

## On some ruminant petrosal bones and their bony labyrinth from Senèze (Villafranchian, France)

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### Abstract

We describe the petrosal bone and its associated bony labyrinth (the bony capsule for the inner ear which is the organ of balance and hearing) of five ruminant species of the emblematic lower Pleistocene French locality Senèze. They include two deer (Cervidae) *Eucladoceros ctenoides senezensis* and *Metacervoceros rhenanus philisi* and three bovids (Bovidae), the bovine *Leptobos (Smertiobos) etruscus*, the antilopine *Gazellospira torticornis* and the caprine *Gallogoral meneghini*. We find new morphological characters of both the petrosal bone and the labyrinth that help distinguish between both ruminant families. They relate to the overall shape of the petrosal bone and to specific areas of the bony labyrinth such as the vestibular aqueduct and endolymphatic sac or the lateral semi-circular canal. It confirms previous observations published recently on deer and tragulids (mouse-deer and chevrotains), and adds bovids to our understanding of this structure. This is only a partial study for Senèze since 6 other ruminant taxa are known from there, but it serves as a preliminary work aiming at more often integrating the petrosal bone and bony labyrinth, now easily available using 3D imaging techniques, into taxonomical and phylogenetic studies.

### Keywords

Ruminantia, Cervidae, Bovidae, inner ear, phylogeny, Pleistocene.

### Résumé

**Description de pétreaux de ruminants et de leurs labyrinthes osseux de Senèze (Villafranchien, France).** - Nous décrivons la portion pétreuse de l'os temporal et le labyrinthe osseux associé de cinq espèces de ruminants de la localité française emblématique du pléistocène inférieur de Senèze. Sont inclus dans cet article deux cerfs (Cervidae) *Eucladoceros ctenoides senezensis* et *Metacervoceros rhenanus philisi* ainsi que trois Bovidae: le boviné *Leptobos (Smertiobos) etruscus*, l'antilopiné *Gazellospira torticornis* et le capriné *Gallogoral meneghini*. Nous mettons en évidence des nouveaux caractères qui permettent de distinguer les deux familles de ruminants étudiées. La forme générale du pétreaux et des zones spécifiques du labyrinthe osseux comme l'aqueduc vestibulaire, le sac endolymphatique ou encore le canal semi-circulaire latéral sont particulièrement informatives. Notre étude confirme des observations publiées récemment sur les cerfs et les Tragulidae (chevrotains), et ajoute les Bovidae à notre compréhension croissante de ces structures. Six autres ruminants non étudiés ici sont connus à Senèze, mais cette étude préliminaire contribue à installer le pétreaux et le labyrinthe osseux dans les études anatomiques et paléontologiques classiques grâce à l'imagerie 3D qui les rend plus facilement accessibles.

### Mots-clés

Ruminantia, Cervidae, Bovidae, oreille interne, phylogénie, Pléistocène.

## 1. INTRODUCTION

With 40 mammal species, Senèze is one of the richest localities of the European Villafranchian and serves as a reference fauna for the biochronological timescale of the European Pleistocene as reference for biozone MNQ18 (Guérin, 2007). The faunal assemblage comes from sediments in a volcanic maar setting where often complete specimens in connexion were found. New

<sup>40</sup>Ar/<sup>39</sup>Ar datings on the abundant volcanic sediments indicate an age bracketed between 2.21 and 2.09 Ma (Pastre *et al.*, 2015). To date 11 species of ruminants are known from this locality including four deer (Cervidae): *Cervalces gallicus* (Azzaroli, 1952), *Eucladoceros ctenoides senezensis* Heintz, 1970, *Metacervoceros rhenanus philisi* (Schaub, 1941 or *M. rhenanus* Dubois, 1904), and *Croizetoceros ramosus minor* Heintz, 1970, and seven bovids (Bovidae): *Leptobos (Smertiobos)*

*etruscus* (Falconer, 1859), *Leptobos* (*Leptobos*) *furtivus* Duvernois, 1989, *Gallogoral meneghinii* (Rütimeyer, 1878), *Gazellospira torticornis* (Aymard, 1854), *Procamptoceros brivatense* Schaub, 1923, *Pliotragus ardeus* (Depéret, 1883), *Megalovis latifrons* Schaub, 1923, and *Ovis* sp. (see up to date faunal list in Delson *et al.*, 2006). The generic, specific or subspecific status of many of the above-mentioned taxa is still discussed, mostly in the framework of biochronological studies in the Pleistocene (e.g., see Kostopoulos & Athanassiou, 2005; Croitor, 2006, 2014; Valli & Palombo, 2005 for the specific status of *Metacervoceros rhenanus philisi*; Duvernois & Guérin, 1989; Duvernois, 1990; Garrido, 2008; Andrés Rodrigo *et al.*, 2010; Masini *et al.*, 2013 for the status of *Leptobos etruscus*; Crégut-Bonnoure, 2007 or Bellucci & Sardella, 2015 for the time range of *Gazellospira torticornis*).

While antlers or horns, teeth, skulls, and postcranial material have usually been described for ruminants in Senèze (e.g., Schaub, 1941; Guérin, 1965; Heintz, 1970; Duvernois & Guérin, 1989; Duvernois, 1990; Crégut-Bonnoure, 2006, 2007; Crégut-Bonnoure & Guérin, 1996; Delpech & Guérin, 1996), no single petrosal bone has ever raised interest despite its known relevance in phylogenetic studies (e.g., Webb & Taylor, 1980; O'Leary, 2010). The bony labyrinth, which is embedded within the petrosal bone, is the bony capsule for the inner ear, the organ of balance and hearing. It long remained vastly unknown for ruminants, both extant and extinct, and recent studies have started to show how significant it could be for phylogenetic analyses (Costeur, 2014; Mennecart & Costeur, 2016a, b; Mennecart *et al.*, 2016; Costeur *et al.*, 2017). With many thousand specimens recovered, Senèze has yielded the whole skeleton of many large mammal species and often isolated petrosal bones exist for many of them.

Very little comparative data on ruminant, either extant or extinct, petrosal bones and bony labyrinths have been published probably because of the difficulty in accessing this bone embedded in the cranial cavity and sometimes not easily identifiable when found isolated. O'Leary (2010) unprecedentedly described detailed and precious morphological data for some extant and one ruminant petrosal bones, but again in a limited sample of 9 taxa, adding data to Webb & Taylor's (1980), Guadelli's (1999), and Mallet & Guadelli's (2013) samples of recent and fossil taxa. Previous attempts at describing the morphology of the bony labyrinth in ruminants occurred in the late 19th and early 20th century (Hyrtl, 1845; Doran, 1878; Gray, 1907, 1908). They are pioneering and seminal works but comparatively contributed little to our knowledge of these structures in ruminants with less than 10 modern species investigated out of more than 200 existing. Before recent works by our team (Costeur, 2014; Mennecart & Costeur, 2016a, b; Mennecart *et al.*, 2016), no single bony labyrinth in a fossil ruminant had ever been studied and only a handful of artiodactyl bony labyrinths were known (e.g., Hürzeler, 1936;

Theodor, 2010; Orliac *et al.*, 2012, 2017). This is thus only the beginning of a deeper knowledge of ruminant petrosal bones and bony labyrinths that allows these phylogenetically relevant structures to be included in more comprehensive studies on the evolutionary study of the group.

With the help of non-invasive imaging techniques, which have encountered a rapid development in the last 20 years enabling the digital reconstruction of otherwise hidden structures, we describe here five petrosal bones and bony labyrinths from five fossil ruminant species from Senèze. This adds morphological data to the description of the deer *Eucladoceros ctenoides senezensis* and *Metacervoceros rhenanus philisi* and of the bovids *Leptobos* (*Smertiobos*) *etruscus*, *Gazellospira torticornis* and *Gallogoral meneghinii*. We hope these data will serve for future research in ruminant phylogeny.

