新疆准噶尔盆地北缘铁尔斯哈巴合晚渐 新世两种啮形类耳区的形态研究¹⁾

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关键词 准噶尔盆地北缘,晚渐新世,啮形类岩骨中图法分类号 Q915.873

我们曾描述过一块与本文描述的标本产自同一地点和层位、可能为 Amphechinus 的猬类岩骨标本(孟津等,1999)。后来新发现的与牙齿属同一个体的 Amphechinus 岩骨标本证明我们根据单体岩骨的分类鉴定无误。此例说明,在一定的条件下,耳区标本在某些哺乳动物类群中可以鉴定到属,甚至种。因此在形态学、生物地层学上都有一定的意义,而且会因有关标本的不断积累而越来越重要。本文记述了另外两块产自新疆准噶尔盆地北缘铁尔斯哈巴合晚渐新世地层中的岩骨。有关地层、地点资料及所用术语见孟津等(1999)以及其中的相关文献。

岩骨 A (? Sinolagomys 或 Desmatolagus)。 耳泡与岩骨体愈合成一体,其外侧部分破损,鼓室内结构暴露 (图版 I a~c)。耳泡壁厚,为海绵状骨质结构,与耳泡愈合的岩骨乳状突部分也呈海绵状。耳泡内壁与岬相连接的部分具许多小隔板。隔板终止于支撑鼓膜的环脊,并与它成 90°角关系。岬已膨大,其表面由一横沟分为前后两个浑圆的部分,前部包含耳蜗管大部;后部包含了耳蜗管基部、前庭腔、蜗窗及前庭窗等。镫骨动脉穿过耳泡后内壁,在鼓室中被一完整的骨管包裹贯穿全程,仅在横越前庭窗段略有收缩。前庭窗呈明显的长椭圆形,与之相吻合的镫骨脚板也应为相应形状。镫骨孔应当较大才能使十分发育的镫骨动脉管通过。镫骨肌窝、鼓室盖等结构因海绵状耳泡壁的发育愈合而不能辨认。岩骨背面弓形小窝破损,内耳及相关结构保存完好。砧骨与锤骨头部呈关联状保存于耳泡中,经修理使二者分开(图版 I d,e)。

根据个体大小、化石的出现频率、海绵状耳泡壁、以及较为前置且穿过耳泡壁的镫骨动脉孔,我们将岩骨A归于?Sinolagomys或 Desmatolagus。如果鉴定无误,这是?Sinolagomys或 Desmatolagus惟一所知的耳区标本,表明某些鼠兔的耳区结构在晚渐新世时已相当特化。

岩骨B(? Yindirtemys(图版 I f, g)。岬相当膨大,表面不光滑但不具沟痕,表明内颈和

¹⁾ 国家自然科学基金(编号:49572080)、中国科学院"九五"重点项目(编号:KZ952-J1-410)和中国科学院古生物学与古人类学科基础研究特别支持基金(编号:9810)资助。

镫骨动脉已不存在。前庭窗椭圆形,位于一深陷的腔中,此也表明不太可能有镫骨动脉穿过镫骨。鼓室盖大,椭圆形穹隆状,其内侧留在岬体上的界线分明,鼓室盖骨体部分破损, 暴露出位于其背面的面神经管,面神经在鼓室中仅部分包裹于骨管中。鼓室隐窝小。岩骨背面弓形小窝深大,内耳内结构保存完好。耳神经穿过的螺旋状筛板等结构十分清楚。

根据个体大小、化石出现频率以及内颈和镫骨动脉缺失等,我们将岩骨B归于? Yindirtemys。虽然已知镫骨及内颈动脉的缺失现象出现于现生梳趾鼠科中,但化石梳趾鼠科成员中有关的耳区结构还未曾报道过。如果我们的鉴定正确,那么岩骨B为早期梳趾鼠耳区提供了初步形态特征。

致谢 本项目得到国家自然科学基金、中国科学院重点项目基金、中国科学院古生物学与古人类学科基础研究特别支持基金和中国科学技术部的资助。中国科学院新疆分院开发处、新疆维吾尔自治区及阿勒泰地区有关各级文物管理部门、新疆建设兵团 182 团和喀拉布勒根乡政府对我们的野外工作给予了大力的支持和协助。孟津的工作得到美国自然科学基金及美国自然历史博物馆资助。新疆地质矿产局测绘队苏剑锋参加了野外考察工作。作者在此表示衷心的谢意。

