | 61                     | skull L: NMB 7060              |
| Bovidae        | <i>Eudorcas</i>     | <i>rufifrons</i>                  | NMB 6414         | 10.23          | 201               | 30                     |                                |
| Bovidae        | <i>Gazella</i>      | <i>dorcas</i>                     | NMB 1724         | 11.61          | 170               | 15.4                   |                                |
| Bovidae        | <i>Gazella</i>      | <i>gazella</i>                    | NMB 11029        | 9.69           | 172               | 23                     |                                |
| Bovidae        | <i>Gazella</i>      | <i>subgutturosa</i>               | NMB 2497         | 10.73          | 182               | 35                     |                                |
| Bovidae        | <i>Hemitragus</i>   | <i>hylocrius</i>                  | NMB 2389         | 10.32          | 220               | 75                     |                                |
| Bovidae        | <i>Hippotragus</i>  | <i>leucophaeus ellipsiprymnus</i> | NMB 2149         | 13.85          | 310               | 225                    |                                |
| Bovidae        | <i>Kobus</i>        | <i>defassa</i>                    | NMB 447          | 14.18          | 385               | 175                    | skull L: NMB 15089             |
| Bovidae        | <i>Litocranius</i>  | <i>walleri</i>                    | NMB 2543         | 10.56          | 225               | 43.5                   |                                |
| Bovidae        | <i>Madoqua</i>      | <i>kirkii</i>                     | NMB 7572         | 8.71           | 114               | 4.9                    |                                |
| Bovidae        | <i>Madoqua</i>      | <i>saltiana</i>                   | NMB 8064         | 7.84           | 106               | 3.3                    |                                |
| Bovidae        | <i>Naemorhedus</i>  | <i>goral</i>                      | NMB 1923         | 10.46          | 209               | 28.5                   | skull L: NMB 4651              |
| Bovidae        | <i>Neotragus</i>    | <i>batesi</i>                     | NMB Z.1536       | 8.09           | 109.5             | 2.5                    |                                |
| Bovidae        | <i>Nesotragus</i>   | <i>moschatus</i>                  | NMB 2122         | 8.15           | 112               | 5.2                    |                                |
| Bovidae        | <i>Neotragus</i>    | <i>pygmaeus</i>                   | NMB 16362        | 8.11           | 101.5             | 2.4                    | skull L: NMB 2123              |
| Bovidae        | <i>Oreamnos</i>     | <i>americanus</i>                 | NMB 11149        | 10.31          | 275               | 90                     |                                |
| Bovidae        | <i>Oreotragus</i>   | <i>oreotragus</i>                 | NMB 8401         | 9.85           | 138               | 13                     |                                |
| Bovidae        | <i>Ourebia</i>      | <i>ourebi</i>                     | NMB 8772         | 8.51           | 166               | 17.5                   |                                |
| Bovidae        | <i>Ovibos</i>       | <i>moschatus</i>                  | NMB 11175        | 12.7           | 410               | 305                    | Skull L: UCMZ M 1978.1.92 (40) |
| Bovidae        | <i>Ovis</i>         | <i>aries</i>                      | NMB 9037         | 9.65           | 246               | 70                     |                                |
| Bovidae        | <i>Pelea</i>        | <i>capreolus</i>                  | NMB 2147         | 11.43          | 195               | 25                     |                                |

