

First Description of the Auditory Region of a Tremarctinae (Ursidae, Mammalia) Bear: The Case of *Arctotherium angustidens*

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Published online: 21 November 2013
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Abstract Here we present the first detailed morphological study of the auditory region of a tremarctine bear, the South American giant short-faced bear *Arctotherium angustidens*. We compared 19 specimens of *A. angustidens* with other tremarctines and ursines. Through the use of CT scans, we confirmed the presence of a recessus epitympanicus and an anterior incomplete septum of uncertain homology, not related with the septum bullae nor with the longitudinal septum formed by the ecto- and the entotympanic. A secondary crus formed by the lateral semicircular canal (LSC) with the posterior semicircular canal (PSC) of the inner ear was observed in *A. angustidens*, *A. bonariense*, *Tremarctos ornatus*, *Ursus spelaeus*, and *Ursus arctos*. This secondary crus was not previously reported for ursids. We also observed that the intraspecific variation in the auditory region of *A. angustidens* is related to 1) the position of the foramen postglenoideum, 2) the anterior projection of the bulla tympanica over the foramen lacerum and over the opening of the Eustachian tube (medial process of the bulla tympanica), and 3) the projection of the bulla tympanica over the posterior surface of the processus postglenoideus (tympanic process). In addition to this variation, we also identified the presence of interspecific variation in the external auditory region among Tremarctinae and Ursidae. These differences are related to the size of the processus mastoideus and the processus paraoccipitalis, the position of the foramen postglenoideum, and the presence/absence of contact between the bulla tympanica and the processus paraoccipitalis.

Keywords Ursidae · *Arctotherium* · Morphology · Auditory region

Introduction

The Tremarctinae represent an endemic monophyletic group of American bears (Trajano and Ferrarezzi 1994; Talbot and Shields 1996). Within this subfamily there are four genera: *Plionarctos*, *Arctodus*, *Arctotherium*, and *Tremarctos*. *Arctotherium angustidens* is a giant bear (Soibelzon and Tarantini 2009; Soibelzon and Schubert 2011), characteristic of the Ensenadan Age (early and middle Pleistocene) of South America (Soibelzon et al. 2005).

The auditory region has been studied widely within Carnivora by numerous authors (e.g., Van Kampen 1905; Pocock 1921, 1922, 1929; Van der Klaauw 1931; Thenius 1949; Hough 1952; Ginsburg 1966; Beaumont 1968; Hunt 1974). The auditory region of carnivorans contains important information for elucidating the phylogeny of the different groups (Hough 1944). This region has been described and is well known in some bears of the subfamilies Ursinae (Hough 1948; Torres 1984, 1987, 1988) and Ailuropodinae (Segall 1943; Davis 1964). However, in tremarctine bears this region has not yet been described. It is noteworthy that the incorporation of auditory features, such as the presence or absence of the septum bullae (Hough 1948), allowed classifying the members of Carnivora into three large groups: Arctoidea, Aeluroidea, and Cynoidea (Flower 1869), although only two suborders Caniformia and Feliformia are recognized now (Eisenberg 1989; Wozencraft 1989, 2005; Wyss and Flynn 1993). These three groups of carnivorans, proposed by Flower (1869), are recognized currently as infraorders. The families of Carnivora following Wozencraft (2005) include Felidae, Viverridae, Eupleridae, Nandiniidae, Herpestidae, Hyaenidae (Feliformia); Canidae, Ursidae, Otariidae, Odobenidae, Phocidae, Mustelidae, Mephitidae, Procyonidae, Ailuridae (Caniformia).

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This study describes the external and internal morphology of the auditory region of a tremarctine bear for the first time, using the South American giant short-faced bear, *Arctotherium angustidens*, as the primary example. We also add significant data to the published record of the anatomy of the auditory region of bears, providing a preliminary interpretation of some internal morphological auditory features (e.g., horizontal anterior septum of the tympanic cavity, accessory crus formed by the lateral and the posterior semicircular canals).

Material and Methods

The comparative study of the external auditory region was carried out through direct observation of specimens, which were photographed in corresponding views. The description of this region follows Torres (1987). The studied sample consisted of 23 skulls of tremarctine bears: 19 specimens of *A. angustidens* (see Table 1), one of *A. bonariense* (MLP 00-VII-1-1), one of *A. tarijense* (MACN 971), and two specimens of *Tremarctos ornatus* (MLP DZV 1-I-03-62 and MLP DZV s/n). Ursine bears used for comparisons include: *Ursus spelaeus* (MLP 10-69; MLP 80-XII-1-1), *U.*

americanus (MACN Zool. 8071; MLP DZV 84; MLP DZV 1011; MNHN AC 1912-441; MNHN AC 2137; MNHN AC 1913-421; MNHN AC 1850-443; MNHN AC 1935-194; MNHN AC 1959-250; MNHN M 1938-125; MNHN M 1902-1415; MNHN M 1990-495; MNHN M 1990-496), *U. arctos* (MNHN AC 1964-231; MNHN AC 1889-174; MNHN AC 1932-485; MNHN AC 1900-78; MNHN AC 1951-261; MNHN AC 1746; MNHN AC 1733; MNHN M 1988-137; MNHN M 1949-517; MNHN M 1902-1019; MNHN M 1947-872; MNHN M 1988-205; MNHN M 1884-1419), *U. maritimus* (MNHN AC 1912-139; MNHN AC 1906-57; MNHN AC 1918-65; MNHN AC 1912-103; MNHN AC 1938-93; MNHN AC 1865-168; MNHN AC 1897-287; MNHN AC 1961-293). All specimens preserved the auditory region.

For the morphological analysis and comparisons of the internal anatomy of the auditory region of *A. angustidens* (middle and inner ear), 3D reconstructions were made by means of computed axial tomography (CT) carried out on the specimen MLP 82-X-22-1. The 3D reconstructions were produced with the free trial version of the Materialise Mimics Software 10.01. This is a non-invasive method to study internal anatomical structures. The internal morphology observed was compared with CTs made on the tremarctines *A. bonariense* (MLP 00-VII-1-1) and *T. ornatus* (MLP DZV. 1-I-03-62), and the ursine *U. spelaeus* (MLP 80-XII-1-1). The CTs were made in a private institution (CIMED, La Plata, Buenos Aires) with a Philips/Brilliance 64 Scanner, of 12 KV, with a slice thickness of 0.670 mm. CTs of *U. arctos* (TMM M-2749), *U. americanus* (USNM 227070), and *U. maritimus* (H 001-05) provided by the Digital Morphology library at the University of Texas (www.digimorph.org) were also studied.