TWO PETROSALS OF GLIRIFORM MAMMALS FROM LATE OLIGOCENE OF TIEERSIHABAHE, XINJIANG UYGUR AUTONOMOUS REGION, CHINA

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Abstract Two petrosals from the Late Oligocene of the northern Junggar Basin, Xinjiang Uygur Autonomous Region of China are described and are assigned to ? Yindirtemys and ? Sinolagomys or Desmatolagus based on sizes and morphologies. The unit formed by a fused bulla and petrosal, the spongy bullar wall and the anterior position of the entrance for the stapedial artery into the tympanic cavity indicate that petrosal A is most likely from an ochotonid. Absence of grooves and foramina for the internal carotid artery around the promontorium suggests petrosal B probably belongs to the ctenodactylid Yindirtemys. If the identifications are confirmed, these specimens represent the first records of ear regions in the two taxa.

Key words Late Oligocene, North Junggar Basin, Gliriform petrosals

1 Introduction

Living lagomorphs contain 12 genera belonging to two families: Leporidae and

Ochotonidae. Leporidae consists of 11 genera, whereas Ochotonidae has only one, namely, *Ochotona*. Fossil records, however, show a different picture: there are 25 genera of ochotonids and 31 of leporids (McKenna and Bell, 1997). Apparently, *Ochotona* is a relic of a once prosperous group in geological history. Although fossil lagomorphs were known in the Tertiary of America, Europe and Africa, only in Asia the record is continuous (Bohlin, 1942; Sych, 1975; McKenna, 1982; Huang, 1987; Tong, 1989). If *Mimotona* is considered a lagomorph (McKenna, 1982; Li and Ting, 1985; 1993), the fossil history of lagomorph can be traced as early as in the Paleocene in Asia. Our knowledge of early lagomorph morphology is unbalanced because fossil lagomorphs, particularly early Tertiary ochotonids, are known primarily from jaws and teeth.

Living members of the rodent family Ctenodactylidae are found in desert or semi-desert areas of North and East Africa; they belong to four genera and 6 species (George, 1974; Nowak and Paradiso, 1991). Fossil ctenodactylids in eastern and central Asia are abundant. About 10 genera including 30 species have been reported from the early Oligocene through Miocene of North China, Mongolia, Kazakhstan, Pakistan, India, Saudi Arabia, Turkey, Israel and Libya (Wang, 1997 and references therein), although views about the content and subdivisions, particularly the fossil taxa, of the family vary from author to author (Flynn et al., 1986; Wang, 1997; McKenna and Bell, 1997; Dashzeveg and Meng, 1998). Nonetheless, the family Ctenodactylidae is important for rodent phylogeny because of its possible sister-group relationship with hystricognathous rodents (Luckett and Hartenberger, 1985; Meng, 1990; Bryant and McKenna, 1995) and in Asian biostratigraphy because of its abundance in fossil records during the mid-Tertiary. Their appearances in the Oligocene are probably related to the environmental changes across the Eocene-Oligocene boundary, an event termed "the Mongolian Remodeling" (Meng and McKenna, 1998). As in the case of ochotonids, most fossil species of the Ctenodactylidae are represented by dental material and only a few poorly preserved cranial specimens have been reported (Bohlin, 1946; Wang, 1997). Auditory region is little known in early ctenodactylids. Ear region plays an important role in understanding the phylogeny of the Ctenodactylidae and is represented almost exclusively by extant taxa whenever that region is involved in phylogenetic analyses(Lavocat and Parent, 1985; Meng, 1990; Bryant and McKenna, 1995).

Here we describe two ear regions, which we believe probably belong to an ochotonid lagomorph, ? Sinolagomys or Desmatolagus, and a ctenodactylid rodent, ? Yindirtemys. Both were collected from the late Oligocene Tieersihabahe locality on the northern rim of the Junggar Basin of Xinjiang, northwest China. In a previous study, a hedgehog petrosal from the same locality and beds has been described (Meng et al., 1999). That petrosal was considered to be from Amphechinus and most likely A.

cf. A. rectus based on the high frequent occurrence of the genus in the fauna, its relative body size and morphology. The assignment is now confirmed by the discovery of a new petrosal being associated with teeth and other bony elements of an individual Amphechinus from the same locality. This demonstrates that an isolated petrosal can be reliably identified, at least in some cases, to generic or even species level.