|            |                    |                       |           |       |       |       |                    |
|------------|--------------------|-----------------------|-----------|-------|-------|-------|--------------------|
| Bovidae    | <i>Philantomba</i> | <i>maxwelli</i>       | NMB 15180 | 8.26  | 134   | 8     |                    |
| Bovidae    | <i>Philantomba</i> | <i>monticola</i>      | NMB 15224 | 8.09  | 126   | 5.2   |                    |
| Bovidae    | <i>Philantomba</i> | <i>walteri</i>        | NMB 15551 | 8.31  | 141   | 8     |                    |
| Bovidae    | <i>Procapra</i>    | <i>gutturosa</i>      | NMB 10435 | 9.83  | 255   | 30    | skull L: NMB 10432 |
| Bovidae    | <i>Pseudois</i>    | <i>nayaur</i>         | NMB 1919  | 10.33 | 241   | 50    |                    |
| Bovidae    | <i>Raphicerus</i>  | <i>campestris</i>     | NMB 16338 | 9.7   | 142   | 11    |                    |
| Bovidae    | <i>Raphicerus</i>  | <i>melanotis</i>      | NMB 4228  | 9.47  | 137   | 10    |                    |
| Bovidae    | <i>Redunca</i>     | <i>arundinum</i>      | NMB 4882  | 11.31 | 265   | 55    | Skull L: NMB 16252 |
| Bovidae    | <i>Redunca</i>     | <i>fulvorufula</i>    | NMB 15091 | 11.62 | 215   | 55    |                    |
| Bovidae    | <i>Rupicapra</i>   | <i>rupicapra</i>      | NMB 320   | 9.36  | 202   | 37    |                    |
| Bovidae    | <i>Saiga</i>       | <i>tatarica</i>       | NMB 10065 | 12.12 | 206   | 45    |                    |
| Bovidae    | <i>Sylvicapra</i>  | <i>grimmia</i>        | NMB 15123 | 9.79  | 160   | 18.5  |                    |
| Bovidae    | <i>Tetracerus</i>  | <i>quadricornis</i>   | NMB 10472 | 10.83 | 195   | 19    |                    |
| Bovidae    | <i>Tragelaphus</i> | <i>scriptus</i>       | NMB 3568  | 11.08 | 195   | 50    |                    |
| Cervidae   | <i>Alces</i>       | <i>alces</i>          | NMB 2198  | 13.8  | 550   | 500   |                    |
| Cervidae   | <i>Axis</i>        | <i>axis</i>           | NMB 3718  | 11.33 | 251   | 68.5  |                    |
| Cervidae   | <i>Capreolus</i>   | <i>capreolus</i>      | NMB 6212  | 8.87  | 186   | 32.5  | skull L: NMB 1243  |
| Cervidae   | <i>Cervus</i>      | <i>elaphus</i>        | NMB 11147 | 12.79 | 290   | 207.5 |                    |
| Cervidae   | <i>Cervus</i>      | <i>nippon</i>         | NMB 6106  | 12.2  | 300   | 30    |                    |
| Cervidae   | <i>Dama</i>        | <i>dama</i>           | NMB 3186  | 11.73 | 250   | 70    |                    |
| Cervidae   | <i>Elaphodus</i>   | <i>cephalophus</i>    | NMB 2067  | 10.4  | 196   | 33.5  |                    |
| Cervidae   | <i>Elaphurus</i>   | <i> davidianus</i>    | NMB 10490 | 11.41 | 405   | 185   | skull L: NMB 10683 |
| Cervidae   | <i>Hydropotes</i>  | <i>inermis</i>        | NMB 9892  | 9.03  | 153   | 12.5  |                    |
| Cervidae   | <i>Mazama</i>      | <i>americana</i>      | NMB 2315  | 10.14 | 198   | 16.5  |                    |
| Cervidae   | <i>Mazama</i>      | <i>gouazoubira</i>    | NMB 6672  | 10.34 | 230   | 16.5  |                    |
| Cervidae   | <i>Muntiacus</i>   | <i>muntyak</i>        | NMB 2408  | 9.76  | 166   | 23.5  |                    |
| Cervidae   | <i>Odocoileus</i>  | <i>virginianus</i>    | NMB 9872  | 11.14 | 270   | 117.5 | skull L: NMB 15109 |
| Cervidae   | <i>Ozotoceros</i>  | <i>bezoarticus</i>    | NMB 2312  | 10.1  | 227   | 32.5  |                    |
| Cervidae   | <i>Pudu</i>        | <i>puda</i>           | NMB 2209  | 7.97  | 152   | 9.5   |                    |
| Cervidae   | <i>Rangifer</i>    | <i>tarandus</i>       | NMB 7552  | 12.27 | 315   | 100   |                    |
| Cervidae   | <i>Rusa</i>        | <i>timorrensis</i>    | NMB 3657  | 11.26 | 255   | 63    |                    |
| Giraffidae | <i>Giraffa</i>     | <i>camelopardalis</i> | NMB 12075 | 15.95 | 600   | 800   |                    |
| Giraffidae | <i>Okapia</i>      | <i>johnstoni</i>      | NMB 10811 | 16.82 | 480   | 250   |                    |
| Moschidae  | <i>Moschus</i>     | <i>moschiferus</i>    | NMB 4201  | 9.5   | 152   | 12.5  |                    |
| Tragulidae | <i>Hyemoschus</i>  | <i>aquaticus</i>      | NMB 2499  | 9.18  | 123.2 | 10    |                    |
| Tragulidae | <i>Moschiola</i>   | <i>meminna</i>        | NMB 1366  | 7.05  | 96    | 2.45  |                    |
| Tragulidae | <i>Tragulus</i>    | <i>javanicus</i>      | NMB 10028 | 8.67  | 110   | 4     |                    |
| Tragulidae | <i>Tragulus</i>    | <i>kanchil</i>        | NMB 3791  | 7.5   | 92    | 4     |                    |
| Tragulidae | <i>Tragulus</i>    | <i>napu</i>           | NMB 10085 | 7.83  | 104.3 | 5     |                    |

