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THE INTERNAL CAROTID ARTERY IN EARLY EUTHERIANS

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Although evidence from comparative anatomy and embryology shows that only one internal carotid artery is present among extant eutherians, numerous early eutherians have two vascular-like grooves on the petrosal suggesting the presence of two separate internal carotids. It is argued here that the most acceptable model for the interpretation of this morphology places the single internal carotid in the lateral groove and a venous channel (inferior petrosal sinus) in the medial one. This lateral course for the internal carotid artery is not necessarily primitive for Eutheria, only widespread among early groups. The earliest known eutherian basicrania have only a medial groove and therefore, a medial course to the internal carotid. However, based on ontogenetic research, this medial course in the earliest known eutherians was most likely not identical with the medial course in non-eutherian mammals.

Key words: internal carotid artery, basicrania, early eutherians, petrosal, inferior petrosal sinus.

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INTRODUCTION

In a report on the middle Eocene fauna from the Bridger Basin of Wyoming, Matthew (1909) proposed that three separate longitudinal arteries — separate lateral and medial internal carotids, plus the stapedia artery — were present in the tympanic region of the carnivore-insectivore ancestor (fig. 1). The presence of three grooves running across the tympanic region in the Bridger miacids led Matthew to this conclusion. One groove ran medially around the promontorium of the petrosal, like the course of the internal carotid artery in extant carnivores. A second groove travelled across the promontorium, like the internal carotid of extant insectivores. Finally, a third groove ran laterally from the second groove to the fenestra vestibuli, like the course of the stapedia artery in modern insectivores. Of these three ancestral arteries, Matthew proposed, extant insectivores presumably retain only the two lateral vessels, while extant carnivores presumably retain the medial one. Therefore, under this scheme the internal carotid artery of extant carnivores with its me-

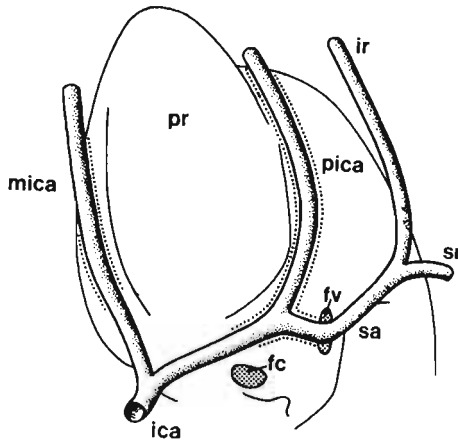


Fig. 1. A schematic representation of Matthew's model for the internal carotid system in the carnivore-insectivore ancestor. A left petrosal bone is shown in ventral aspect with a medial groove and internal carotid artery (*mica*), a lateral groove and internal carotid artery (*pica*) and a stapedial groove and artery (*sa*). Presumably both the medial and lateral internal carotids supply the brain, while the stapedial artery divides into a superior ramus (*sr*) feeding the dura and orbit and an inferior ramus (*ir*) feeding the upper and lower jaws. Abbreviations as on page: 291.

dial course is not the homologue of the laterally placed internal carotid artery of extant insectivores.

In recent years a number of researchers (McKenna 1966; Van Valen 1966; Szalay 1972, 1975; Archibald 1977; Bugge 1978, 1979) have adopted Matthew's scheme as the model of the primitive eutherian internal carotid system. The terms medial internal carotid artery and promontory artery have been coined to distinguish the two carotids of Matthew's scheme. Support for this model lies in the widespread occurrence of "miacid-like" tympanic morphologies among diverse late Cretaceous-early Tertiary eutherian groups (Table 1).

Table 1

Late Cretaceous-early Tertiary eutherian groups exhibiting a morphology consistent with Matthew's "two-carotid" scheme ¹⁾

"Bug Creek Petrosals"	— MacIntyre 1972
<i>Palaeoryctes</i>	— Van Valen 1966, McKenna 1966
Leptictidae	— Butler 1956, McKenna 1966
Hyaenodontidae	— Piveteau 1935
Carnivora	— Matthew 1909
Oxyaenidae	— Matthew 1909
Artiodactyla	— Whitmore 1953, Dechaseaux 1974
Arctocyonidae	— Russell 1964
Condylarthra	— Russell 1964, Gazin 1965
Rodentia	— Lavocat 1967, Wahlert 1974, Parent 1980.