2 Identification

We have identified the following genera and species from the Tieersihabahe fauna collected during last two field seasons: Insectivora (Amphechinus kansuensis, Aminimus, A. cf. A. rectus, Talpinae gen. et sp. indet., Heterosoricinae gen. et sp. indet., Crocidosoricinae gen. et sp. indet.), Chiroptera Incertae familiae, Lagomorpha (Desmatolagus sp. (? shargaltensis), D. cf. D. gobiensis, Desmatolagus sp. nov., Sinolagomys major, S. kansuensis), Rodentia (Eutamias sp., Sciuridae gen. et sp. indet., Yindirtemys cf. Y. deflexus, Y. ambiguus, Eucricetodon sp. nov., Vasseuromys sp. (=Glirulus sp., Wu et al., 2000), Gliridae gen. et sp. indet., Tachyoryctoides brutschewi, Pseudotheridomys asiaticus, Parasminthus tangingoli, P. asiae-cetralis, P. parvulus, Plesiosminthus sp., Litodonomys sp., Ansomyinae gen. et sp. nov.), other taxa include: Didymoconus sp., Indricotheriinae gen. et sp. indet., Eumeryx sp. (large), Eumeryx sp. (small) and Bovidae gen. et sp. indet.

Comparing the size and morphology among the taxa discovered from the locality, the two petrosals do not belong to Insectivora (Erinaceidae, Talpidae, Soricidae), Chiroptera, Perissodactyla (Indricotheriinae), Artiodactyla (Cervidae, Didymoconidae. Nor do they likely belong to Eomyidae, Cricetidae, Zapodidae, and Gliridae of Rodentia, because the species of these rodents from the locality are too small to match the size of either petrosal. Among the rest species, petrosal A, which is a unit formed by a fused bulla and petrosal, most likely belongs to Sinolagomys. As in Ochotona, the bullar wall is spongy and fused to the petrosal to form a unit that has a relatively loose connection with surrounding cranial elements. The entrance foramen for the stapedial artery into the middle tympanic cavity penetrates the bullar wall and is located relatively anterior to the jugular foramen as in lagomorphs in which the stapedial is present. Although Desmatolagus is also placed in Ochotonidae (McKenna and Bell, 1997), it is represented by fewer specimens and has a lower chance to match petrosal A. Petrosal B probably belongs to Yindirtemys because the genus is represented by the large number of specimens among large-sized taxa from this locality. In addition to size, lack of grooves on the promontorium for the internal carotid or stapedial arteries also suggests this taxonomic assignment, because the internal carotid system is totally lost in Ctenodactylidae, whereas it is usually present in relatives of other rodents found in this locality.

3 Description

Petrosal A (? Sinolagomys or Desmatolagus), IVPP V 12432, pl. I a~e)—As we did in the previous paper about an isolated petrosal of an erinaceid (Meng et al., 1999), the petrosal is orientated in such that the cranial side is referred to as the dorsal and the promontorium side as the ventral. The bulla is fused to the petrosal so that the ear region can be considered as one unit for convenience of description. Due to breakage to the lateral portions of the bulla and petrosal, the external auditory meatus, the epitympanic recess, the lateral wall of the vestibule, and the stylomastoid foramen are gone but the tympanic cavity is exposed. The external surfaces of the bulla and the mastoid were worn, revealing the spongy structure of the bullar wall that surrounds the entire ventral side of the tympanic cavity. Through the breakage, loose sands that filled the tympanic cavity were removed and structures within the tympanic cavity can be observed. The intact incus and the head of the malleus were articulated in preservation and were displaced from their anatomical position. These minute bones were removed from the cavity and separated during preparation.

The ectotympanic bulla is fused to the petrosal. On the dorsal side of the ear region, the suture between the petrosal and the bulla is recognizable. posteromedial side of the ear unit, the conjunction between the bulla and the mastoid of the petrosal is indicated by a notch, which can be traced to the dorsal side of the ear. This is also confirmed within the tympanic cavity by the position of the tympanic ridge that held the tympanic membrane in life and the relationship of the mastoid part with other structures such as the bony connection with the promontorium. Externally, the bulla appears inflated but internally the tympanic cavity is not very large. This is because the bullar wall is thick, particularly at its anterior end and lateral portion. The bullar wall consists of spongy or porous bony structures. The anterior end of the bulla extends more anteriorly than the anterior tip of the petrosal. At the antero-ventral aspect, the bulla appears flat and the bullar wall of this region is the thinnest. The external auditory meatus must have been located lateral to this flat area, judging by the position of the tympanic ridge for the eardrum within the bulla. At the medial aspect of the bulla, there is a circular foramen for the stapedial artery. This foramen is entirely within the ectotympanic and is relatively anterior than the jugular foramen. The foramen continues into the tympanic cavity as a bony tube for the stapedial artery.