## 2. MATERIAL AND METHODS

Table 1 lists the specimens described in this study with scanning information. They all come from the collection of the Natural History Museum Basel (hereafter NMB) and represent only a subset of the ruminant species known from Senèze because the petrosal bone was not found for several of them. We CT-scanned the petrosal bones at the Biomaterials Science Center in Basel (University Basel) using a Phoenix Nanotom® (General Electric Wunstorf, Germany) equipped with a 180 kV / 15 W nanofocus X-ray source. Scanning resolution (Table 1) varies from 35 µm to 55 µm but this has no influence on the final renderings and on measurements taken. The bony labyrinths were segmented using AVIZO 7.0 and AVIZO LITE 9.0 (FEI Visualization Group). Nomenclature follows O'Leary (2010) for the petrosal bone, and Orliac *et al.* (2012) and Costeur (2014) for the bony labyrinths. The identification of isolated petrosal bones can prove difficult because of the lack of comparative material and of studies that have described some. The present material was identified thanks to associated identifiable cranial specimens like teeth or cranial appendages. Senèze is known for the preservation of complete specimens and the isolated petrosals are often the product of broken skulls that were found in pieces but all in the vicinity to each other so that all isolated petrosal bones could be attributed to tooth or cranial material, which made their identification easy.

Nomenclature at higher taxonomic levels such as subfamily or tribe follows Groves & Grubb (2011).

### Abbreviations for the bony labyrinth

**aa**, asc ampulla; **asc**, anterior semi-circular canal; **ca**, cochlear aqueduct; **cc**, common crus; **co**, cochlea; **es**, endolymphatic sac; **fc**, *fenestra cochleae*; **fv**, *fenestra vestibuli*; **la**, lsc ampulla; **lsc**, lateral semi-circular canal; **pa**, psc ampulla; **psc**, posterior semi-circular canal; **sac**,

Table 1: Linear, volumetric, angular, and scanning data for the bony labyrinths of the five specimens described in this study. ASC, anterior semi-circular canal; PSC, posterior semi-circular canal; LSC, lateral semi-circular canal.

	<i>E. ctenoides</i> <i>senezensis</i>	<i>M. rhenanus</i> <i>philisi</i>	<i>L. etruscus</i>	<i>G. torticornis</i>	<i>G. meneghinii</i>
specimen number	NMB Se.1797	NMB Se.583	NMB Se.1712	NMB Se.1704	NMB Se.313
scanning resolution (µm)	45	45	35	55	45
number of cochlear turns	2.25	2.50	2.50	2.50	2.25
volume (mm <sup>3</sup> )	135.0	113.6	88.0	145.6	136.6
stapedial ratio	2.00	1.64	1.74	-	1.90
cochlear aspect ratio	0.51	0.50	0.55	0.47	0.48
ASC height (mm)	5.18	4.78	4.91	6.84	6.64
ASC width (mm)	5.08	4.60	5.19	5.96	5.75
PSC height (mm)	4.81	4.40	4.57	5.32	5.26
PSC width (mm)	4.60	4.40	4.19	5.67	5.37
LSC length (mm)	4.28	4.12	4.11	4.70	4.96
LSC width (mm)	5.04	4.51	3.93	4.95	5.30
angle ASC-PSC (°)	85	89	84	90	83
angle ASC-LSC (°)	81	70	71	86.5	78
angle PSC-LSC (°)	88	85	86	93.2	78

*sacculus*; **sl**, secondary bony lamina; **ut**, *utricle*; **va**, vestibular aqueduct.

### 3. RESULTS

#### Systematics

Order Artiodactyla Owen, 1848  
Family Cervidae Goldfuss, 1820  
Subfamily Cervinae Goldfuss, 1820

#### *Eucladoceros ctenoides senezensis* Heintz, 1970

**Material:** NMB Se 1797

#### Petrosal bone (Fig 1a, b)

The petrosal bone has an overall elongated shape and its apex is here broken but it is pointy in another specimen not described here (NMB Se. 557). Both conditions are as in *Cervus elaphus* Linnæus, 1758 (O'Leary, 2010) or *Odocoileus virginianus* (Zimmermann, 1780) (Costeur, 2014) and unlike in bovids where the overall shape is more massive and compact.

**Lateral surface (Fig. 1a):** The promontorium has a hemi-ellipsoid shape. The epitympanic wing is present but limited in extent anteriorly. Its apex is pointy. A transpromontorial sulcus cannot be observed as in *Cervus elaphus* and *Odocoileus virginianus* (O'Leary, 2010) although this condition may occur on some specimens of the latter indicating the variability of this character (Costeur, 2014).

The *fenestra cochleae* (i.e., round window) is not very big and is separated from the *fenestra vestibuli* (i.e., oval window) by a large and smooth *crista interfenestralis*. The fossa for the tensor tympani muscle is ellipsoid in shape and does not excavate the tegmen tympani. It does compress the promontorium laterally. The contact to the posterior bulla is prominent and forms a sharp blade running next to the posterior part of the promontorium. The secondary facial foramen is well visible and forms a large hole lateral to the oval window. The stapedial muscle fossa is a small and rather deep hole and lies posterior to the oval window. The tegmen tympani, constituting the roof of the tympanic cavity on the rostral surface (*facies rostralis*) of the petrosal bone, is large in size and recalls the condition seen in *Cervus elaphus* in its extent (O'Leary, 2010) more than in *Odocoileus virginianus* (Costeur, 2014) although its anterior process is less blunt than in *Cervus* and is here sharper. The tegmen tympani forms a straight wall on the rostral surface of the petrosal extending posteriorly to the level of the facial sulcus. Its anterior process (*sensu* O'Leary, 2010) lies well below the level of the apex of the petrosal. The *hiatus Fallopii* is a small hole at the anterior of the tegmen tympani on the rostral surface and is ventrally positioned.

**Medial surface (Fig. 1b):** No prefacial commissure fossa (*sensu* O'Leary, 2010) is visible. The internal acoustic meatus is broad and occupies a large space of the *pars cochlearis*. The visible *foramina acustica* (*superius* and *inferius*) are large openings separated by a sharp *crista transversa*. An incipient basicapsular groove seems to occupy the flange between the medial and lateral surfaces.

The *fossa cerebellaris* containing the subarcuate fossa, is elongated and shallow, but deeper than in the bovids described below (*Gazellospira* and *Gallogoral*). The cochlear aqueduct opens ventrally posterior to the level of the internal acoustic meatus. It is an elongated hole. The opening for the vestibular aqueduct is situated below that for the cochlear aqueduct at the level of the middle part of the *fossa cerebellaris* containing the subarcuate

fossa. It lies far away posteriorly (not laterally) from the internal acoustic meatus attesting to the long and straight vestibular aqueduct (see Fig. 1c, d). The mastoid region is well preserved, elongated and wedge-like in shape.

**Bony labyrinth (Fig. 1c, d)**

Measurements are given in Table 1. The cochlea completes 2.25 turns. It is well detached from the vestibule. Both