For the anatomical descriptions, we generally used the Nomina Anatomica Veterinaria, International Committee on Veterinary Gross Anatomical Nomenclature (2012) and we follow the terminology of Davis (1964) and Torres (1987) for the description of some specific anatomical structures. For age and sex determination, we used the method proposed by Soibelzon (2002) and Soibelzon et al. (2009). For the interpretation of the anterior horizontal septum in the cavum tympani observed in most of the bears studied here, CTs of other Carnivora taxa, *Procyon lotor* (LACM 52261) and *Puma concolor* (LACM 87430 and LACM 85440), were also examined (also provided by the Digital Morphology library).

Institutional Abbreviations

H: Illinois State Museum, United States. LACM: Los Angeles County Museum of Natural History, United States. MACN: Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina. MACN Zool: Museo Argentino de Ciencias Naturales, Departamento de Zoología, Buenos Aires,

Table 1 List of the specimens of *Arctotherium angustidens* studied in this contribution, relative age and sex (modified from Soibelzon 2002)

Specimens	Relative age				Sex
	Young	Young adult	Adult	Senile adult	
MHN 32915				x	F
MMMP 26S			x		F
MMMP 3980			x		F
MACN 12529				x	F
MLP 82-X-22-1			x		F
MACN 43				x	F
MMMP 1491		x			F
MLP 00-VII-15-1	x				M
MMMP 018		x			M
MACN 5132				x	M
MLP 00-VII-10-1			x		M
MMMP 3981	x				M
MMMP 3982	x				M
MLP 97-I-5-1			x		M
MLP 10-4				x	a
MLP 96-XII-1-1					a
MACN 974			x		a
MMMP 162S				x	a
MMMP 1232	x				a

Sex was determined by the width of the canine teeth, the relative age by the wear of the crowns of the molars and the degree of fusion of the cranial sutures (see Soibelzon 2002; Soibelzon and Schubert 2011)

^a It is impossible to determine the relative age for lack of canines

Argentina. MHN: Natural History Museum, London, UK. MLP: Museo de La Plata, División Paleontología Vertebrados, La Plata, Argentina. MLP DZV: Museo de La Plata, Departamento de Zoología, La Plata, Argentina. MMP: Museo Municipal de Mar del Plata “Lorenzo Scaglia”, Mar del Plata, Argentina. MMPH: Museo Municipal “Punta Hermengo”, Miramar, Argentina. MNHN AC: Muséum National d’Histoire Naturelle, Collection de Anatomie Comparée, Paris, France. MNHN M: Muséum National d’Histoire Naturelle, Collection des Mammifères, Paris, France. TMM: Texas Memorial Museum, United States. USNM: United States National Museum.

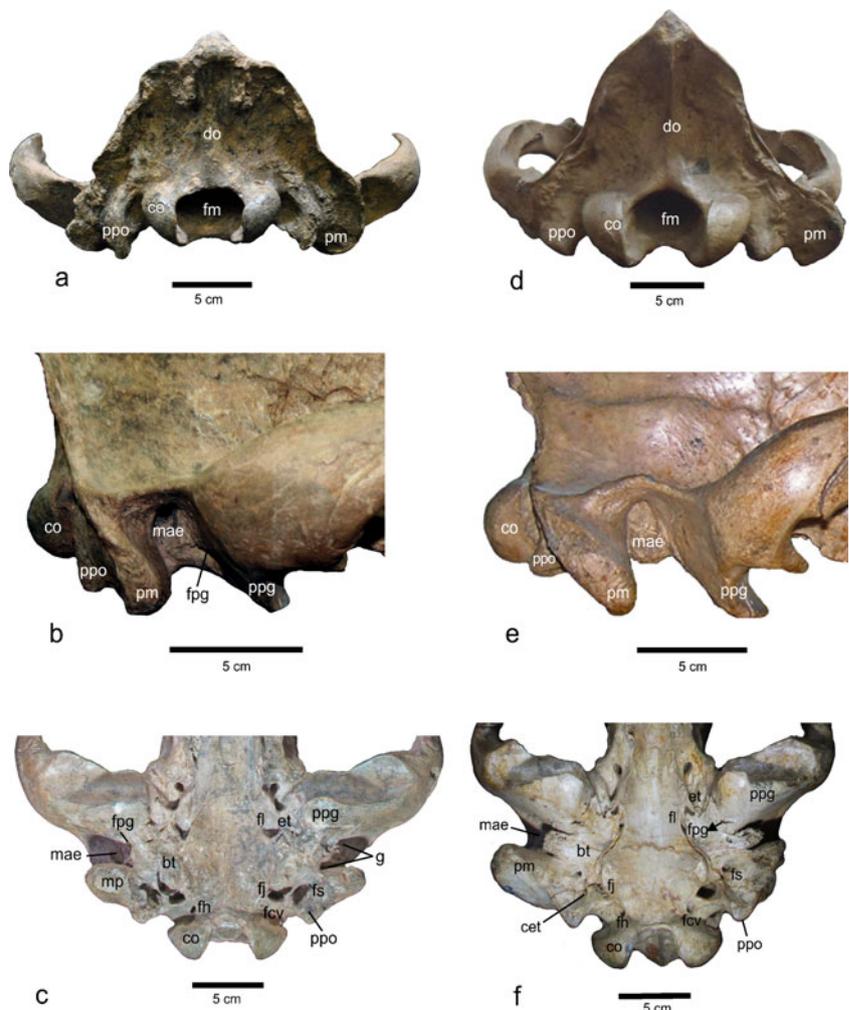
Results

External Auditory Region

The external auditory region of *A. angustidens* is shown in Fig. 1. In occipital view (Fig. 1a), the processus mastoideus is

robust, ventrolaterally oriented and it extends more ventrally than the processus paraoccipitalis (sensu Davis 1964). This process is laterally expanded, anteroposteriorly compressed, and does not reach the height of the processus postglenoideus (sensu Davis 1964). The processus paraoccipitalis is relatively small, conical, and ventrally oriented. The processus mastoideus is generally wider than the processus paraoccipitalis and the condylus occipitalis. Attached to the processus mastoideus are the lateral flexors of the head muscles (Sisson 1977): the *M. sternomastoideus*, which inserts in the lateral and ventral borders of this process; the *M. rectus capitis lateralis*, which inserts on the posterior surface of this process near its lateral edge and one of the two heads of the *M. longissimus capitis*, which arises from the transverse processes of the last three cervical vertebrae. The *M. digastricus* attaches to the processus paraoccipitalis and the ridge connecting this process with the processus mastoideus (see Davis 1964 for a detailed description of muscles and soft tissues of this region).