¹⁾ This morphology is most often present in the form of vascularlike grooves on the petrosal bone. In some cases, for instance, *Palaeoryctes*, the presence of an artery is inferred from foramina alone.

Three recent articles raise serious questions about the validity of the distinction between the medial internal carotid and promontory arteries made by Matthew's scheme. Cartmill and MacPhee (1980) suggest that these two vessels may be homologues differing only in their positions relative to the promontorium. Providing support for this, Presley (1979) shows that embryologically the mammalian internal carotid is always a derivative of the dorsal aorta and that its medial or promontorial position can be interpreted as a mere result of differential growth rates in the surrounding chondrocranial elements. MacPhee (1981) notes that the internal carotid artery in living eutherians occupies a range of positions from near the midline to the lateral side of the promontorium (cf. Werner 1960; Wible 1980). Further, in its course, this vessel is always accompanied by the internal carotid nerve, a significant point considering the very conservative nature of nerve pathways. This combined with other evidence from comparative anatomy suggests to MacPhee that there is, in homological terms, only one internal carotid artery with variant pathways.

According to the comparative anatomical and embryological evidence, the medial internal carotid and promontory arteries are merely two character states of the eutherian internal carotid artery. Yet, if one accepts the existence of a single eutherian artery, the problem of the two "internal carotid" grooves in the fossil basicrania is left unanswered. If only a single internal carotid artery could have been present in these early eutherians, in addition to the stapedia artery, then which groove did the internal carotid occupy and what occupied the other groove?

MORPHOLOGICAL ALTERNATIVES

With the rejection of Matthew's "two-carotid" model, two plausible interpretations of the "miacid-like" basicranial morphology remain: (1) a medial; or (2) a lateral (or promontorial) course for the single internal carotid artery. Both of these alternatives have been suggested to account for the morphology in particular fossils. However, a careful evaluation shows that one of these alternatives offers a more acceptable model.

(1) A medial course: In his description of *Meniscotherium*, an early Eocene condylarth, Gazin (1965) placed the internal carotid artery in the medial groove and branches of the tympanic nerve plexus in the lateral (or promontorial) one. However, evidence from comparative anatomy shows that this is an unlikely interpretation. The lateral groove in *Meniscotherium* and other early eutherians runs forward toward the apex of the petrosal anteromedially across the promontorium, while the tympanic nerve and its rostral continuation, the lesser petrosal nerve, follow

a more lateral course across the promontorium forward to the foramen ovale (MacPhee 1977, 1981; personal observations). Also, the tympanic nerve rarely leaves any bony trace in living eutherians and then, certainly not of a broad vascular-like variety (personal observations).

The problem with any model calling for a medial course to the internal carotid artery in the "miacid-like" basicrania is in filling the lateral groove. When a lateral groove is present in extant eutherians, it normally contains an internal carotid artery (promontorial character state). There is only one structure besides an internal carotid artery that has been found by itself in a lateral groove in extant eutherians; this is the internal carotid nerve (Conroy and Wible 1978). However, the internal carotid artery in this animal, *Lemur variegatus*, was lacking; in other specimens of this same species, the internal carotid artery has been found in the lateral groove (Tandler 1899). It is highly unlikely that the early eutherian internal carotid artery was in the medial groove and the internal carotid nerve in the lateral one, since these two structures travel together in living eutherians.

It appears that a medially placed internal carotid artery is an unlikely alternative for early eutherians possessing a lateral groove. However, there is another possibility that must be considered; the lateral groove may have contained a structure not found among living mammals. Such a structure is a collateral arterial branch, that is, an artery running collaterally to the medially placed internal carotid (cf. Presley 1979; Parent 1980). Although this possibility cannot be ruled out entirely, it is not necessary to rely on the formation of a *de novo* collateral artery when the following model can fill the fossil morphology with structures known to occur in extant eutherians.

(2) A lateral course: Whitmore (1953) suggested that the inferior petrosal sinus ran in the medial groove and that the internal carotid artery ran across the promontorium in *Merycoidon culbertsonii*, a White River Oligocene artiodactyl. In addition, Butler (1956), Lavocat (1967) and Wahlert (1974) have offered the inferior petrosal sinus as an alternative to the medial internal carotid artery in their interpretations of the basicranial morphology in particular fossils. This model (fig. 2) fills the lateral groove with the only structure known to run in the lateral groove in extant eutherians: an internal carotid artery (promontorial character state). Also, based on its morphology in extant forms, the inferior petrosal sinus is a plausible occupant of the "miacid-like" medial groove.