Within the bulla, the tympanic cavity and the space formed by expansion of the mastoid are confluent posterior to the promontorium. On the ectotympanic part, there are numerous septa on the medial or dorsal side of the tympanic ridge. These septa are roughly perpendicular to the circular tympanic ridge and externally they merge with the porous bony structures. A large portion of the tympanic ridge is preserved, from which a diameter of 5 mm of the tympanic membrane is measured. The space

between the ridge and the lateral portion of the bulla is narrow and the external meatus is assumed not elongated. Between the ridge and the external acoustic meatus, the surface of the bullar wall is smooth. Because the ectotympanic curves inward to cover extensively the roof of the tympanic cavity on the medial and anterior sides of the promontorium, therefore, structures such as the tegmen tympani on the anterolateral side of the promontorium is not observed. The eustachian canal exists in the tympanic cavity at its anterior corner; the canal is entirely enclosed in the bullar wall and has a circular cross-section.

On the mastoid part of the inflated bulla, there are only a few irregular septa bracing the bony gyrus of the lateral semicircular canal; the latter projects out of the bony wall of the petrosal. Usually, the gyrus of the lateral semicircular canal surrounds the fossa for the stapedius muscle (Meng and Fox, 1995). In petrosal A, however, the space surrounded by the canal is also porous, suggesting that a stapedius muscle may not attach to this area or may be absent. A small bridge of the mastoid that connects to the posterior rim of the oval window consists part of a larger plate that fused to the promontorium and the bony canal for the facial nerve; but the lateral portion of that plate and part of the facial canal were broken. This connection suggests that the mastoid tubercle (probably including the tympanohyal) is connected with the promontorium.

The promontorium is perfectly preserved. Its medial and anterior sides are covered by the spongy ectotympanic. The promontorium has two parts, represented by two bulged areas on the ventral surface. The anterior part apparently houses most of the cochlear canal and the posterior one contains primarily the vestibule of the inner ear and the basal portion of the cochlear canal. They are separated externally by a distinctive groove. Judging from the external shape of the promontorium, the cochlear canal coils around an axis that points anteriorly and has more than two turns.

The most prominent feature on the promontorium is a large, complete bony tube for the stapedial artery. This tube starts at the posteromedial corner of the cavity and extends laterally to across over the fenestra vestibuli (or oval window). It continues anterolaterally, crossing the ventral side of the bony canal for the facial nerve, and exits from the tympanic cavity. The entire course of the stapedial artery within the tympanic cavity is enclosed in the bony tube. The tube is constant in its size except a narrower neck at the section where it passes over the fenestra vestibuli, or through the stapedial foramen of the stapes. In this region, the wall of the tube is thinner; the internal diameter of the tube may not change. Owing to breakage, the fate of the stapedial artery on the dorsal side of the petrosal is unknown, but the bifurcation of the ramus superior and ramus inferior, if present, must be in the braincase.

The fenestra vestibuli is greatly elongated, with its central part blocked by the stapedial tube and its long axis at a ca. 30 degree angle to the frontal plane of the

skull. The plane of the fenestra vestibuli faces ventrolaterally. The shape of the fenestra vestibuli dictates that the footplate of the stapes must be elongated and the stapedial foramen must be very large. The fenestra cochlea at the posterior end of promontorium is much smaller than the oval window. Its ventral rim is formed by the bony tube for the stapedial artery, but is not shielded by the latter. Posterior to the fenestra cochleae, the gyrus for the lateral semicircular canal juts out the surrounding petrosal bone and encloses a fossa that is commonly for the attachment of the stapedius muscle (Meng and Fox, 1995). The fossa faces lateroventrally and its bottom is also formed by the spongy bone.