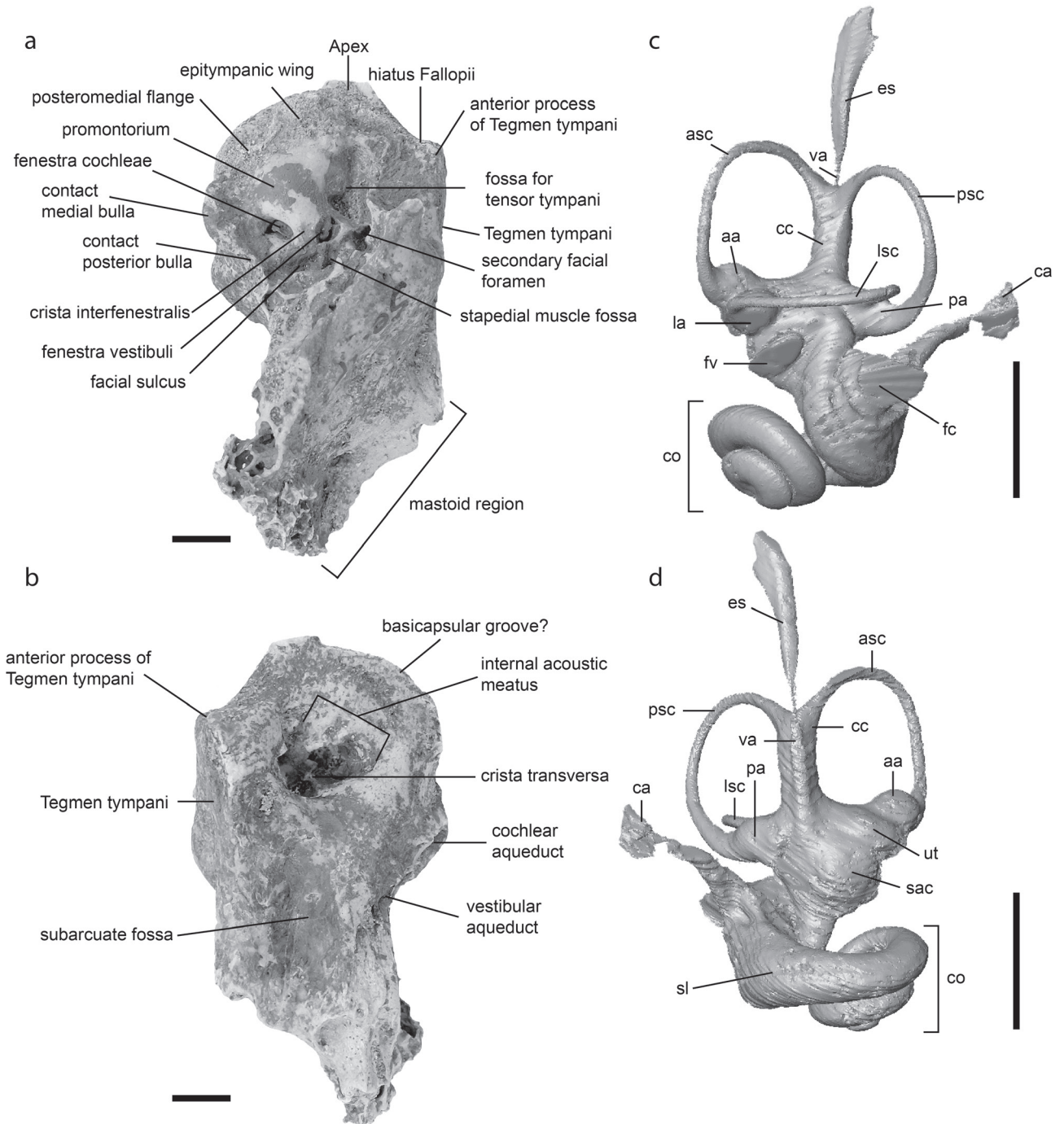


Fig. 1: Left petrosal bone and digital reconstruction of the bony labyrinth of the deer *E. teneoides senezensis* from Senèze (specimen NMB Se. 1797). a, lateral view of the petrosal bone. b, medial view of the petrosal bone. c, posterolateral view of the bony labyrinth. d, anteromedial view of the bony labyrinth. See text for abbreviations. Scale bars: 5 mm.

turns are of similar thickness, the second one being only slightly thinner. The aspect ratio (total height divided by total width) is 0.51 classifying the cochlea as a low cochlea (*sensu* Gray, 1907, 1908) in comparison to high cochleas in tragulids characterized by a higher number of turns making it more conical in side view (Mennecart & Costeur, 2016a, b). The cochlear aqueduct is long, rather flat in diameter, and mostly straight to slightly posteriorly curved. The secondary bony lamina is visible over about a quarter of the basal turn. Both *fenestrae* are clearly reconstructed. The *fenestra cochleae* is quite dorsally positioned, almost at the level of the *fenestra vestibuli*. The latter is very ellipsoid in shape with a stapedial ratio of 2, being thus twice as long as large. On the vestibule, both the *utricle* and *sacculus* are well defined (Fig. 1d), the latter being rounded in shape. The anterior semi-circular canal is the most dorsally expanded canal although not extremely more than the posterior semi-circular canal; it expands above the level of the common crus as does the posterior semi-circular canal but to a lesser extent. The common crus is broad. The lateral semi-circular canal is straight. It branches in the posterior ampulla slightly dorsally, a typical characteristic of cervid bony labyrinths (Mennecart *et al.*, 2016). The vestibular aqueduct is broad too and forms a straight canal running close to the common crus. It originates at its base, in the dorsalmost extent of the *sacculus*, and is aligned with its midline such as in most deer where it is known (Mennecart *et al.*, 2016). It is longer than the common crus. The endolymphatic sac at the end of the vestibular aqueduct is a thin, long, and funnel-shape structure, slightly undulating and ending largely above the dorsal extent of the anterior and posterior semi-circular canals. This explains why its opening on the petrosal bone is positioned far posteriorly from the internal acoustic meatus.

#### *Metacervocerus rhenanus philisi* (Schaub, 1941)

**Material:** NMB Se 583

#### **Petrosal bone (Fig. 2a, b)**

The petrosal bone shares several characteristics with that of *Eucladoceros*. It has an overall elongated shape and its apex is pointy as in *Cervus elaphus* (O'Leary, 2010) or *Odocoileus virginianus* (Costeur, 2014) and again unlike in bovids.

**Lateral surface (Fig. 2a):** The promontorium has a hemi-ellipsoid shape. The epitympanic wing is present but large anteriorly and prolonged by a broad posteromedial flange. A transpromontorial sulcus cannot be observed. The *fenestra cochleae* (i.e., round window) is not bigger than the *fenestra vestibuli* (i.e., oval window) and separated from it by a large *crista interfenestralis*. The fossa for the tensor tympani muscle is round in shape and does not excavate the tegmen tympani. It extends laterally above the oval window. The contact to the posterior

bulla is prominent like in *Eucladoceros* and forms here too a sharp blade running next to the posterior part of the promontorium. The contact to the medial bulla is a high elongated zone running parallel to the edge of the posteromedial flange of the petrosal, somehow creating a groove that could be mistaken with a basicapsular groove. The secondary facial foramen is well visible and forms a hole posterolaterally to the oval window. The stapedial muscle fossa is not well visible because of a preservation problem that created some breakage in the area of the facial sulcus. The tegmen tympani is wide and not very long, contrary to the bovids described below. It recalls the condition seen in *Cervus elaphus* in its extent (O'Leary, 2010). Its anterior process is blunt (*sensu* O'Leary, 2010), rounded in shape and little protruding. It lies well below the level of the apex of the petrosal, even more posteriorly than in *Eucladoceros*. The *hiatus Fallopii* is a very large, ventrally positioned, hole at the anterior of the tegmen tympani.

**Medial surface (Fig. 2b):** No prefacial commissure fossa (*sensu* O'Leary, 2010) is visible. The internal acoustic meatus is broad and occupies a large space of the *pars cochlearis*. Both *foramina acusticus (superius and inferius)* are large openings. A flatter area running parallel to the anterior and ventral edge of the petrosal could be the trace of the basicapsular groove. The *fossa cerebellaris* containing the subarcuate fossa is rather small when compared to that in *Eucladoceros*. It is shallow as in all ruminants (O'Leary, 2010), but deeper than in the bovids described below (*Gazellospira* and *Gallogoral*). The cochlear aqueduct opens ventrally at the level of the internal acoustic meatus. It is a rather large rounded hole. The rather large opening for the vestibular aqueduct is situated well below that for the cochlear aqueduct at the level of the middle part of the *fossa cerebellaris* as in *Eucladoceros*. It lies away posteriorly (not laterally) from the internal acoustic meatus attesting to the long and straight vestibular aqueduct (see Fig. 2c, d) exactly like in *Eucladoceros*. The mastoid region is well preserved, elongated and wedge-like in shape, such as in most ruminants (O'Leary, 2010).