Among extant eutherians, there are three different pathways followed by venous channels running medial to the promontorium. This is best understood in terms of the ontogeny of this region. In the chondrocranium of an eutherian embryo (fig. 3), the cochlear capsule (a precursor of the petrosal bone) and parachordal plate (the future basioccipital in this region) are separated by the basicapsular fenestra and joined by anterior

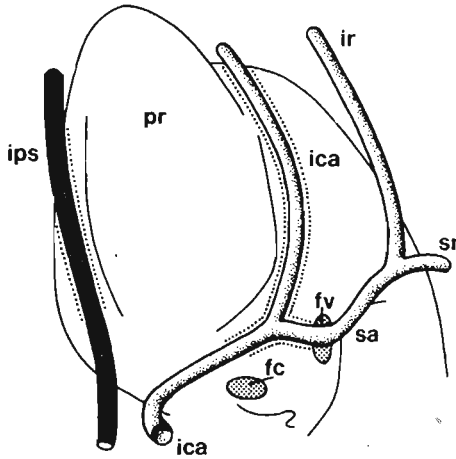


Fig. 2. The interpretation of the early eutherian "miacid-like" basicranial morphology accepted here. The single internal carotid artery (promontorial character state) occupies the lateral groove, while an inferior petrosal sinus runs medial to the promontorium. Abbreviations as on page: 291.

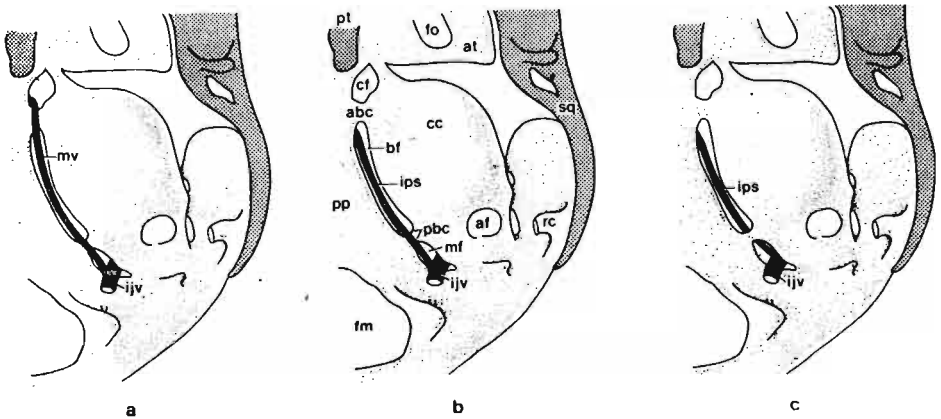


Fig 3. Schematic representations of three left tympanic regions of an idealized eutherian chondrocranium in ventral aspect (modified after MacPhee 1981), showing the three pathways for the embryonic medial venous channel: a an extracranial course; b a course through the basicapsular fenestra; c an intracranial course. Terminology for the venous channel is as in the adult. The regular stipple indicates membrane bone. Abbreviations as on page: 291.

and posterior basicapsular commissures.²⁾ A complex system of venous channels connecting the internal jugular vein and cavernous sinus runs through this region. Three possible pathways, occurring singly or in combination, have been found in embryos studied to date: (1) an extracranial course (ventral to both commissures and through the carotid foramen) (fig. 3a); (2) a course through the basicapsular fenestra (ventral to the posterior commissure and dorsal to the anterior one) (fig. 3b); and (3) an

²⁾ See Beer (1937) for variations on this morphology in eutherian chondrocrania.

intracranial course (dorsal to both commissures) (fig. 3c). These same three pathways are found among adult eutherians: (1) an extracranial medial vein entering the cranial cavity *via* the carotid foramen, as in *Canis familiaris* (Miller *et al.* 1964); (2) an inferior petrosal sinus running through the patent basicapsular fenestra, as in *Tupaia* (MacPhee 1981), soricomorph insectivores (McDowell 1958; MacPhee 1981) and megachiropterans (personal observations); and (3) an intracranial inferior petrosal sinus, as in *Canis familiaris* (Miller *et al.* 1964) and *Homo*. It is not clear which of these pathways represents the primitive state for Eutheria, but as is shown below, this is not essential for interpreting the fossil morphology.