Because the breakage went through the foramen acousticum superius within the internal acoustic meatus and the lateral part of the vestibule, some features are undeterminable, whereas others are revealed. The epitympanic recess is unknown. The facial canal penetrates the petrosal and enters a bony canal on the dorsal side of the stapedial canal. The space for the genicular ganglion is visible, from which the canal for the facial nerve extends posteriorly through the tympanic cavity; most of the facial canal, however, was broken. From the relation of the facial canal with the mastoid of the petrosal, it is plausible that the facial nerve is completely enclosed in the bony canal until it exits the tympanic region at the stylomastoid foramen. From the space for the genicular ganglion a smaller canal for the greater petrosal nerve stretches anteriorly and enters the braincase through a slit-like opening at the anterior edge of the petrosal. The pathway between the superior vestibular area of the cochlear canal and the vestibule is also exposed. The vestibule is spatial, within which the primary and secondary spiral laminae and the vestibular fissure between the laminae (see Meng and Fox, 1995) at the basal part of the cochlear are visible.

On the dorsal side of the ear region, although the mastoid and the petrosal medial to the subarcuate fossa and the internal acoustic meatus are porous, the surface of the bone is smooth. The partially preserved subarcuate fossa suggests a moderate size and depth. At its posterior rim, the anterior semicircular canal is exposed. The cochlear area within the acoustic meatus is in a good condition, in which the foraminous spiral tract, the inferior vestibular area and the foramen singulare are all visible. On the medial side of the dorsal petrosal, a small aquaeductus cochleae opens lateral to the petrosal-ectotympanic suture.

The incus is intact and the malleus head was preserved. Before preparation, the incus articulated with the malleus in their original anatomic relation, although both elements have been displaced within the tympanic cavity. Preparation easily separated the two minute elements. The maximum length of the incus is about 1.5 mm. Its body can be roughly divided into two parts. The dorsal part that bears the short process is thick and rounded, and together with the conical short process it is tear-drop shaped. As a common case in mammals, the short process is anchored to the incudal

fossa in the epitympanic recess by the posterior ligament of the incus. However, because of the breakage, it is unknown whether the epitympanic recess was normal or inflated as in some extant rodents. The ventral part of the incus body that bears the long process is thinner; therefore, the medial surface of the body is gently convex, whereas the lateral shows some unevenness. The incudomalleolar facet faces anteriorly and extends on the lateral surface of the incus body. The dorsal and medial rim of the articulation facet is well defined. The long process is about twice as long as the incus body and is curved, with a pointed tip. The lentiform process, which articulates to the head of the stapes in life, is absent.

The malleus was broken from its neck and the manubrium was missing. The head of the malleus is normal in size and bears a short anterior process. From what left at the neck, there is a thin lamina that forms the basal part of the neck. How much this lamina extends anteriorly is undeterminable.

Petrosal B (? Yindirtemys, IVPP V 12433, pl. I f,g)—The morphology of petrosal B is relatively simple. The promontorium is somewhat inflated and its surface is not smooth but bears no grooves for the internal carotid and stapedial arteries. fenestra cochleae is roughly circular, with its medial edge slightly extended medially. Through the fenestra cochleae, the primary and secondary spiral laminae within the cochlear canal are visible. On the lateral side of the promontorium, the fenestra vestibuli is located. The entire rim for attachment of the footplate of the stapes is oval and is deeply socketed. The bony bridge between the two fenestrae is broad. A blunt process dorsolateral to the fenestra cochleae and dorsomedial to the fenestra vestibuli is developed. Posterior to the process is the deep stapedius fossa. Anterior to the fenestra vestibuli is a large, concave fossa, the tegmen tympani; its medial edge is curved and well defined on the lateral side of promontorium. The thin bony lamina forming part of the tegmen tympani, which is the floor for the canal housing the facial nerve, is broken. Because of the breakage, the space for the geniculate ganglion, the canal for the facial nerve that courses posteriorly, and a smaller canal for the greater petrosal nerve that extends anteriorly, are exposed. Lateral to the fenestra vestibuli, the floor of the canal for the facial nerve is originally incomplete. The canal extends to the stapedius fossa. The facial nerve in life should have existed in the ear region through the stylomastoid foramen. Lateral to the canal for the facial nerve is the epitympanic recess, which in life houses the articulation of the malleus and incus. The fossa is roughly oval with its long axis oriented anteroposteriorly.