The species with the longest BL are also those showing the longest skulls (480 mm in the okapi specimen *Okapia johnstoni*, 600 mm in the giraffe specimen *Giraffa camelopardalis*, or 495 mm in the cow specimen *Bos taurus*, see Tab. 1). The same is true for the smallest BL of chevrotains (genera *Tragulus* and *Moschiola*), which show skull lengths of less than 100 mm (Tab. 1).

The longest BL are found in species with the largest body masses (the Giraffe with average body mass of 800 kg, but reaching up to more than 1500 kg in some individuals, or the cow with average body mass of 900 kg) with the notable exception of the Okapi (only 250 kg on average for a very long BL). The smallest BL are found in the smallest species, the chevrotains weighing less than 5 kg on average (and even less than 3 kg for *Moschiola meminna*).

The longest BL are found in species with the largest body masses (the giraffe with average body mass of 800 kg, but reaching up to more than 1,500 kg in some individuals, or the cow with average body mass of 900 kg) with the notable exception of the okapi (only 250 kg on average for a very long BL). The smallest BL are found in the smallest species, the chevrotains weighing less than 5 kg on average and even less than 3 kg for *Moschiola meminna*.

Figure 2 shows the scaling relationship between BL length and skull length. This relationship confirms the qualitative description. Plotting the data on a double-logarithmic scale, one finds a clear correlation between the parameters. The coefficient of allometry is  $0.378 \pm 0.015$ . The scaling is below unity, which verifies that species with a large skull have relatively small BL and species with a small skull have relatively large BL.