These three pathways for the medial venous channel may account for the variable morphologies of the medial groove in the fossil basicrania. In some fossils, for instance, *Meniscotherium* (Gazin 1965) and *Viveravus minutus* (Matthew 1909), the medial groove is merely an open channel between the basioccipital and petrosal. This medial groove may have contained an extracranial medial vein as in *Canis familiaris*. In other fossils, for instance, *Pleuraspidothorium aumonieri* (Russell 1964), *Arctocyonides arenae* (Russell 1964) and *Dichobune leporina* (Dechaseaux 1974), the medial groove actually leads to a patent basicapsular fenestra (personal observations); this structure has been mistakenly identified as a posterior carotid foramen in these forms. An inferior petrosal sinus as present in soricomorph insectivores may have passed through this opening.³⁾ Finally, in other fossils, like *Vulpavus ovatus* (Matthew 1909; personal observations), the medial groove is actually a closed canal between the basioccipital and petrosal; this may have given passage to an inferior petrosal sinus as in *Homo*. It is interesting that of these three medial "groove" morphologies⁴⁾, only one, the open channel between the petrosal and basioccipital, gives passage to an internal carotid artery among living eutherians, while all three are known to give passage to a venous channel.

Although a venous channel fits the medial "groove" morphology in the fossil basicrania, another possibility must be considered here. The medial "groove" may have (also?) contained an artery running collaterally to the laterally placed internal carotid artery (cf. Presley 1979; Parent 1980). The ascending pharyngeal artery follows a somewhat analogous pathway in some extant eutherians (cf. Daniel *et al.* 1953; Cartmill 1975) and was likely present in early eutherians (MacPhee 1981). However, it is

³⁾ However, a patent basicapsular fenestra is found in various adult extant eutherians, for instance microchiropterans, without transmitting any structures (personal observations).

⁴⁾ There is in fact a fourth morphology exhibited by the isolated petrosals from the late Cretaceous Bug Creek Anthills of Montana. These fossils apparently have two medial grooves (MacIntyre 1972). This morphology may have housed two venous channels as in *Canis*. However, the interpretation of these fossils awaits further study.

argued here that this vessel was an unlikely occupant of the medial "groove" in the fossils. First of all, the course of the ascending pharyngeal artery, like that of a medially placed internal carotid, cannot account for the three different medial "groove" morphologies found in early eutherians. The ascending pharyngeal artery in extant forms always follows an extracranial course. Therefore, of the three different medial "groove" morphologies, only an open groove between the basioccipital and petrosal could have housed an ascending pharyngeal artery. Further, when the ascending pharyngeal artery runs medial to the auditory bulla in extant eutherians, it does not run in a groove between the basioccipital and petrosal. Its course is more superficial along the medial bullar wall and not in the area of the basioccipital-petrosal junction (personal observations). Although the ascending pharyngeal artery was likely a part of the primitive eutherian carotid system, its course among extant forms makes it an unlikely choice for the medial "groove".

THE PRIMITIVE COURSE OF THE EUTHERIAN INTERNAL CAROTID ARTERY

Based on the above, it seems most likely that the internal carotid artery occupied the lateral groove in the "miacid-like" basicrania and that a venous channel ran medial to the promontorium. This does not necessarily imply that a lateral course for the internal carotid artery is primitive for Eutheria, only that it was widespread among early groups (see Table 1). In fact, the earliest known eutherian basicrania, *Kennalestes*, *Asioryctes* and *Barunlestes* from the late Cretaceous of Asia (Kielan-Jaworowska 1981; Kielan-Jaworowska and Trofimov 1980), lack a lateral groove. With the presence of a groove medial to the promontorium in *Kennalestes* and *Asioryctes*, Kielan-Jaworowska (1981:58) suggests that an internal carotid artery "as characteristic of marsupials" was present. However, this cannot be determined from the fossil evidence. In marsupials, the internal carotid artery runs medial to the auditory bulla (Tandler 1899; Archer 1976); *Kennalestes*, *Asioryctes* and most early eutherians lack bony bullae and likely had only membranous bullae as adults (Novacek 1977; Archibald 1977; MacPhee 1981). Although the presence of a medial groove (and the absence of a lateral one) in *Kennalestes* and *Asioryctes* suggests a medial course for the internal carotid artery, it does not show the relationship between that vessel and a membranous auditory bulla. However, such a membranous covering is present in mammalian embryos as the precursor of the auditory bulla (MacPhee 1977, 1981) and so, ontogeny provides a possible model for the fossil morphology.