Fig. 1 Comparisons between *Arctotherium angustidens* (MLP 82-X-22-1); **a** occipital view; **b** lateral view; **c** ventral view of the skull, and *Ursus spelaeus* (MLP 80-XII-1-1); **d** occipital view; **e** lateral view; **f** ventral view of the skull. Abbreviations: bt, bulla tympanica; cet, contact exoccipital-tympanic (medial ridge); co, condylus occipitalis; do, dorsal surface of the os occipitale; et, Eustachian tube; fcv, fossa condylaris ventralis; fh, foramen n. hypoglossis; fj, foramen jugulare; fl, foramen lacerum; fm, foramen magnum; fpg, foramen postglenoideum; fs, foramen stylomastoideum; g, groove separating tympanic projection of processus postglenoideus and processus mastoideus; mae, meatus acusticus externus; pm, processus mastoideus; ppg, processus postglenoideus; ppo, processus paraoccipitalis



The dorsal margin of the os occipitale is rounded and the foramen magnum is ellipsoidal in cross-section.

In some mammals, the os temporale is a composite bone formed by the fusion of three or more individual elements and divided into three parts: the pars squamosa, pars petrosa, and pars tympanica. The first one corresponds to the squamosal bone, which includes the processus zygomaticus. The pars petrosa corresponds to the petrosal, which is the complex bone housing the inner ear. Finally, the pars tympanica encloses the cavum tympani (middle ear region). In Carnivora, this pars forms the bulla tympanica, composed of three or sometimes four ontogenetic elements: one lateral dermal ectotympanic (= tympanic), to which the tympanic membrane is attached, and two or three chondral entotympanics (rostral and caudal/s), which form the medial and posterior aspects of the bulla (Hunt 1974). In adult specimens of *Ursus americanus*, the bulla tympanica is formed by four ossifications: ectotympanic, rostral entotympanic, anterior caudal entotympanic, and posterior caudal entotympanic (Hunt 1974). The fusion of the rostral entotympanic with the anterior caudal entotympanic forms the bony canalis caroticus that enclosed the internal carotid artery (Hunt 1974). In all the specimens described here sutures are obscured, so we are unable to discriminate the number of bones forming the bulla. Thus, we will describe the bulla tympanica as a single entity.

In lateral view (Fig. 1b), the bulla tympanica forms a short meatus acusticus externus, which does not laterally surpass the processus mastoideus. It is a dorsally open tube, ellipsoidal in cross-section and sub-horizontally oriented, slightly tilted in dorsal-medial-lateral direction. The meatus acusticus externus is separated from the processus paraoccipitalis (posteriorly) and the processus postglenoideus (anteriorly) by two narrow and deep sulci (Fig. 1c). Anteroventral to the aperture of the meatus acusticus externus is the sub-circular foramen postglenoideum (sensu Davis 1964). It is ventrolaterally oriented; however, in some specimens (MMP 1232, MMP 1491, MMP 3980) it is placed on the ventral surface of the braincase.

In ventral view (Fig. 1c), the bulla tympanica is slightly globular and its medial wall is formed by the pars basilaris of the os occipitale (basioccipital). Posteriorly, the medial ridge of the foramen stylomastoideum is slightly developed, so it is placed in a shallow recess together with the foramen jugulare. The latter is the orifice where the canalis caroticus (anterior) and the canal for the exit of the N. glossopharyngeus (IX), N. vagus (X), and N. accessorius spinalis (XI) nerves open. Posteromedial to these is the foramen n. hypoglossis, which connects with the canalis n. hypoglossi (XII) and it is placed in the fossa condylaris ventralis (Fig. 1c). Projecting medially from the processus paraoccipitalis is a transverse ridge, which delimits posteriorly the foramen jugulare. The latter opens independently from the posterior orifice of the canalis caroticus (Fig. 1c). Only a single aperture for the entrance of

the foramen stylomastoideum is observed (Fig. 1c), through which runs the N. facialis (VII) and probably the A. (artery) and V. (vein) stylomastoidea (Davis 1964).