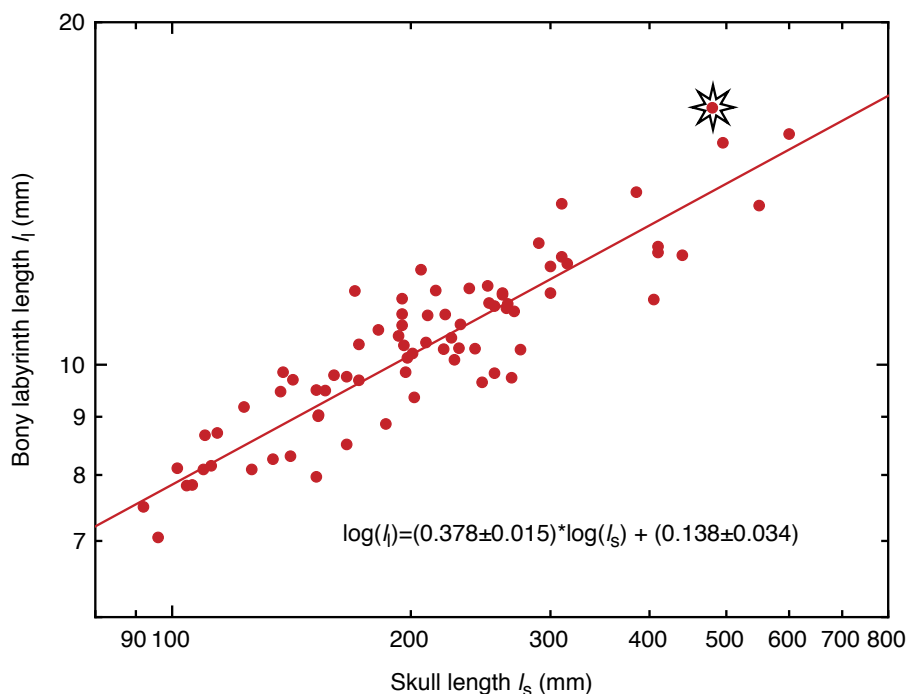


Figure 2. The diagram shows the double-logarithmic plot of bony labyrinth length against skull length for the 77 ruminants investigated. One finds the expected relationship. The star highlights the okapi specimen.

Figure 3 elucidates the scaling relationship between BL length and species body mass. Here, the relationship also demonstrates a clear correlation between the quantities. The coefficient of allometry is  $0.115 \pm 0.005$ . The scaling relationship is also below unity, which confirms that large species have relatively small BL and vice versa. As stated above the okapi specimen studied had a relatively large BL for its body mass and stands slightly out of the data cloud, see data point highlighted by the star. It should be noted that the allometry coefficient is smaller for the body mass than for the skull related to the labyrinth length.