#### **Bony labyrinth (Fig. 2c, d)**

Measurements are given in Table 1. The cochlea completes 2.5 turns. It is well detached from the vestibule and similar to that of *Eucladoceros*. The aspect ratio (total height divided by total width) is 0.5 attesting to a low cochlea (*sensu* Gray, 1907, 1908). The cochlear aqueduct is thick and rather short, much shorter than in *Eucladoceros*, but ontogeny can play a role here (see Costeur *et al.*, 2017). It has a circular diameter and takes a slight bend at mid-course. The secondary bony lamina is hardly visible but seems to run over about a quarter of the basal turn. The *fenestra cochleae* faces slightly laterally. The *fenestra vestibuli* is much less ellipsoid in shape than in *Eucladoceros* with a stapedial ratio of 1.64. On the vestibule, both the *utricle* and *sacculus* are well defined

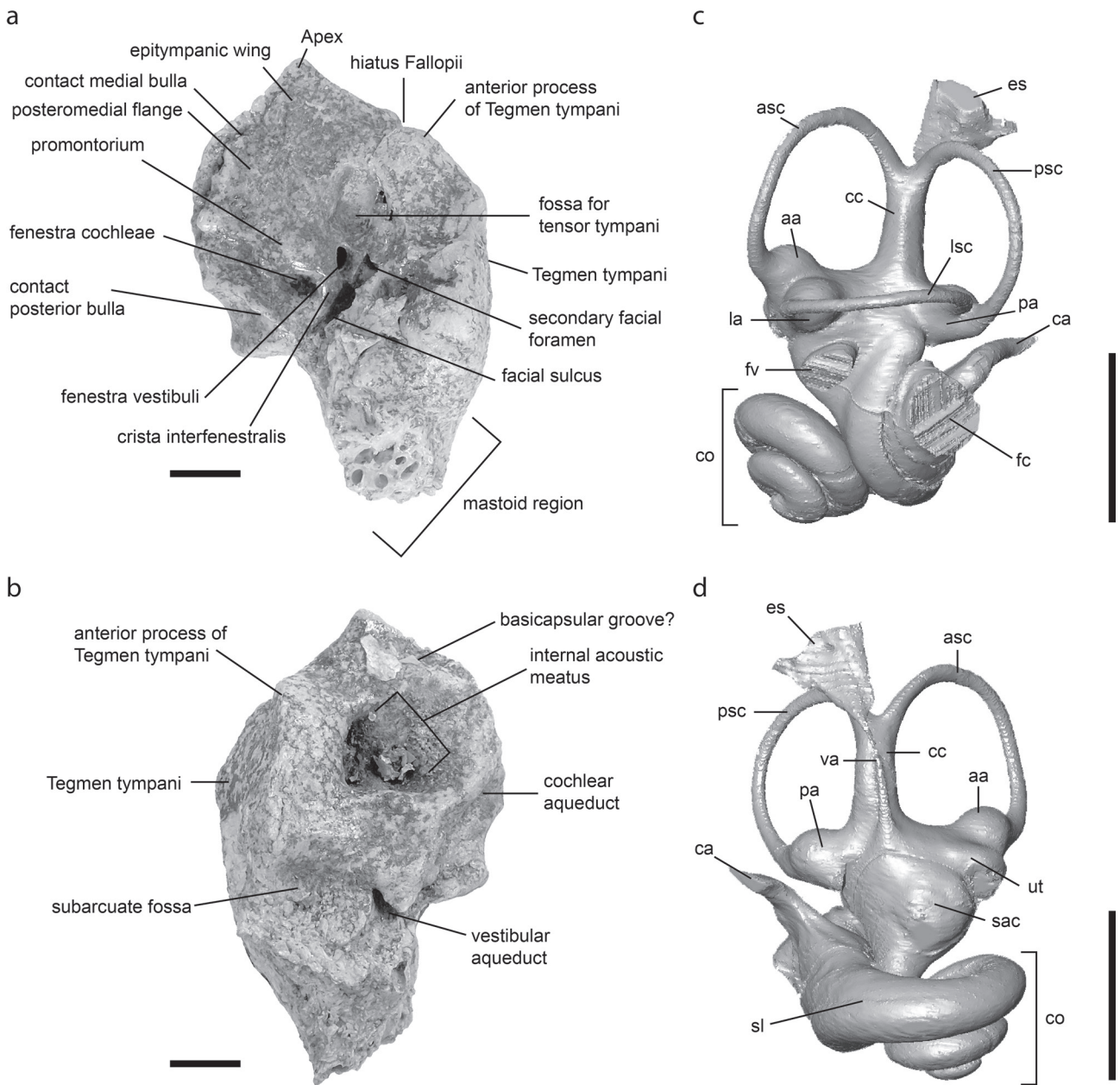


Fig. 2: Left petrosal bone and digital reconstruction of the bony labyrinth of the deer *M. rhenanus philisi* from Senèze (specimen NMB Se. 583). a, lateral view of the petrosal bone. b, medial view of the petrosal bone. c, posterolateral view of the bony labyrinth. d, anteromedial view of the bony labyrinth. See text for abbreviations. Scale bars: 5 mm.

and look as in *Eucladoceros* (Fig. 2d); the *sacculus* being rounded in shape here too. The anterior semi-circular canal is the most dorsally expanded canal; it expands above the level of the common crus as does the posterior semi-circular canal but to a lesser extent. Both canals are smaller than in *Eucladoceros*. The common crus is broad. The lateral semi-circular canal is straight. It branches clearly within the posterior ampulla, again a typical characteristic of cervid bony labyrinths (Mennecart *et al.*, 2016). The vestibular aqueduct is a broad canal that

runs along the length of the common crus, being almost attached to it. It is slightly bent and thus not as straight as in *Eucladoceros*, which is not very typical for deer where it is often straight (Mennecart *et al.*, 2016). It originates at the base of the common crus, here again at the level of the dorsalmost extent of the *sacculus*. Its length is similar as that of the common crus. The endolymphatic sac at the end of the vestibular aqueduct is broad and triangular in shape and ends just above the dorsal extent of the anterior and posterior semi-circular canals.

Family Bovidae Gray, 1821  
 Subfamily Bovinae Gray, 1821

***Leptobos (Smertiobos) etruscus* (Falconer, 1859)**

**Material:** NMB Se 1712

**Petrosal bone (Fig. 3a, b)**

The surface of petrosal bone on the *pars cochlearis* is slightly broken so that the promontorium is not complete. The petrosal has an overall massive and rounded shape, especially anteriorly, as in *Bos taurus* Linnaeus, 1758 (O’Leary, 2010), *Bos primigenius* and fossil *Bison* sp.

(Guadelli, 1999), or as in the following bovids described here *Gazellospira* and *Gallogoral*, and unlike the above mentioned cervids where it is longer anteriorly.

**Lateral surface (Fig. 3a):** The promontorium has a bulbous shape and is not elongated. The epitympanic wing is present but limited in extent anteriorly. Its apex is blunt. The posteromedial flange of the promontorium is present but not as expanded as in *Gallogoral* (see below and Fig. 5a). No transpromontorial sulcus is visible unlike in *Bos taurus* (O’Leary, 2010).

The *fenestra cochleae* (i.e., round window) is broken (a process that happened after the scan of the specimen, hence the well reconstructed *fenestra cochleae* on the