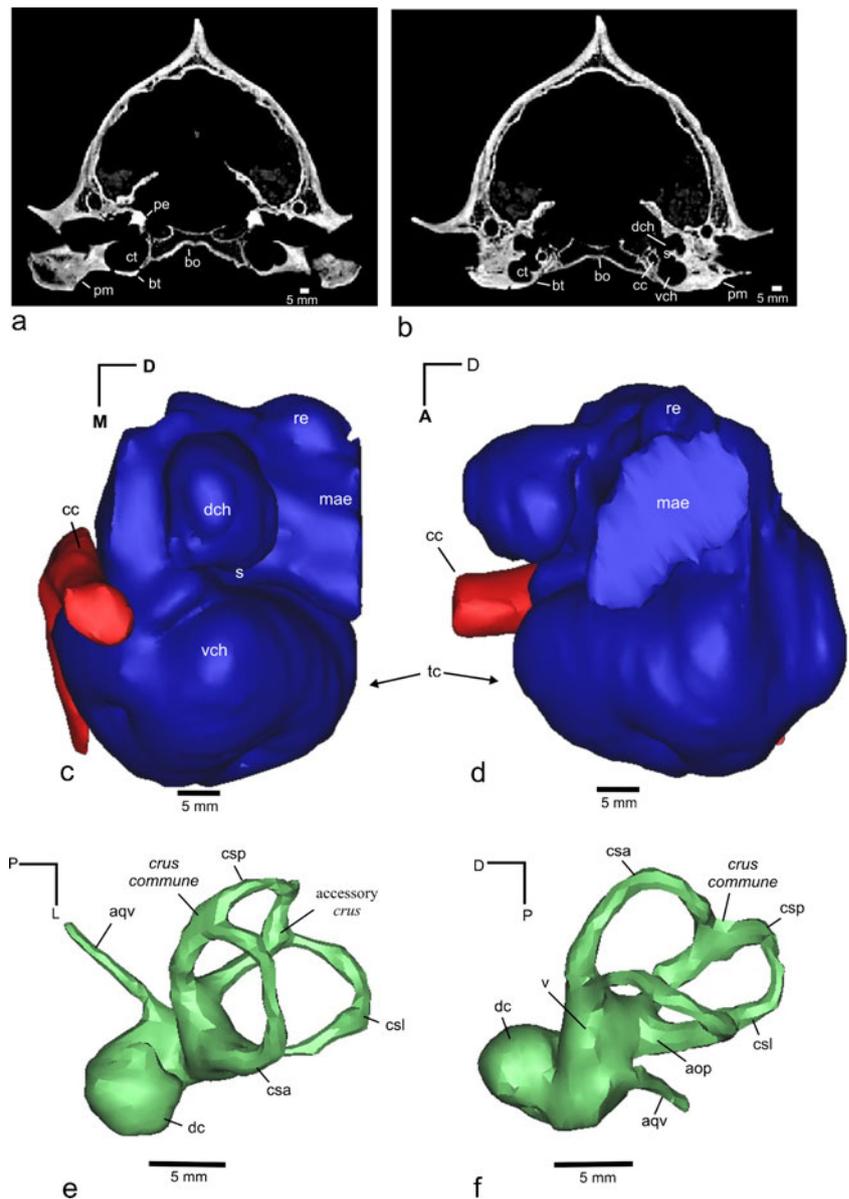
The floor of the cavum tympani is formed by the tympanic bones (see above). In ventral view, in most specimens, the bulla tympanica slightly overlaps the posterior surface of the processus postglenoideus, without forming a canal as occurs in other bears (see discussion below; Fig. 1c). In the anteromedial edge of the bulla tympanica there is an aperture where the foramen lacerum and the Eustachian (auditory) tube (sensu Davis 1964) open. The Eustachian tube connects the nasopharynx with the cavum tympani. Posterolaterally, the bulla tympanica contacts the processus mastoideus. In some specimens of *A. angustidens* (MACN 43; MLP 10-4; MLP 00-VII-10-1; MMP 162S; MMP 1232; MMP 1491), the foramen lacerum and the opening of the Eustachian tube are partially covered by a variable expansion of the bulla tympanica. The medial edge of the bulla tympanica borders on the lateral edge of the pars basilaris of the os occipitale, so that the lateral margins of the os occipitale are convex.

Middle Ear Region

As mentioned above, the bulla tympanica in *A. angustidens* is slightly globular. It delimits a voluminous cavum tympani; the approximate volume in specimen MLP 82-X-22-1 is 11561.665 mm³ and represents 0.5 % of the total volume of the skull (Fig. 2a). The medial, ventral, and lateral walls of the cavum tympani are formed by the tympanic bones (see above), whereas dorsally it is delimited by the pars petrosa of the os temporale, which extends posterolaterally, forming in occipital view a triangular shaped mastoid surface and projecting ventrally in a wide processus mastoideus (Fig. 2a).

In the anterior region, the cavum tympani is incompletely divided by a horizontal septum into dorsal and ventral recesses. The ventral recess is more developed (Fig. 2b, c). This septum is formed by an evagination of the lateral wall of the bulla tympanica. As stated above, tympanic bones are fused, and the limits between them cannot be established; however, given that it is formed by the lateralmost part of the bulla tympanica, we interpret that it could be formed only by the ectotympanic. This septum is not homologous with the septum described in other carnivorans, the septum bullae (Flower 1869), which is transverse to the bulla tympanica, or the longitudinal (vertical) septum, formed by the ectotympanic and the entotympanic (Ivanoff 2000). While the horizontal septum divides the cavum tympani into dorsal and ventral recesses, the septum bullae divides it into an anterior and posterior recesses and the longitudinal septum into lateral and medial recesses. These two last septa were not observed in *A. angustidens*. The cavum tympani is more developed posterior to the meatus acusticus externus. In this sector, the bulla tympanica is a single chamber (Fig. 2d). The

Fig. 2 *Arctotherium angustidens* (MLP 82-X-22-1). CT images of the skull. **a** coronal view of the medial region of the tympanic cavity; **b** coronal view of the anterior region of the tympanic cavity. Endocast of the left middle ear (cavum tympani in blue and canalis caroticus in red), **c** anterior view; **d** lateral view. Endocast of the left inner ear **e** lateral view, **f** dorsal view. Abbreviations; aop, ampulla ossea posterior; aqv, aqueductus vestibuli; bo pars basilaris of os occipitale; bt, bulla tympanica; cc, canalis caroticus; csa, canalis semicircularis anterior; csl, canalis semicircularis lateralis; csp, canalis semicircularis posterior; ct; cavum tympani; dc, ductus cochlearis; dch, dorsal chamber in anterior region of bullae tympanica; mae, meatus acusticus externus; pe, pars petrosa of os temporale; pm processus mastoideus; re, recessus epitympanicus; s septum; v, vestibule; vch ventral chamber in anterior region of bullae tympanica



canalis caroticus is placed on the medial wall of the cavum tympani, below the pars petrosa of the os temporale, and given its location it may be completely formed by the entotympanic (Fig. 2b–d).

Dorsal to the cavum tympani is observed a recessus epitympanicus. This is a small chamber that opens at the cavum tympani dorsal to the articulation between the malleus and incus (Van der Klaauw 1931), medial to the meatus acusticus extenus (Fig. 2c, d).

Anteromedial to the meatus acusticus externus is the pars petrosa of the os temporale, the most prominent part of which is the promontorium. Located on the anterior sector of this bone is the fenestra vestibuli (oval window), which contained the footplate of the stapes in life. In specimen MLP 96-XII-1-1, the right side of the pars petrosa of the os temporale is

partially preserved, and it is possible to observe that in *A. angustidens* the fenestra cochleae (round window) opens in the posterior part of the promontorium. In this specimen, posterior to the fenestra cochleae is the aperture of the foramen stylomastoideum. The ventral surface of the pars petrosa of the os temporale is divided in two regions, the anteroventral pars cochlearis, which enclosed the cochlea, and the posterodorsal pars canicularis, which housed the vestibule and the canales semicirculares. The surface of the pars canicularis is irregular, showing an area of muscle attachment.

In the aperture of the meatus acusticus externus the annulus tympanicus can be seen representing the attachment of the membrana tympani to the ectotympanic bone. On the lateral and ventral wall of the cavum tympani are curved ridges (transverse ridges sensu Torres 1987), which diverge from

the annulus tympanicus to the medial wall of the cavum tympani (Fig. 3a).