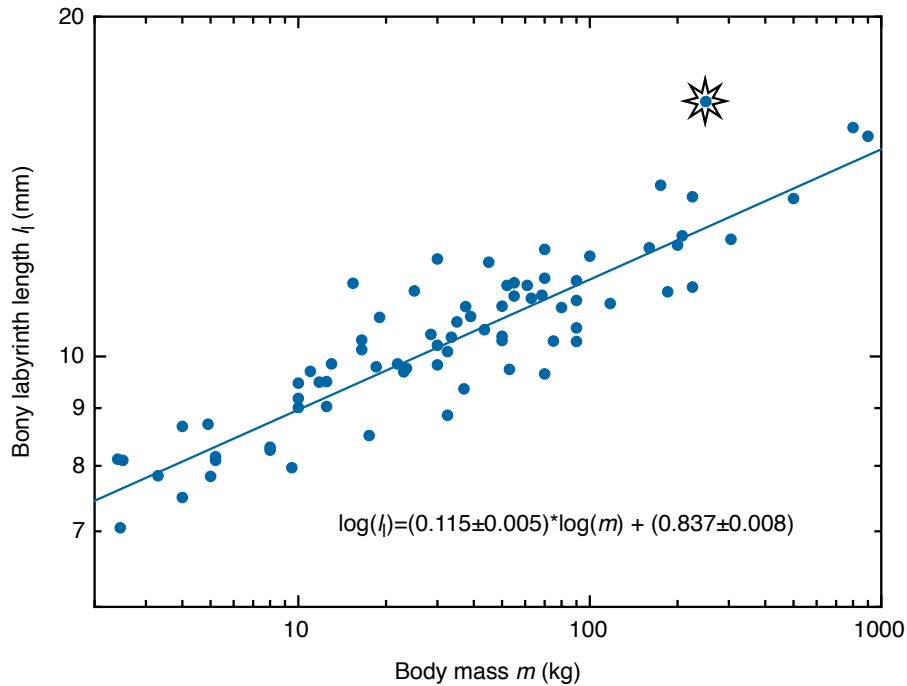


Figure 3. The left diagram shows the double-logarithmic plot of bony labyrinth length against skull length for the 77 ruminants investigated. One finds the expected relationship. The right diagram displays the double-logarithmic plot of bony labyrinth length against body mass for the same species. The star indicates the okapi specimen.

Allometry is a major factor that has the potential for channeling morphological variation or constraining phenotypic evolution, as already pointed out in ref. [28]. It has been assumed that allometric variation thus defines lines of least resistance to evolution, see e.g. refs. [4, 29], along which morphological evolution preferentially occurs. As such investigating allometric relationships between body parts and body mass has great potential in providing critical information on the evolution of organisms.

Allometric relationships have been investigated in ruminants almost exclusively in order to understand how representatives of this highly specialized group of mammals feed, digest, or use their home range [30-34]. Since body mass is a major ecological parameter, reconstructing body masses of extinct taxa based on linear measurements of long bones or teeth has also been an important aim involving allometric relationships [35, 36]. On the other side, scaling relationships have rarely been investigated in ruminant research in order to understand how morphological traits evolved in the clade. A notable exception is a study of the antelope skull [37]. It shows that large species have proportionally longer skulls, a pattern holding true at the level of mammals [37]. This study concluded that allometry channeled the evolution of facial shapes and promoted morphological variation for dietary adaptations [37].

Sense organs are known to scale negatively with body mass in mammals [12]. Such as reminded in [6], the achievement of key structures such as the individualization of three middle ear bones in the ear of mammals in their early evolutionary stages is partly the result of developmental timing allowing them to fully ossify before other skull bones. This implies a negative ontogenetic allometric growth, other skull bones continuing to grow until adult size. This timing and allometry allowed mammals evolving their very specific ear adapted to a wide hearing frequency range. The same developmental pattern of the BL in ruminants was evidenced where full ossification, and thus full adult size and volume of the BL, is achieved at mid gestation, well before birth [18, 22]. The authors further indicated that the BL of the cow shows a negative ontogenetic allometric growth relative to the petrosal bone and to skull length [18]. Expanding to the evolutionary level, the present study shows that the BL scales negatively with body mass in ruminants. A similar result was reached [16] by showing that the BL scales negatively with petrosal bone size in a limited sample of mammals. A more detailed study [7] had already anticipated this relationship by revealing the negative allometry of the semi-circular



canals (SCC) using a large sample at the mammal clade level, where the SCC scaled with an allometric coefficient of 0.14, a very close coefficient to the one found here. The similarity of both allometric coefficients implies a possible isometry in the internal development of the BL, a feature likely to occur in highly integrated structures promoting phenotypic stability [38]. Altogether, the allometric relationship evidenced here is probably fundamental in explaining the evolution of the diversified hearing and locomotor capacities of mammals.

That the BL occupies a relatively large space in the petrosal bone and eventually in the brain cavity of smaller mammals could be related to functional demands. Miniaturization is impossible beyond a certain level without impacting the function of the organ of balance such as shown in ref. [39], even if ruminants fall largely beyond the size threshold necessary in small vertebrates investigated in ref. [39]. The lightest mammal, the Etruscan shrew weighing about 2 g has a BL length, as measured in this study, of 3 mm occupying a huge space in the brain cavity, i.e. more than half the length of the skull, personal data and see Figure 1. This is only half the size of the smallest ruminant for a body mass difference of an order of magnitude. On the other side of the spectrum the BL of the Indian elephant, the second largest land mammal with a body mass of about 4,000 kg, measures only about 22 mm (personal data), occupying a tiny space in the enormous one meter long skull of the animal. As hypothesized in ref. [40], the thin mammalian tympanic membrane of large mammals does not grow very large to prevent breakage imposing a constraint on the size of the middle ear ossicles. There may thus be a cascade effect preventing the inner ear and thus the BL in becoming very large in very large species. As hypothesized in ref. [16], the allometry linking the BL to the petrosal bone, to the skull and ultimately to body mass may impose constraints on the size and shape of the whole auditory region.