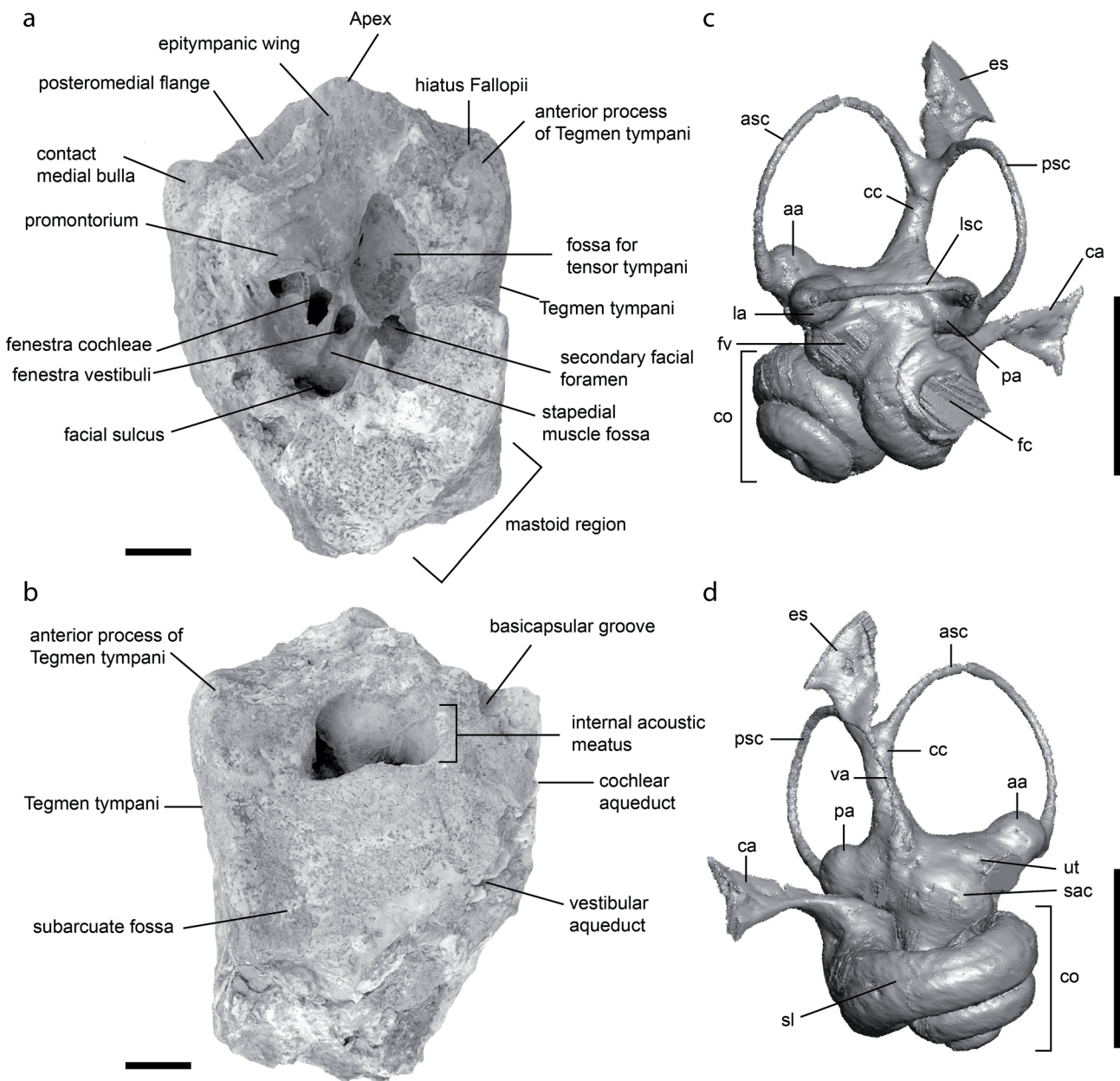


Fig. 3: Right petrosal bone and digital reconstruction of the bony labyrinth of the bovid *L. (Smertiobos) etruscus* from Senèze (specimen NMB Se. 1712, mirrored). a, lateral view of the petrosal bone. b, medial view of the petrosal bone. c, posterolateral view of the bony labyrinth. d, anteromedial view of the bony labyrinth. See text for abbreviations. Scale bars: 5 mm.

bony labyrinth). The *fenestra vestibuli* (i.e., oval window) is oval in shape like in all studied specimens. The fossa for the tensor tympani muscle is elongated and very large. It deeply excavates the *pars cochlearis* and the tegmen tympani, to a lesser extent though. The secondary facial foramen is a large pit lying directly posterior to the fossa for the tensor tympani muscle. The stapedial muscle fossa is small not very deep and lies posterior to the oval window. The tegmen tympani is large in size, very broad, but not inflated (O'Leary, 2010). Its anterior process, *sensu* O'Leary (2010), lies below the level of the apex of the petrosal. The anterior process is blunt in shape. The *hiatus Fallopii* is a small hole at the anterior of the tegmen tympani; it is less ventral than on the deer described before, being situated more at mid-width of the tegmen tympani.

**Medial surface (Fig. 3b):** No prefacial commissure fossa (*sensu* O'Leary, 2010) is visible. The internal acoustic meatus is very broad and occupies much of the *pars cochlearis*. Both *foramina acusticus* (*superius* and *inferius*) are very large openings separated by a thin and very internally positioned *crista transversa* (not visible on Fig. 3b). There is a well-defined deep basicapsular groove. The *fossa cerebellaris* containing the subarcuate fossa is very shallow. The cochlear aqueduct opens ventrally slightly posterior to the level of the internal acoustic meatus. The small opening for the vestibular aqueduct is circular in shape. It is a small pit situated below the opening of the cochlear aqueduct. The mastoid region is broad and clearly wedge-like in shape.

#### **Bony labyrinth (Fig. 3c, d)**

Measurements are given in Table 1. The cochlea completes 2.5 turns. It is large and massive and very close to the vestibule, contrary to all other specimens studied here, which is reminiscent to plesiomorphic stages in early pecoran ruminants (Mennecart *et al.*, 2016). The aspect ratio (total height divided by total width) is 0.55 classifying the cochlea at the limit between high and low cochleas (*sensu* Gray, 1907, 1908). It is close to the level reached by *Bos taurus* (0.57, pers. data based on published specimens from Costeur *et al.*, 2017). The cochlear spiral is tight and the second turn is much thinner than the basal turn. The cochlear aqueduct is long and thick; it flattens at mid-course as it bends. It ends in a large triangular-in-shape. The secondary bony lamina is visible over a quarter of the basal turn. Both *fenestrae* are nicely preserved. The *fenestra cochleae* is more posteriorly positioned than the *fenestra vestibuli*. The latter is ellipsoid in shape, intermediate between the very ellipsoid *Gallogoral* (stapedial ratio of 1.9 for the latter, see below, versus 1.74 in *Leptobos*) and *Metacervoceros* (stapedial ratio of 1.64, see above). On the vestibule, both the *utricle* and *sacculus* are well defined (Fig. 3d), the latter being oval in shape. The anterior semi-circular canal is by far the most dorsally expanded canal; it expands above the level of the common crus while the

posterior semi-circular canal extends only slightly above the latter. The common crus is rather thin, straight and not very long. The lateral semi-circular canal is straight. It branches at the level of the posterior ampulla, but not in it as seen in the deer, but rather in front of it in the vestibule. The vestibular aqueduct is a thin and slightly curved canal close to the common crus. It originates at the base of the common crus, slightly anteriorly. It is almost as long as the common crus. The endolymphatic sac at the end of the vestibular aqueduct is a broad and triangular in shape extending more dorsally than the anterior semi-circular canal.

Subfamily Antilopinae Gray, 1821

#### ***Gazellospira torticornis* (Aymard, 1854)**

**Material:** NMB Se 1704

#### **Petrosal bone (Fig. 4a, b)**

The petrosal bone has an overall massive and rounded shape, especially anteriorly, as in *Bos taurus* (O'Leary, 2010) and unlike most cervids where it is longer anteriorly (O'Leary, 2010; Costeur, 2014; Mennecart *et al.*, 2016). The petrosal bone was partly embedded in the matrix of the skull so that the lateral surface was more complicated to reconstruct. Some of the details are thus unavailable.

**Lateral surface (Fig. 4a):** The promontorium has a rounded shape and is not elongated. The epitympanic wing is present but limited in extent anteriorly. Its apex is smooth and blunt. The posteromedial flange of the promontorium is present but not as expanded as in *Gallogoral* (see below and Fig. 5a). An anteriorly positioned transpromontorial sulcus on the anteriormost part of the promontorium seems to be imprinted in the bone.

The *fenestra cochleae* (i.e., round window) is not very big and is separated from the *fenestra vestibuli* (i.e., oval window) by a small *crista interfenestralis*. The fossa for the tensor tympani muscle is oval and broad but does not excavate the tegmen tympani itself. It lies directly anterolaterally to the oval window. The secondary facial foramen is not well visible because of the reconstruction. The stapedial muscle fossa is small and lies posterior to the oval window. The tegmen tympani on the rostral surface is large in size, less than in *Gallogoral* (see below and Fig. 5), but not inflated (*sensu* O'Leary, 2010). It forms a straight wall on the rostral surface of the petrosal. Its anterior process, *sensu* O'Leary (2010), lies below the level of the apex of the petrosal. The anterior process is blunt in shape. The *hiatus Fallopii* is a small hole at the anterior of the tegmen tympani.