Inner Ear Region

The inner ear is enclosed within the pars petrosa of the os temporale. The ventral portion of this bone is divided in an anterior cochlear part and a posterior pyramidal part (Torres 1987). As mentioned above, the most noticeable region of the pars petrosa of the os temporale in its ventral face is the promontorium, which corresponds to the first turn of the cochlear canal spiral. Posteroventral to this is the fenestra vestibuli (Fig. 3b). Dorsally, at the promontorium, is the fenestra cochleae (Fig. 3c), which is closed from the middle ear by the membrana tympani secundaria. The fenestra vestibuli is larger than the fenestra cochleae.

In the cochlea there is another aperture that corresponds to the meatus acusticus internus and it is placed dorsomedially in the anterior third of the pars petrosa of the os temporale. In the specimen MLP 82-X-22-1 this opening could not be accurately reconstructed due to the poor preservation of that region. In the posterior region of the inner ear is the aqueductus vestibuli, which transmits the ductus endolymphaticus (Fig. 2e, f). Unlike other mammals such as marsupials (Schmelzle et al. 2007) or notoungulates (Macrini

et al. 2010), in *A. angustidens* the diameter of the aqueductus vestibuli (and probably of the ductus endolymphaticus) and that of the canalis semicircularis is similar. This aqueductus extends along the pars petrosa of the temporal bone and emerges in the posterior cranial fossa. In that region the aqueductus vestibuli becomes wider, probably also coinciding with the increase in size of the ductus endolymphaticus, which forms an extradural bag, the saccus endolymphaticus.

From the tomography of specimen MLP 82-X-22-1, the semicircular canals were reconstructed (Fig. 2e, f). The area of the arc comprised by the canalis semicircularis posterior (CSP) is oval in shape with the major axis oriented obliquely laterodorsally to ventromedially/posterodorsally. The area of the arc enclosed by the canalis semicircularis anterior (CSA) is rounded in shape. As is well known, the CSA forms a crus commune with the CSP; its other end expands in the ampullae membranaceae, which is connected with the vestibule. The CSA is oriented dorsomedially to ventrolaterally. The canalis semicircularis lateralis (CSL) is slightly horizontal, oriented obliquely dorsoventrolaterally; the path described by the CSL encloses an area oval in shape. Close to the ampullae membranacea anterior is the ampullae membranacea of the CSL. Noticeably, we were able to reconstruct the inner ear in *A. bonariense* MLP 00-VII-1-1, *T. ornatus* MLP DZV 1-I-03-62 and MLP DZV s/n, and *U. spelaeus* MLP 80-XII-1-1. As

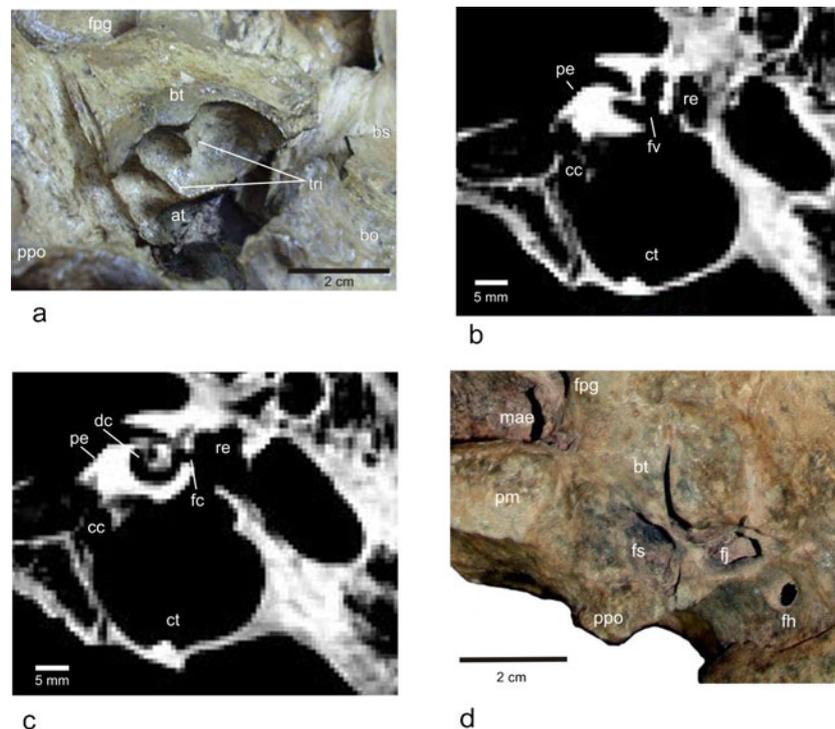


Fig. 3 *Arctotherium angustidens*. **a** detailed image of the posterior view of the left auditory region of MACN 43; **b**, **c** MLP 82-X-22-1, coronal CT images of the middle and inner auditory region; **d** enlarged view of the posterior left of external auditory region (MLP 82-X-22-1). Abbreviations; at, annulus tympanicus; bo, pars basilaris of os occipitale; bs, os basisphenoidale; bt, bulla tympanica; cc, canalis caroticus; ct,

cavum tympani; dc, ductus cochlearis; fc, fenestra cochleae; fh, foramen n. hypoglossicus; fj, foramen jugulare; fpg, foramen postglenoideum; fs, foramen stylomastoideum; fv, fenestra vestibuli; ma, meatus acusticus externus; pe, pars petrosa of os temporale; pm, processus mastoideus; ppo, processus paraoccipitalis; re, recessus epitympanicus; tri, transverse ridges

in *A. angustidens*, in all those specimens the lateral and posterior semicircular canals form the secondary crus commune, also present in other mammals (e.g., Luo et al. 2011). The arc radii of the CSA, CSP, and CSL are 1.23 mm, 1.34 mm, and 1.02 mm, respectively.

The bony recess of the sacculus and the utriculus (= vestibular part of the inner ear) were reconstructed. Although it was not possible to see a discernible separation between them, the bulge for the utriculus is ventral to the CSA (see Macrini et al. 2010; Fig. 2e).

Finally, the cochlea of *A. angustidens* is rounded and is placed anterior to the semicircular canals (Fig. 2e, f). Given the resolution of the CT scans (see **Material and Methods**), the bony recess of cochlear duct of MLP 82-X-22-1 was reconstructed without higher detail, so we were able to infer that in *A. angustidens* the coiled cochlea has two spiral turns (counted following West 1985). The primary and secondary bony lamina at the cochlea are also present in this specimen.