This study is a preliminary approach to the scaling relationships of the BL in ruminants. Further investigation will use three-dimensional morphometric data, see ref. [21] and centroid size of the BL to explore the relationship in more detail. Analyses at the level of the clade as well as within the clade at the level of the different families will be carried out to check if different allometric relationships are similar or not. In addition, the inclusion of extinct members down to the origin of the clade as a whole may bring more insights into the morphological evolution of the bony labyrinth. Here, the precise tomographic imaging with the necessary contrast is a prerequisite. The advanced CT-system nanotom<sup>®</sup> m is perfectly suited for such high-precision studies, see e.g. refs. [41-43].

#### 4. CONCLUSIONS

Advanced laboratory-based high-resolution computed tomography systems are well suited to yield three-dimensional data of dozens of species. In this study, we analyzed 77 species of ruminants, for which the bony labyrinth was non-destructively extracted. Both the body mass and the skull length were gathered for the 77 species and correlated with the measurement of bony labyrinth length. A strong negative evolutionary allometry relates the parameters indicating that the bony labyrinth is relatively larger in smaller species and vice versa. This result was expected from previous studies that had shown both a negative ontogenetic allometry relating bony labyrinth length to skull length and a negative evolutionary allometry relating bony labyrinth length to petrosal bone length. Previous investigation of the size of the semi-circular canals plotted against body mass in mammals also came to this conclusion. Our results show that an early timing of ossification of the bony labyrinth is necessary to achieve the negative ontogenetic and evolutionary allometries. The latter are thus critical in the evolution of the diversified hearing and locomotor capacities of mammals.