**Medial surface (Fig. 4b):** No prefacial commissure fossa (*sensu* O'Leary, 2010) is visible. The internal acoustic meatus is broad and occupies much of the *pars cochlearis*. Both *foramina acusticus* (*superius* and *inferius*) are large openings separated by a broad and flat *crista transversa*.

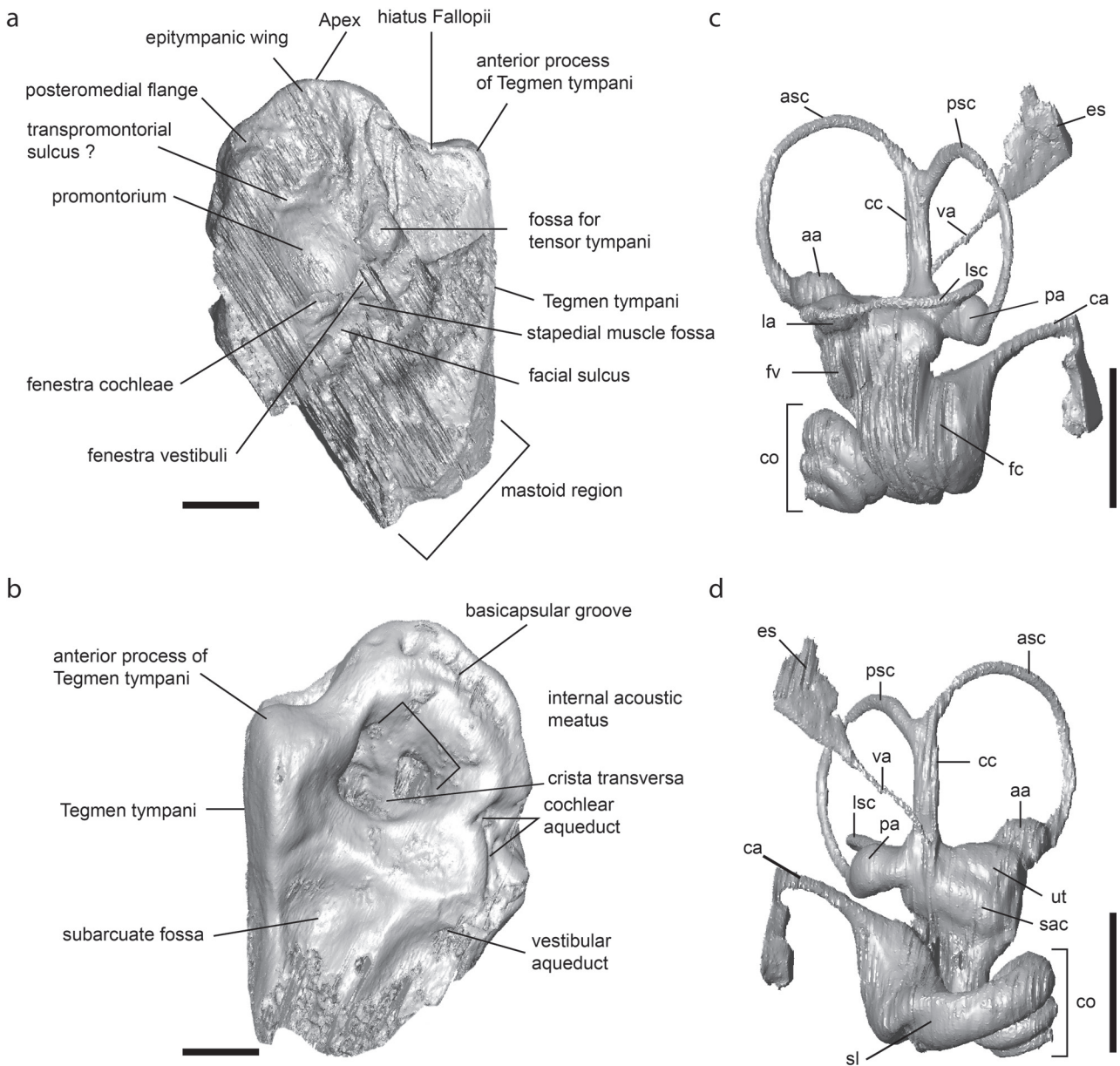


Fig. 4: Digital reconstructions of the left petrosal bone and bony labyrinth of the bovid *Gazellospira torticornis* from Senèze (specimen NMB Se. 1704). a, lateral view of the petrosal bone. b, medial view of the petrosal bone. c, posterolateral view of the bony labyrinth. d, anteromedial view of the bony labyrinth. See text for abbreviations. Scale bars: 5 mm.

There is a well-defined basicapsular groove occupying most of the anterior part of the medial surface. The *fossa cerebellaris* containing the subarcuate fossa is shallow but not particularly wide. The cochlear aqueduct opens ventrally almost at the level of the internal acoustic meatus. It is elongated and slit like to accommodate the bizarre end of the cochlear aqueduct of the bony labyrinth (see Fig. 4c, d). The thin and small opening for the vestibular aqueduct is situated just below at the level of the anteriormost part of the *fossa cerebellaris*, laterally with regards to the internal acoustic meatus. The mastoid region is not well preserved on this reconstruction but seems wedge-like in shape.

**Bony labyrinth (Fig. 4c, d)**

Measurements are given in Table 1. The cochlea completes 2.5 turns. It is reduced in extent compared to the overall size of the bony labyrinth. The aspect ratio (total height divided by total width) is 0.47 classifying the cochlea as a low cochlea (*sensu* Gray, 1907, 1908). The cochlear spiral is tight and the second turn is only slightly smaller than the basal turn, but is twice as thin. The cochlear aqueduct is long, thin and mostly straight to slightly posteriorly curved over its whole course. It ends in a bizarre anteriorly projecting pouch like structure that constitutes the thin slit-like opening visible on the medial surface of the petrosal bone. The secondary bony lamina

is hardly visible but seems to arise from an overlapping scala tympani part of the beginning basal turn. Both *fenestrae* are hardly visible because of the reconstruction problems. The *fenestra cochleae* seems more posteriorly positioned than the *fenestra vestibuli*. On the vestibule, both the *utriculus* and *sacculus* are well defined (Fig. 4d), the latter being ellipsoid in shape. The anterior semi-circular canal is the most dorsally expanded canal; it expands above the level of the common crus while the posterior semi-circular canal extends only slightly above the latter. The common crus is thin, straight and elongated. The lateral semi-circular canal is straight, being only slightly bent anteriorly close the posterior ampulla. It branches dorsally at the dorsalmost level of the posterior ampulla but in the vestibule in front of the latter like in *Tetracerus* or *Bos* (Costeur, 2014; Costeur *et al.*, 2017), a characteristic of bovid bony labyrinths when compared to deer (see above for a comparison, Figs 1 and 2, a-b). The vestibular aqueduct is a thin and straight canal detached from the common crus. It originates at the base of the common crus, aligned with its midline. It quickly diverges from the midline of the common crus as in most bovids where it is known (Costeur, 2014; Costeur *et al.*, 2017) and unlike in most deer (Mennecart *et al.*, 2016). It is short ending well before the end of the common crus dorsally. The endolymphatic sac at the end of the vestibular aqueduct is a thin and flat triangular structure ending at about the level of the anterior semi-circular canal.

Subfamily Caprinae Gill, 1872

***Gallogoral meneghenii* (Rütimeyer, 1878)**

**Material:** NMB Se313

**Petrosal bone (Fig. 5a, b)**

The petrosal bone has an overall massive and compact shape with no anterior expansion, much like in *Bos taurus* (O'Leary, 2010) and unlike most cervids as for *Gazellospira* (O'Leary, 2010; Costeur, 2014; Mennecart *et al.*, 2016).