Discussion

In *Arctotherium* the bulla tympanica has been described as posteriorly flat and used as a diagnostic feature of the genus by Hough (1948). Hough (1948) did not specify which species this character was based on, and in the present study the posterior portion of the bulla tympanica is not flatter in *A. angustidens* than that of other bears (e.g., *T. ornatus*). It was also noted by Hough (1948) that the posterior region of the bulla tympanica is less developed in *Ursus* than in *Arctotherium*. However, in the sample here the bulla tympanica presents similar proportions for these taxa (Fig. 1c, f).

As stated above, the septa of the cavum tympani of carnivorans have been studied by several authors and used in taxonomy (Flower 1869; Wińcza 1896, 1898; Van Kampen 1905; Segall 1943; Hough 1948, 1952; Petter 1966; Ginsburg 1982; Hunt 1974, 1987, 1991; Ivanoff 2000, 2001). Nevertheless, controversies arise about these septa due to their uncertain homology and variability among taxa (see Segall 1943; Hough 1948; Torres 1987; Ivanoff 2000, 2001). There are some septa in Carnivora of uncertain homology: 1) septum bullae, longitudinal (vertical) and formed by the ectotympanic and the entotympanic (Ivanoff 2000), present in some groups such as Felidae; 2) a transverse septum that (when complete) divides the cavum tympani in two chambers (anterior and posterior), present in cynoids and aeluroids (sensu Flower 1869); and 3) an horizontal, anterior, and incomplete septum that divides the anterior region of the cavum tympani in a ventral and dorsal recesses. This last septum is described by Segall (1943) as typically present in mustelids, procyonids, and canids. Noticeably, we observed this septum in other carnivorans such as Ursidae (e.g., *A. angustidens*, *T. ornatus*, *U. arctos*, *U. maritimus*, *U. americanus*) and Felidae (*Puma*

concolor), and we did not find it in *Procyon lotor*. Ivanoff (2001) mentioned the presence of a septum in ursids pointing out the probable homology with Segall's septum. As mentioned above, in *A. angustidens* the ventral recess is larger than the dorsal recess, like in other carnivorans such as *P. concolor*, whereas in other bears, such as *Ursus* and *Tremarctos*, the dorsal recess is more developed.

A secondary crus formed by the LSC with the PSC was observed in *A. angustidens*, *A. bonariense*, *T. ornatus*, *U. spelaeus*, and *U. arctos* (species studied by us from CT scans, see **Material and Methods**). This crus was not previously reported in ursids. A "second crus commune" for these semicircular canals was reported in extinct methaterian mammals (e.g., Sánchez-Villagra and Schmelzle 2007; Sánchez-Villagra et al. 2007; Luo et al. 2011).

Intraspecific Variation of the External Auditory Region in *Arctotherium angustidens*

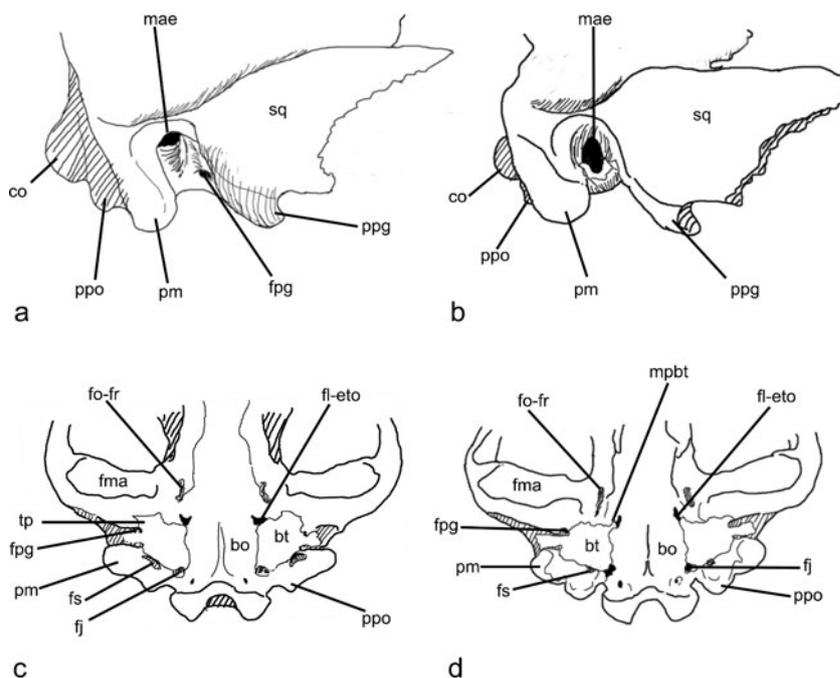
Intraspecific variation in *A. angustidens* is related to 1) the position of the foramen postglenoideum, 2) the projection of the bulla tympanica over the foramen lacerum and over the opening of the Eustachian tube (medial process of the tympanic process), and 3) the projection of the bulla tympanica over the posterior surface of the processus postglenoideus (tympanic process) (Fig. 4). The foramen postglenoideum is normally located in the pars basilaris of the os occipitale, so it is visible in both ventral and lateral views (Fig. 4), but in some specimens (e.g., MLP 1491, MMP 1232, MMP 3980) it is ventrally confined (Fig. 4b). In most specimens (e.g., except MLP 82-X-22-1; Figs. 1c and 4c) the bulla tympanica presents an anterior projection over the foramen lacerum and over the opening of the Eustachian tube (Fig. 4d). The anterior projection of the bulla tympanica over the posterior surface of the processus postglenoideus was not observed in some specimens (e.g., MMP1232, MMP 162S and MMP 1491; Fig. 4d). This morphological variation is not related to sexual dimorphism or age at least in known specimens (see **Results** and Table 1).

Interspecific Variation of the External Auditory Region in Bears

Variation Among Studied Tremarctines

It is noteworthy that the features discussed above also vary within the Tremarctinae. For example, in *A. tarijense* the foramen postglenoideum is observed in ventral view and the anterior margin of the bulla tympanica is not anteriorly projected; this last condition is verified also in *T. ornatus*, but in this species the foramen postglenoideum is observed in lateral view. In this regard, *A. bonariense* is similar to *A. angustidens*.