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## REFERENCES

- [1] Klingenberg, C. P., "Size, shape, and form: concepts of allometry in geometric morphometrics," *Dev. Genes Evol.* **226**, 113-137 (2016).
- [2] Damuth, J., "Scaling of Growth: Plants and animals are not so different," *Proc. Natl. Acad. Sci. USA* **98**(5), 2113-2114 (2001).
- [3] Klingenberg, C. P., "There's something afoot in the evolution of ontogenies," *BMC Evol.Biol.* **10**, 2212010a (2010).
- [4] Pélabon, C., Firmat, C., Bolstad, G. H., Voje, K. L., Houle, D., Cassara, J., Rouzic, A. L., and F., H. T., "Evolution of morphological allometry," *Ann. N. Y. Acad. Sci.* **1320**, 58-75 (2014).
- [5] Peters, R. H., [The ecological implications of body size] Cambridge University Press, (1983).
- [6] Luo, Z. X., "Developmental patterns in Mesozoic evolution of mammal ears," *Annu. Rev. Ecol. Evol. S.* **42**, 355-380 (2011).
- [7] Spoor, F., Garland, T. J., Krovitz, G., Ryan, T. M., Silcox, M. T., and Walker, A., "The primate semicircular canal system and locomotion," *Proc. Natl. Acad. Sci. USA* **104**, 10808-10812 (2007).
- [8] Wilson, L. A. B., and R., S.-V. M., "Diversity trends and their ontogenetic basis: an exploration of allometric disparity in rodents," *Proc. R. Soc. London B Biol. Sci.* **277**, 1227-1234 (2010).
- [9] Wilson, L. A. B., "Allometric disparity in rodent evolution," *Ecol. Evol.* **3**(4), 971-984 (2013).
- [10] McGrosky, A., Codron, D., Müller, D. W. H., Navarrete, A., Isler, K., Hofmann, R. R., and Clauss, M., "Gross intestinal morphometry and allometry in ruminants," *J. Morphol.* **280**(9), 1254-1266 (2019).
- [11] Klingenberg, C. P., "Evolution and development of shape: integrating quantitative approaches," *Nat. Rev. Genet.* **11**, 623-635 (2010).
- [12] Sánchez-Villagra, M. R., [Embryos in deep time: the rock record of biological development] University of California Press, Berkeley and Los Angeles(2012).
- [13] Csiki-Sava, Z., Vremir, M., Jin Meng, J., Brusatte, S. L., and Norell, M. A., "Dome-headed, small-brained island mammal from the Late Cretaceous of Romania," *Proc. Natl. Acad. Sci. USA* **115**(19), 4857-4862 (2018).
- [14] Costeur, L., Schulz, G., and Müller, B., "High-resolution X-ray computed tomography to understand ruminant phylogeny," *Proc. SPIE* **9212**, 921216 (2014).
- [15] Costeur, L., Mennecart, B., Khimchenko, A., Müller, B., and Schulz, G., "Innervation of the cow's inner ear derived from micro-computed tomography," *Proc. SPIE* **10391**, 103911I (2017).
- [16] Billet, G., Muizon, C., Schellhorn, R., Ruf, I., Ladevèze, S., and Bergkvist, L., "Petrosal and inner ear anatomy and allometry amongst specimens referred to *Litopterna* (Placentalia)," *Zool. J. Linn. Soc.* **173**, 956-987 (2015).
- [17] Costeur, L., Mennecart, B., Müller, B., and Schulz, G., "Middle ear bones of a mid-gestation ruminant foetus extracted from X-Ray computed tomography," *Proc. SPIE* **9967**, 99671Q (2016).
- [18] Costeur, L., Mennecart, B., Müller, B., and Schulz, G., "Prenatal growth stages show the development of the ruminant bony labyrinth and petrosal bone," *J. Anat.* **230**, 347-353 (2017).
- [19] Costeur, L., Valli, A. M., Beaudouin, C., and Mennecart, B., "On some ruminant petrosal bones and their bony labyrinth from Senèze (Villafranchian, France)," *Rev. Paléobiol.* **32**(2), 443-456 (2018).
- [20] Mennecart, B., Rössner, G. E., Métais, G., DeMiguel, D., Schulz, G., Müller, B., and Costeur, L., "The petrosal bone and bony labyrinth of early to middle Miocene European deer (Mammalia, Cervidae) reveal their phylogeny," *J. Morphol.* **277**(10), 1329-1338 (2016).
- [21] Mennecart, B., DeMiguel, D., Bibi, F., Rössner, G. E., Métais, G., Neenan, J. M., Wang, S., Schulz, G., Müller, B., and Costeur, L., "Bony labyrinth morphology clarifies the origin and evolution of deer," *Sci. Rep.* **7**, 13176 (2017).