**Lateral surface (Fig. 5a):** The promontorium has a hemi-ellipsoid shape and is rather bulky and not elongated. The epitympanic wing is present but limited in extent. It ends in a blunt and broad apex as in *Bos taurus* (O'Leary, 2010). The posteromedial flange of the promontorium is broad and expanded, which prolongs the epitympanic wing. No transpromontorial sulcus on the promontorium was observed as in *Ovis aries* Linnæus, 1758 but contrary to *Bos taurus* (O'Leary, 2010).

The *fenestra cochleae* (i.e., round window) is at least twice as big as the *fenestra vestibuli* (i.e., oval window); both are rather oval in shape. They are oriented almost perpendicularly to one another as in *Ovis aries* but not as in *Bos taurus* where the round window is anterolaterally oriented and forms an acute angle with the oval window.

The interfenestral crest forms a large and smooth bridge between both *fenestrae*. The fossa for the tensor tympani muscle is oval and broad but does not excavate the tegmen tympani itself. The secondary facial foramen is large and anteriorly positioned at the level of the anteriormost end of the oval window. The anterior, medial and posterior contacts with the bulla are high and large, almost pillar-like, on the lateral side of the petrosal surrounding the promontorium. The stapedial muscle fossa is also large and directly posterior to the oval window. The tegmen tympani is large in size, but not inflated (*sensu* O'Leary, 2010), forming a strong straight wall on the rostral side of the petrosal, it is long anteriorly and its anterior process, *sensu* O'Leary (2010), lies at the level of the apex of the petrosal. The anterior process is pointy to blunt in shape. The *hiatus Fallopii* is visible on this side and forms a small hole just above the contact to the anterior bulla.

**Medial surface (Fig. 5b):** No prefacial commissure fossa (*sensu* O'Leary, 2010) is visible. The internal acoustic meatus is elongated and laterally tilted with regards to the axis of the petrosal, recalling the situation in *Ovis aries* rather than in *Bos taurus* where it is more perpendicular to the axis of the bone (O'Leary, 2010). Both *foramina acustica* (*superius* and *inferius*) are set largely apart to one another. There is no apparent basicapsular groove. The *fossa cerebellaris* containing the subarcuate fossa is shallow and wide. The cochlear aqueduct opens posteroventrally to the internal acoustic meatus, it is thus ventral (*sensu* O'Leary, 2010). It is also large and is situated above a strong spike (*sensu* O'Leary, 2010) of the occipital side (*sensu* Mallet & Guadelli, 2013) of the petrosal. The opening for the vestibular aqueduct is situated just below this spike. It is an elongated and thin slit that runs next to the *fossa cerebellaris*, laterally with regards to the internal acoustic meatus. The mastoid region is large and wedge-shaped as in all ruminants where it is known (O'Leary, 2010; Costeur, 2014; Mennecart & Costeur, 2016a, b; Mennecart *et al.*, 2016).

**Bony labyrinth (Fig. 5c, d)**

Measurements are given in Table 1. The cochlea completes 2.25 turns. It is small compared to the overall size of the bony labyrinth. The aspect ratio (total height divided by total width) is 0.48 in the range of low or "flat" cochleas (*sensu* Gray, 1907, 1908). The cochlear spiral is tight and the second turn is much smaller than the basal turn. The cochlear aqueduct is long and thick; it is oval in diameter and takes a slight lateral bend at half length. The secondary bony lamina is visible over about a quarter of the basal turn. The *fenestra cochleae* is rounded in shape and faces ventrally. The *fenestra vestibuli* is ellipsoid in shape, with a stapedial ratio of 1.9. It is more dorsally positioned than the *fenestra cochleae*. On the vestibule, both the *utriculus* and *sacculus* are well defined (Fig. 5d), the latter being rounded in shape. The anterior semi-circular canal is the most dorsally expanded canal; it expands largely above the level of the

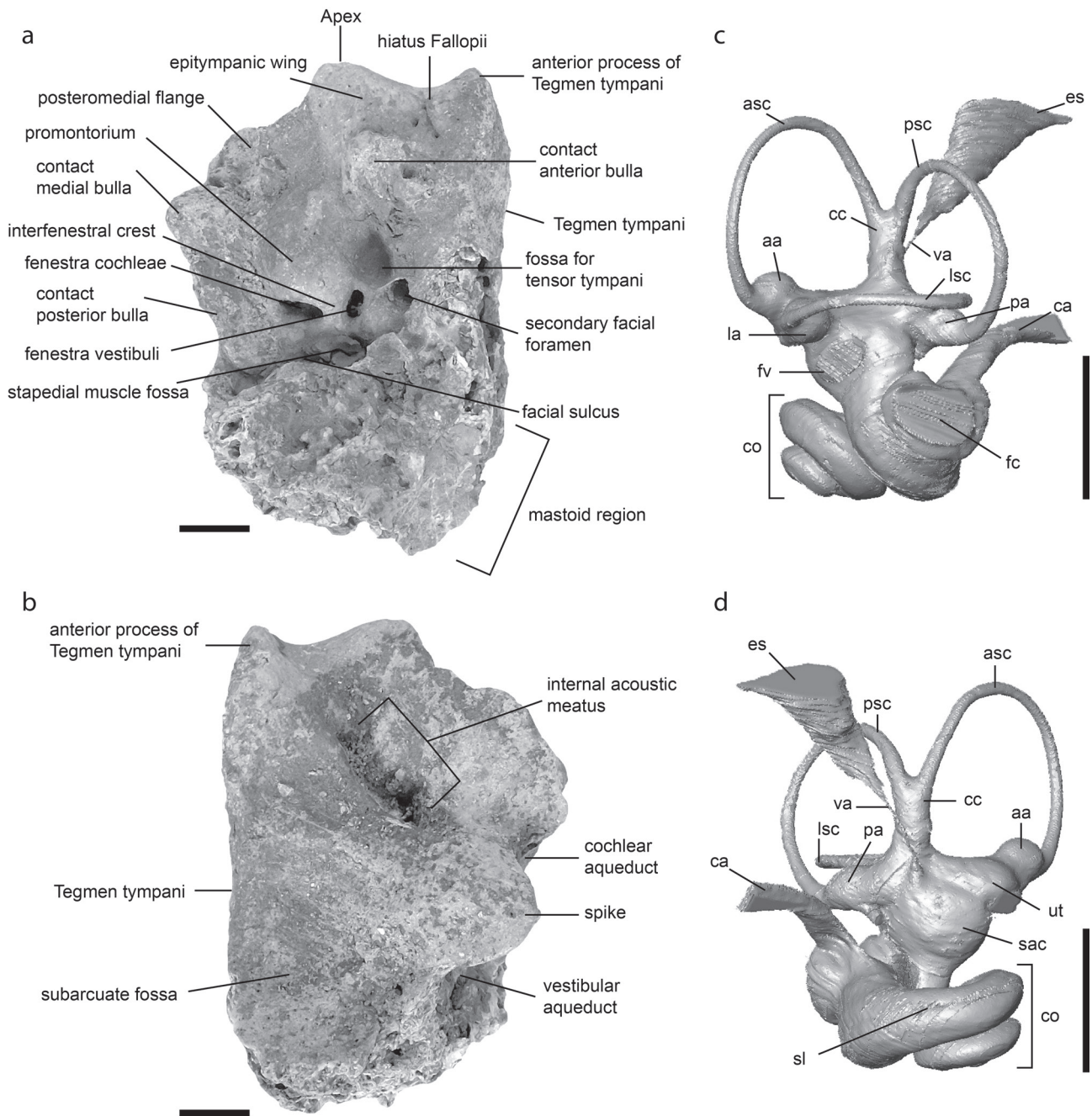


Fig. 5: Left petrosal bone and digital reconstruction of the bony labyrinth of the bovid *Gallogoral meneghini* from Senèze (specimen NMB Se. 313). a, lateral view of the petrosal bone. b, medial view of the petrosal bone. c, posterolateral view of the bony labyrinth. d, anteromedial view of the bony labyrinth. See text for abbreviations. Scale bars: 5 mm.

common crus, as for the posterior semi-circular canal but to a lesser extent for the latter. The common crus thus forms an indentation between both canals and is thick but of limited length. The lateral semi-circular canal is straight. It branches dorsally at the dorsalmost level of the posterior ampulla but in the vestibule in front of the latter like in *Tetracerus* or *Bos* (Costeur, 2014; Costeur *et al.*, 2017), or even *Gazellospira* (see above and Fig. 4c), a characteristic of bovid bony labyrinths when compared

to deer. The vestibular aqueduct is a thin and straight canal detached from the common crus. It originates in the vestibule at the base of the common crus, aligned with its midline, and within the dorsal extent of the *sacculus*. It quickly diverges from the midline of the common crus along its course as in most bovids where it is known (Costeur, 2014; Costeur *et al.*, 2017) and unlike in most deer (Mennecart *et al.*, 2016). It is also short, even shorter than in *Gazellospira* (Fig. 4d), ending well before the end

of the common crus dorsally. The endolymphatic sac at the end of the vestibular aqueduct is large, rather funnel-shaped with a dorsal broadening. It ends after the dorsal extent of the large anterior semi-circular canal.