In mammalian embryos, the developing auditory bulla makes its first appearance in the form of a connective tissue membrane, the fibrous

membrane of the tympanic cavity or FMTC of MacPhee (1977, 1981). The embryonic internal carotid artery follows one of three possible courses with respect to this membrane (fig. 4): (1) medial to the FMTC (and therefore, outside of the tympanic cavity); (2) within the substance of the FMTC; and (3) lateral to the FMTC (and so, within the tympanic

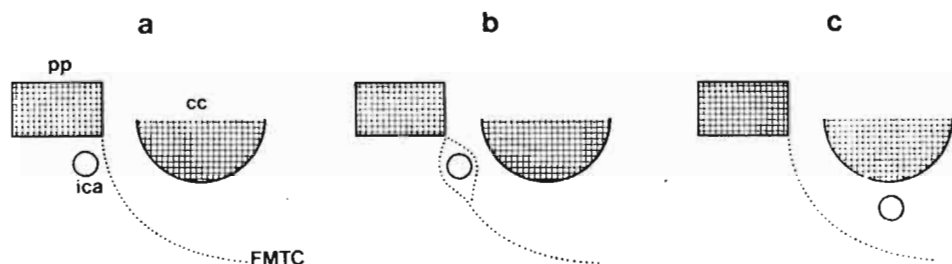


Fig. 4. Schematic representations of transverse sections through the tympanic region of three mammalian embryos, showing the relationship between the internal carotid artery and FMTC, the precursor of the auditory bulla: **a** the internal carotid runs medial to the FMTC; **b** the internal carotid runs through the substance of the FMTC; **c** the internal carotid runs lateral to the FMTC. Note that in **c**, the internal carotid can occupy a range of positions from the medial to the lateral side of the cochlear capsule. Abbreviations as on page: 291.

Table 2

	medial to FMTC	within FMTC	lateral to FMTC
Monotremata	★		
Marsupialia	★		
Edentata		★	
Macroscelidea			★
Lagomorpha			★
Carnivora			★
Insectivora			★
Scandentia			★
Dermoptera			★
Chiroptera			★
Primates			★
Artiodactyla			★
Cetacea			★
Pholidota		★	
Rodentia		★	

Incidence of internal carotid-FMTC relationships among mammalian embryos studied to date. In representatives of some eutherian orders, i.e., Lagomorpha and Carnivora, the internal carotid is enclosed within the FMTC in late ontogenetic stages for the formation of a carotid canal.

cavity). Preliminary observations on the incidence of internal carotid-FMTC relationships among mammalian embryos (Table 2) show the following: (1) in non-eutherian mammalian embryos, the internal carotid is excluded from the tympanic cavity by the FMTC (the morphology in *Tachyglossus*, the only monotreme studied to date, is not exactly comparable to that in marsupials, as relationships are somewhat altered by the posterior expansion of the nasopharynx and auditory tube); and (2) in eutherian embryos, the internal carotid artery follows a more lateral course either within the substance of the FMTC or included within the tympanic cavity by the FMTC.