- [22] Mennecart, B., and Costeur, L., "Shape variation and ontogeny of the ruminant bony labyrinth, an example in Tragulidae," *J. Anat.* **229**(3), 422-435 (2016).
- [23] Nowak, R. M., [Walker's Mammals of the World.] The John Hopkins University Press, London and Baltimore(1999).
- [24] Kingdon, J., and Hoffmann, M., [Mammals of Africa] Bloomsbury Publishing, London(2013).
- [25] Welker, K. L., Orkin, J. D., and Ryan, T. M., "Analysis of intraindividual and intraspecific variation in semicircular canal dimensions using high-resolution x-ray computed tomography," *J. Anat.* **215**(4), 444-451 (2009).
- [26] Osipov, B., Harvati, K., Nathana, D., Spanakis, K., Karantanas, A., and Kranioti, E. F., "Sexual dimorphism of the bony labyrinth: a new age-independent method," *Am. J. Phys. Anthropol.* **151**(2), 290-301 (2013).
- [27] Snively, E., and Theodor, J. M., "Common Functional Correlates of Head-Strike Behavior in the Pachycephalosaur *Stegoceras validum* (Ornithischia, Dinosauria) and Combative Artiodactyls," *PLoS ONE* **6**(6), e21422 (2011).
- [28] Sansalone, G., Colangelo, P., Kotsakis, T., Loy, A., Castiglia, R., Bannikova, A. A., Zemlemerova, E. D., and Piras, P., "Influence of Evolutionary Allometry on Rates of Morphological Evolution and Disparity in strictly Subterranean Moles (Talpinae, Talpidae, Lipotyphla, Mammalia)," *J. Mammal.* **25**(1), 1-14 (2017).
- [29] Brombacher, A., Wilson, P. A., Bailey, I., and Ezard, T. H. G., "The Breakdown of Static and Evolutionary Allometries during Climatic Upheaval," *The Am. Nat.* **190**(3), 350-362 (2017).
- [30] du Toit, J., "Home range—body mass relations: a field study on African browsing ruminants," *Oecologia* **85**, 301-303 (1990).
- [31] Gordon, I. J., Illiust, A. W., and Milne, J. D., "Sources of variation in the foraging efficiency of grazing ruminants," *Funct. Ecol.* **10**, 219-226 (1996).
- [32] Van Soest, P. J., "Allometry and Ecology of Feeding Behavior and Digestive Capacity in Herbivores: A Review," *Zoo Biol.* **15**, 455-479 (1996).
- [33] Hudson, R. J., and White, R. G., [Bioenergetics of wild herbivores] CRC Press, Boca Raton(1985).
- [34] Clauss, M., Steuer, P., Müller, D. W. H., Codron, D., and Hummel, J., "Herbivory and Body Size: Allometries of Diet Quality and Gastrointestinal Physiology, and Implications for Herbivore Ecology and Dinosaur Gigantism," *PLoS ONE* **8**(10), e68714 (2013).
- [35] Legendre, S., "Les communautés de mammifères du Paléogène (Eocène supérieur et Oligocène) d'Europe occidentale: Structures, milieux et évolution," *Münch. Geowiss. Abh.* **A16**, 1-110 (1989).
- [36] Janis, C. M., [Correlation of cranial and dental variables with body size in ungulates and macropodids] Cambridge University Press, (1990).
- [37] Cardini, A., and Polly, P. D., "Larger mammals have longer faces because of size-related constraints on skull form," *Nat. Commun.* **4**, 2458 (2013).
- [38] Wagner, G. P., and Schwenk, K., [Evolutionarily Stable Configurations: functional integration and the evolution of phenotypic stability] Springer, (2000).
- [39] Lambert, F. M., Beck, J. C., Baker, R., and Straka, H., "Semicircular Canal Size Determines the Developmental Onset of Angular Vestibuloocular Reflexes in Larval *Xenopus*," *J. Neurosci.* **28**(32), 8086–8095 (2008).
- [40] Nummela, S., "Scaling of the mammalian middle ear," *Hear. Res.* **85**(1-2), (1995).
- [41] Vöggtlin, C., Schulz, G., Deyhle, H., Jäger, K., Liebrich, T., Weikert, S., and Müller, B., "Comparison of denture models by means of micro computed tomography," *Proc. SPIE* **8506**, 85061S (2012).
- [42] Vöggtlin, C., Schulz, G., Jäger, K., and Müller, B., "Comparing the accuracy of master models based on digital intra-oral scanners with conventional plaster casts " *Phys. Med.* **1**, 20-26 (2016).
- [43] Sacher, M., Schulz, G., Deyhle, H., Jäger, K., and Müller, B., "Comparing the accuracy of intraoral scanners, using advanced micro computed tomography," *Proc. SPIE* **11113**, 111131Q (2019).