#### 4. DISCUSSION

The opportunity of describing several fossil petrosal bones and their associated bony labyrinths from different taxa of the same locality is rare. Senèze enables it thanks to the fantastic amount of well-preserved specimens. While 11 ruminant taxa are known from Senèze (Guérin, 2007), not all were available as petrosal bones for this study but 5 could be described and CT-scanned to access the cast of the inner ear. This enables to compare several specimens belonging to two distinct emblematic families of ruminants: Cervidae and Bovidae. While characters of the skull, cranial appendages, teeth, and metatarsals are classical characters used to differentiate both families in the fossil record, the petrosal bone and bony labyrinth add significant data that may help in separating older members of the families, maybe even some close to their divergence. Indeed if Pleistocene bovids and cervids are easily identifiable, much older taxa in the Early Miocene did not bear any cranial appendages and had plesiomorphic teeth and postcranial elements that may be limited in their discriminative power. We set here the bases of the use of characters of the inner ear that can be used in future studies of 42 morphological characters, O'Leary (2010) could only find very few in her limited sample (2 characters in 4 taxa, related to the ventral tuberosity hardly visible on our specimens), which were different between deer and bovids. Our study gives here more details and shows first that the overall shape of the petrosal bone is very different between both families, bovids generally having a massive and round petrosal bone while it is often, albeit not always, more elongated in cervids. The latter generally have a pointy apex while it is blunt in bovids contributing to the overall round morphology. The tegmen tympani on the rostral surface is in general more anteriorly expanded in bovids and its anterior process (*sensu* O'Leary, 2010) reaches a higher point, being even as anteriorly extended as the apex in *Gallogoral*. A great variability of shape of the internal acoustic meatus is observed in the studied taxa but it generally seems similar in the two deer and is more variable in the bovids. Some characters of the petrosal bone that discriminate both families, such as the position of the opening for the vestibular aqueduct more anterolateral in bovids, are directly related to the length and orientation of this structure on the bony labyrinth. It is mostly straight and long in both deer and mostly curved to clearly tilted in bovids so that its opening outside the petrosal bone cannot occur at the same level of the medial side of the bone. The lengths of the endolymphatic sac and cochlear aqueduct have been

shown to increase with ontogeny (Costeur *et al.*, 2017) and the variability observed here could be the result of different ages. The petrosal bone increases in size through ontogeny to stay in contact with the growing skull and bone is added on its periphery such as clearly evidenced on the cow (Costeur *et al.*, 2017). This has an impact on these “open structures”, which elongate as the bone grows. As evidenced on tragulid and cervid ruminants (Mennecart & Costeur, 2016a, b; Mennecart *et al.*, 2016), the branching pattern of the lateral semi-circular canal bears a strong phylogenetic signal. It is here confirmed with bovids which show a unique branching pattern, different from deer, where the lateral semi-circular canal branches in the vestibule anteromedially “in front” of the posterior ampulla, while it branches essentially within the posterior ampulla in deer.

The length of the cochlea is similar between all the taxa studied here and a quarter of a turn of difference enters the natural variability observed in other ruminants (Mennecart & Costeur, 2016b). Strong differences are otherwise observed such as the overall shape of the cochlea in *Leptobos* which is massive and very close to the vestibule. It retains a plesiomorphic morphology, different from those of the Antilopinae *Gazellospira* and Caprinae *Gallogoral* and also very different from that of the Bovinae *Bos taurus* (Costeur *et al.*, 2017). The cochlear aqueduct, shape of the common crus, and anteriorly positioned origin of vestibular aqueduct are otherwise strikingly similar between *Leptobos* and *Bos* probably confirming the strong phylogenetic power of the bony labyrinth in general. The shape of the cochlea is also more similar between both deer than it is with the other ruminants studied here, with a wide basal turn and turns that are in general of similar thickness while the second turn in the bovids from Senèze is much thinner than the basal turn.

The morphology of *Eucladoceros*'s bony labyrinth supports affinities with *Cervus elaphus* (Mennecart *et al.*, 2016, 2017; but also see Croitor, 2014, for a different hypothesis). Both taxa share a very similar long vestibular aqueduct and thin funnel-shape endolymphatic sac. Likewise, the insertion of the lateral semi-circular canal in the posterior ampulla is very similar too. The striking similarities of the slightly curved vestibular aqueduct overlain by a triangular endolymphatic sac and of the shape of the cochlear aqueduct of *M. rhenanus philisi* with *Dama dama* Linnæus, 1758 (Mennecart *et al.*, 2017) lends credence to previous hypotheses which related both taxa (Pfeiffer, 2002; Breda & Lister, 2013). Providing close phylogenetic affinities of the three bovids studied here based on the bony labyrinth is not possible at this point since the 3D morphology of the bony labyrinth of bovids is vastly unknown [apart from the less than ten species where it is known out of the more than 140 existing: *Rupicapra* and *Gazella* in Hyrtl (1845), *Oryx*, *Gazella* and *Ovis* in Gray (1907) but the illustrations in both these studies are not easy to interpret, and apart from

*Tetracerus* in Costeur, 2014, *Ovis*, *Capra*, *Rupicapra*, *Bos* and *Bison* in Guadelli (1999) and Mallet & Guadelli (2013), or again *Bos* in Costeur *et al.*, 2017]. More work has to be carried out before closer conclusions can be reached.

## 5. CONCLUSIONS

As part of our understanding of Plio-pleistocene European ruminants, we described the morphology of some petrosal bones and associated bony labyrinths found in the MNQ18 reference locality Senèze. Five species including two deer (Cervidae) *Eucladoceros ctenoides senezensis* and *Metacervoceros rhenanus philisi* and 3 bovids (Bovidae), the bovine *Leptobos (Smertiobos) etruscus*, the antilopine *Gazellospira torticornis* and the caprine *Gallogoral meneghini* are described. The main results show a suite of morphological characters of the bony labyrinth that distinguish both families such as the orientation of the vestibular aqueduct, tilted or curved in bovids and straighter in cervids, or the insertion of the lateral semi-circular canal in the vestibule in bovids and in the posterior ampulla in cervids. In addition the petrosal bone of bovids is often more massive-looking, being generally more rounded in shape, especially anteriorly where a blunt apex departs from the rather general condition of a pointy apex in cervids. This adds to the morphological differences in both taxa and could be incorporated in future phylogenetic analyses, especially for earlier bovids and cervids closer to their divergence in the Early Miocene.

## ACKNOWLEDGEMENTS

We dedicate this work to Claude Guérin who was a great anatomist and palaeontologist. He largely contributed to our interest for vertebrate palaeontology and accompanied the first professional steps of most of us. He also led us on the field in Senèze from which the material described here comes.

We chose to limit this work to the ruminants of this locality as a tribute to his contribution to our understanding of this famous locality. We thank Martine Faure for her invitation to participate to this tribute to Claude as well as for her comments and editorial work. We are very grateful to Evelyne Crégut-Bonnoure and Jean-Luc Guadelli for their constructive comments that helped improve this article. This is a contribution to SNF Project 200021\_159854/1. We thank the Swiss National Foundation for funding.

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