Fig. 4 Intraspecific variation of the external auditory region in *Arctotherium angustidens*. **a** MLP 82-X-22-1 in lateral view; **b** MMP 1491 in lateral view; **c** MLP 82-X-22-1 in ventral view; **d** MMP 162S in ventral view. Abbreviations; bo, pars basilaris of os occipitale; bt, bulla tympanica; co, condylus occipitalis; eto, eustachian tube opening; fj, foramen jugulare; fl, foramen lacerum; fma, fossa mandibularis; fo, foramen ovale; fpg, foramen postglenoideum; fr, foramen rotundum; fs, foramen stylomastoideum; mae, meatus acusticus externus; mpbt, medial process of bullae tympanica; pm, processus mastoideus; ppg, processus postglenoideus; ppo, processus paraoccipitalis; sq, pars squamosa of os temporale; tp, tympanic process



Another feature observed only in *A. tarijense* is that the ridge that contacts the processus paraoccipitalis with the bulla tympanica is conspicuous and separates the foramen stylomastoideum from the foramen jugulare.

In relation to the processus paraoccipitalis, the main difference observed between *A. angustidens* and *A. bonariensis*—*A. tarijense* is that the processus paraoccipitalis is posteriorly oriented in the last two species. In *T. ornatus* the processus mastoideus is to some extent larger than the processus paraoccipitalis and oriented in the same way as in *A. angustidens*. The processus paraoccipitalis in *T. ornatus* is clearly oriented posteroventrally.

Comparisons Between Tremarctines and Studied Ursines

As in some specimens of *A. angustidens* and *A. tarijense*, in *U. spelaeus*, *U. arctos*, *U. maritimus*, and *U. americanus* the foramen postglenoideum is only observed in ventral view (Fig. 1e, f). It seems that the position of the foramen postglenoideum does not vary within Ursinae, while in *Arctotherium* it varies as described above. Nevertheless, this statement should be tested in a larger sample.

As in *A. angustidens*, in *U. spelaeus* the processus mastoideus is more robust than the processus paraoccipitalis and reaches the height of the processus postglenoideus (Fig. 1d); in *U. arctos* and *U. maritimus* the processus mastoideus is more robust than the processus paraoccipitalis and is slightly taller than the processus postglenoideus. This is not the case of *U. americanus* where the two processes are similar in size to that of *T. ornatus*. The processus paraoccipitalis in *U. americanus* and *U. maritimus* is

antero-posteriorly compressed and laterally expanded (not conical) and its apex is posteroventrally oriented producing a concave posterior surface. In turn, the processus mastoideus in *U. arctos* is conical and ventrally oriented, while in *U. spelaeus* is conical and posteroventrally oriented (Fig. 1d, e).

The bulla tympanica of ursine bears widely contacts the processus paraoccipitalis via a ridge that separates the foramen stylomastoideum and the foramen jugulare (Fig. 1f). Hough (1948) observed in tremarctines (except *A. tarijense*) that this ridge is less developed and the foramen stylomastoideum lies in a common fossa with the foramen jugulare (see description; Fig. 1c); thus, the contact between the processus paraoccipitalis and the bulla tympanica is very restricted.

Conclusions

Here we provide the first description of the auditory region of *A. angustidens* with comparisons to other Tremarctinae and with Ursinae. From the description and the comparative study we conclude that the intra- and interspecific variability of the auditory region is higher than previously known.

The use of CT scans for the study of the middle and inner ear is a non-invasive tool. Using this method we determined the presence of an anterior incomplete septum and a recessus epitympanicus. However, these structures require further comparative study in order to establish their homology among Carnivora (a first step to analyze the implication of those middle ear structures in the phylogeny of the group). Another novel feature that requires more detailed comparisons is the presence of an accessory crus in the inner ear of ursids.

We believe that this type of study, using 3D modeling, should be extended to other groups to interpret the morphology of the auditory region in the context of the evolutionary history of the Carnivora and its relationship with the life styles of the different groups.

Acknowledgments We thank the two anonymous reviewers and John R. Wible (Editor-in-Chief) for valuable and useful suggestions on an early version of this manuscript. We thank to the Dr. Juan F. Cuesta, Téc. Leonardo Bandiera and Téc. Juan Pablo Merino from CIMED for their help with the CT scans. We thank the following persons and institutions for allowing the examination of the material: Marcelo Reguero, Museo de La Plata; Alejandro Dondas, Museo Municipal de Mar del Plata “Lorenzo Scaglia” and Alejandro Kramarz, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia.” We also thank to B. Pianzola (Photograph Laboratory of the MLP) for the photographs and M. Tomeo for the editing figures. We acknowledge the Digital Morphology library (DIGIMORPH) at the University of Texas at Austin for access to CT scans housed at their library. We are grateful Dr. Federico Degrange for the helpful instructions about the software used for 3D reconstructions. ANPCyT PICT 0804 BID and CONICET PIP 0436 are acknowledged for financial support.