Both lateral and medial edges of the petrosal are broken. On the medial side, a distinctive aquaeductus cochlea is observed. A curved sulcus leading to a blind canal around the anteromedial edge of the petrosal is of unknown function. On the dorsal side of the petrosal, the subarcuate fossa is deep. Its posterior edge is broken, exposing part of the anterior semicircular canal. Anterior to the subarcuate fossa is the

internal acoustic meatus. Within the meatus, the transverse crest divides the meatus into dorsal and ventral portions. The dorsal orifice is for the outgoing facial nerve and the area cribrosa superior that is for passage of a branch of the vestibular nerve. The ventral orifice contains the foramen singulare transmitting a branch of the vestibular nerve to the posterior ampulla of the semicircular canal and the spiral, cribriform belt, that is, the foraminous spiral tract for the passage of the cochlear nerve (see Meng and Fox, 1995; Fox and Meng, 1997).

4 Discussion

Petrosal A (?Sinolagomys or Desmatolagus) apparently represents a type of derived ear because of the following features. First, the bullar wall fuses to the petrosal so that the ear region forms a unit. As in Ochotona, this unit probably has a weak connection with surrounding cranial elements and would be easily detached from the cranium during the preservation. Second, numerous septa within the bulla are developed. In this regard, petrosal A differs from the ear of Ochotona, in which the internal septa are absent. Third, the bullar wall is thick and spongy, similar to that of Ochotona. However, in early leporid such as Palaeolagus (Meng, 1991) and ochotonid such as Prolagus (Dawson, 1969), the bullar wall is thin and solid. Fourth, the promontory artery is lost. Presence of the promontory artery is a primitive condition in mammals (Wible, 1986) and in rodents (Meng, 1990). A laterally placed internal carotid artery is reported from Palaeolagus and is considered primitive for lagomorphs (Meng, 1991). Fifth, the carotid foramen within the bullar is derived compared with a condition in which the course of the artery is between the bullar wall and the petrosal (Wible, 1986). As in Prolagus and Lepus the carotid foramen in petrosal A penetrates the bullar wall. In addition, the carotid foramen is primitive ventral to the jugular foramen but in lagomorphs in which the foramen exists in it is shifted more anteriorly. In Ochotona, however, the carotid foramen is absent. Sixth, the promontorium is inflated and shows two sections. Finally, the fenestra vestibuli and, by implication, the footplate of the stapes are elongated. All these features indicate that petrosal A is morphologically advanced. If the identification is correct, this suggests that late Oligocene ochotonids already showed specialization of the ear region.

Petrosal B (? Yindirtemys) is also derived primarily in that the promontorium is inflated, the fenestra vestibuli is deeply socketed, and the internal carotid system is lost. Although lack of the internal carotid artery is a derived condition found in Ctenodactylidae and hystricognathous rodents (Meng, 1990; Bryant and McKenna, 1995), this condition in fossil ctenodactylid is unknown. If our identification of petrosal B as ? Yindirtemys is correct, it shows that loss of the internal carotic artery already occurred in early ctenodactylids.

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Explanations of Plate I

Petrosals and ear ossicles of two gliriform mammals from the late Oligocene of North Junggar Basin, Xinjiang a~e, ?Sinolagomys or Desmatolagus (IVPP V 12432); f~g, ?Yindirtemys (IVPP V 12433)

In a~c, the upper is anterior for the specimens; in g~f, the left is toward the anterior

d1~3, medial, posterior and lateral sides of the malleus head (d2 showing the articular facet to the incus)

e1~5, lateral, posterodorsal, anterior (artiuclar facet for the malleus), medial, and posteroventral sides of the incus (See text for descriptions)

Abbreviations: aqc, aquaeductus cochleae; bmc, contact region for the bulla and mastoid; bu, bulla (with spongy structures); bus, internal bullar septa; con, canal for the cochlear nerve within the internal acoustic meatus; csa, canal (foramen) for the entrance of the stapedial artery; er, epitympanic recess; euc, eustachian canal; fac, canal for the facial nerve; faci, canal for the facial nerve within the internal acoustic meatus; fc, fenestra cochleae; fsm, fossa for the stapedius muscle; fv, fenestra vestibuli; gpc, canal for the greater petrosal nerve; iam, internal acoustic meatus; mas, mastoid of the petrosal; pm, promontorium; sf, subarcuate fossa; stc, bony canal for the stapedial artery; std, dorsal exit of the stapedial artery; tc, transverse crest; tt, tegmen tympani; ves, vestibule

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