References

- Beaumont G (1968) Note sur la region auditive de quelques Carnivores. *Arch des Sci Genève* 21:211–224
- Davis DD (1964) The giant panda. A morphological study of evolutionary mechanism. *Fieldiana Zool Mem* 3:1–399
- Eisenberg JF (1989) An introduction to the Carnivora. In: Gittleman JL (ed) *Carnivore Behavior, Ecology, and Evolution*. Cornell University Press, Ithaca, pp 1–9
- Flower WH (1869) On the value of the characters of the base of the cranium in the classification of the Order Carnivora, and on the systematic position of *Bassaris* and other disputed forms. *Proc Zool Soc Lond* 37:4–37
- Ginsburg L (1966) Les amphicyons des Phosphorites du Quercy. *Ann Paléontol* 52:23–64
- Ginsburg L (1982) Sur la position systématique du petit panda, *Ailurus fulgens* (Carnivora, Mammalia). *Gébios Mém Spéc* 6:247–258
- Hough JR (1948) The auditory region in some members of the Procyonidae, Canidae, and Ursidae. Its significance in the phylogeny of the Carnivora. *Bull Am Mus Nat Hist* 92:67–118
- Hough JR (1952) Auditory region in North American Felidae: significance in phylogeny. *Geol Surv Prof Pap* 243:95–115
- Hough MJ (1944) The auditory region in some Miocene carnivores. *J Palaeontol* 18:470–479
- Hunt RM Jr (1974) The auditory bulla in Carnivora: an anatomical basis for reappraisal of carnivore evolution. *J Morphol* 143:21–76
- Hunt RM Jr (1987) Evolution of the aeluroid Carnivora: significance of auditory structure in the nimravid cat *Dinictis*. *Am Mus Novitates* 2886:1–74
- Hunt RM Jr (1991) Evolution of the aeluroid Carnivora: viverrid affinities of the Miocene carnivoran *Herpestides*. *Am Mus Novitates* 3023:1–34
- International Committee on Veterinary Gross Anatomical Nomenclature (2012) *Nomina Anatomica Veterinaria*, 5th Edition. Department of Veterinary Anatomy, Cornell Univ, Ithaca
- Ivanoff DV (2000) Origin of the septum in the canid auditory bulla: evidence from morphogenesis. *Acta Theriol* 45:253–270
- Ivanoff DV (2001) Partitions in the carnivoran auditory bulla: their formation and significance for systematics. *Mammal Rev* 31:1–16
- Luo ZX, Ruf I, Schultz JA, Martin T (2011) Fossil evidence on evolution of inner ear cochlea in Jurassic mammals. *Proc R Soc B* 278:28–34
- Macrini TE, Flynn JJ, Croft DA, Wyss AR (2010) Inner ear of a notoungulate placental mammal: anatomical description and examination of potentially phylogenetically informative characters. *J Anat* 216:600–610
- Petter G (1966) *Cynodictis*, canidé oligocène d’Europe: région tympanique et affinités. *Ann Paléontol (Vertébrés)* 52:3–19
- Pocock RI (1921) The external characters and classification of the Procyonidae. *Proc Zool Soc Lond* 91:389–422
- Pocock RI (1922) The external characters and classification of the Mustelidae. *Proc Zool Soc Lond* 91:803–837
- Pocock RI (1929) The structure of the auditory bulla in the Procyonidae and the Ursidae, with a note on the bulla of *Hyaena*. *Proc Zool Soc Lond* 98:963–974
- Sánchez-Villagra MR, Ladevèze S, Horovitz I (2007) Exceptionally preserved North American Paleogene metatherians: adaptations and discovery of a major gap in the opossum fossil record. *Proc R Soc Biol Lett* 3:318–322
- Sánchez-Villagra MR, Schmelzle T (2007) Anatomy and development of the bony inner ear in the woolly opossum, *Caluromys philander* (Didelphimorphia, Marsupialia). *Mastozool Neotrop* 14:53–60
- Schmelzle T, Sánchez-Villagra MR, Maier W (2007) Vestibular labyrinth evolution in diprotodontian marsupial mammals. *Mammal Study* 32:83–97
- Segall W (1943) The auditory region of the arctoid carnivores. *Zool Ser Field Mus Nat Hist* 29:33–59
- Sisson S (1977) *Anatomía de los Animales Domésticos*. Salvat, Barcelona
- Soibelzon LH (2002) Los Ursidae (Carnivora, Fissipedia) fósiles de la República Argentina. Aspectos Sistemáticos y Paleocológicos. PhD dissertation. Universidad Nacional de La Plata
- Soibelzon LH, Pomi LH, Tonni EP, Rodríguez S, Dondas A (2009) ‘First report of a South American short-faced bears’ den (*Arctotherium angustidens*): palaeobiological and palaeoecological implications. *Alcheringa* 33:211–222
- Soibelzon LH, Schubert BW (2011) The largest known bear, *Arctotherium angustidens*, from the early Pleistocene Pampean Region of Argentina: with a discussion of size and diet trends in bears. *J Paleontol* 85:69–75
- Soibelzon LH, Tarantini VB (2009) Estimación de la masa corporal de las especies de osos fósiles y actuales (Ursidae, Tremarctinae) de América del Sur. *Rev Museo Argent Cienc Nat* 11:243–254
- Soibelzon LH, Tonni EP, Bond M (2005) The fossil record of the South American short-faced bears (Ursidae, Tremarctinae). *J S Am Earth Sci* 20:105–113
- Talbot SL, Shields GF (1996) Phylogeography of brown bears (*Ursus arctos*) of Alaska and paraphyly within the Ursidae. *Mol Phylogen Evol* 5:477–494
- Thenius E (1949) Zur Revision der Insektivoren des steirischen Tertiärs II. *Sitzungsberichte der Österreichischen Akad Wissensch math-naturwissensch Klasse Abt I* 159:671–693
- Torres T (1984) Los Úrsidos del Pleistoceno- Holoceno de la Península Ibérica. PhD dissertation. Tesis Doctoral Escuela Técnica Superior de Ingenieros de Minas de Madrid, Madrid
- Torres T (1987) La Región Auditiva en los Osos del Pleistoceno Europeo. *Rev Esp Paleontol* 2:41–47
- Torres T (1988) Osos (Mammalia, Carnivora, Ursidae) del Pleistoceno de la Península Ibérica. Publicación especial del Boletín Geológico y Minero, Instituto Geológico y Minero de España 94:1–316
- Trajano E, Ferrarezzi H (1994) A fossil bear from northeastern Brazil, with a phylogenetic analysis of the South American extinct Tremarctinae (Ursidae). *J Vertebr Paleontol* 14:552–561
- Van Der Klaauw CJ (1931) The auditory region of some fossil mammals with a general introduction to this region of the skull. *Bull Am Mus Nat Hist* 62:1–352
- Van Kampen PN (1905) Die Tympanalgegend des Säugetierschädels. *Morphol Jahrb* 34:321–722

- West CD (1985) The relationship of the spiral turns of the cochlea and the length of the basilar membrane to the range of audible frequencies in ground dwelling mammals. *J Acoust Soc Am* 77:1091–1101.
- Wińcza H (1896) Über einige Entwicklungsveränderungen in der Gegend des Schädelgrundes bei den Säugethieren. *Bull Int Acad Sci Crac* 1896:326–337
- Wińcza H (1898) On some changes during the development of the base of the head in mammals. *Rozpr Akad Umiejet, Wydz Matematyczno-Przyrodniczy, Serya 2*, 13:10–26
- Wozencraft WC (1989) The phylogeny of the recent Carnivora. In: Gittleman JL (ed) *Carnivore Behavior, Ecology, and Evolution*. Cornell University Press, Ithaca, pp 495–535
- Wozencraft WC (2005) Order Carnivora. In: Wilson DE, Reeder DM (eds) *Mammal Species of the World, Third Edition*. The Johns Hopkins University Press, Baltimore, pp 532–628
- Wyss AR, Flynn JJ (1993) A phylogenetic analysis and definition of the Carnivora. In: Szalay FS, Novacek MJ, McKenna MC (eds) *Mammal Phylogeny: Placentals*. Springer-Verlag, NY, pp 32–52