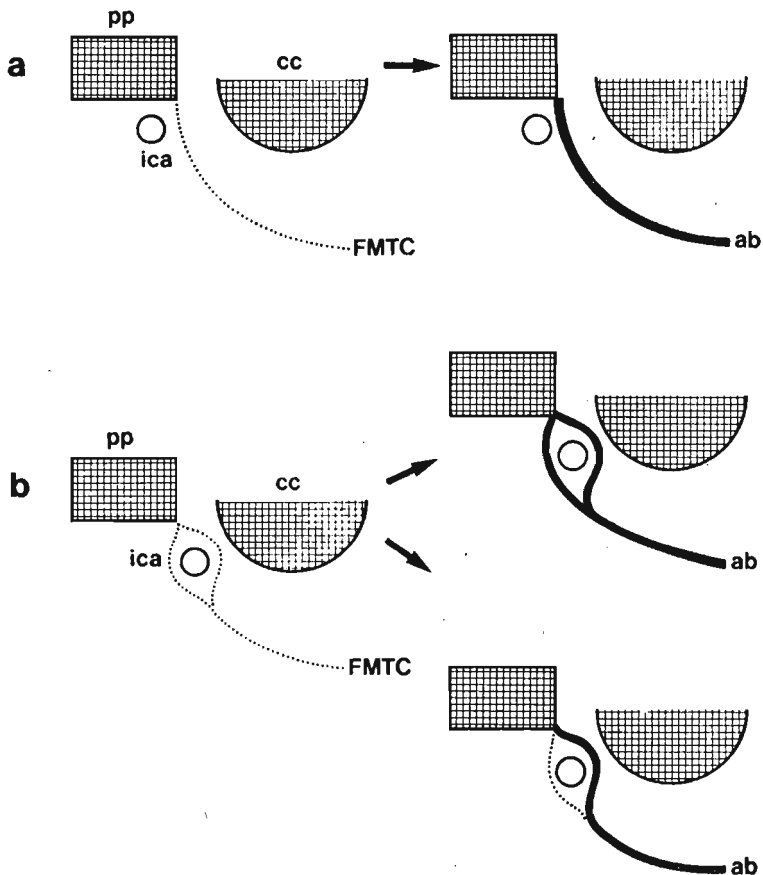


Fig. 5. Schematic representations of two developmental processes for the formation of an internal carotid artery running medial to the auditory bulla in the adult. In non-eutherian mammals (a), the internal carotid lies medial to the FMTC in the embryo. In later ontogenetic stages, the internal carotid is still excluded from the tympanic cavity by the formation of a bony bulla (the ectopterygoid in *Tachyglossus* and the alisphenoid in marsupials). In edentates (b), the internal carotid runs through the substance of the FMTC in the embryo. Later, the entotympanic can either form a complete or incomplete carotid canal around the artery. Abbreviations as on page: 291.

It is generally accepted that the primitive course of the mammalian internal carotid was medial to the promontorium and the auditory bulla as this is the condition in monotremes, marsupials, and some eutherians, including edentates (cf. Presley 1979). However, ontogenetic research shows that the edentate artery running medial to the bulla develops in a very different way than the artery in monotremes and marsupials. In non-eutherian mammals, the internal carotid is always excluded from the tympanic cavity, either by the FMTC or the bony bulla (fig. 5a). In contrast, the internal carotid in edentate embryos (*Dasypus novemcinctus* and *Bradypus*) runs through the substance of the FMTC (fig. 5b). Later, the entotympanic bullar elements form within the FMTC (cf. MacPhee 1979) around the internal carotid artery. The extent of entotympanic formation is variable; the internal carotid can either be enclosed within a canal in the entotympanic or merely excluded from the tympanic cavity by the entotympanic. This variable degree of entotympanic formation accounts for the observations in adult edentate skulls of complete and incomplete carotid canals (Kampen 1905; personal observations).

These preliminary ontogenetic observations confirm that the primitive course of the internal carotid artery in mammals was likely medial to the bulla (FMTC), the condition found in monotremes and marsupials. However, it is unlikely that this was also the primitive course of the eutherian artery, as this same pathway is not found among extant eutherians. The primitive eutherian internal carotid artery followed a more lateral course either through the substance of the FMTC or lateral to the FMTC within the tympanic cavity. The presence of a medial groove in *Kennalestes* and *Asioryctes* suggests a medial course for the primitive eutherian internal carotid. Yet, based on the above ontogenetic observations, this medial course was most likely not identical with the medial course of non-eutherian mammals.

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Abbreviations:

ab	auditory bulla
abc	anterior basicapsular commissure
af	aperture of fossula of cochlear fenestra
at	ala temporalis
bf	basicapsular fenestra
cc	cochlear capsule
cf	carotid foramen
fc	fenestra cochleae
fo	foramen ovale
fm	foramen magnum
FMTC	fibrous membrane of the tympanic cavity
fv	fenestra vestibuli
ica	internal carotid artery
ijv	internal jugular vein
ips	inferior petrosal sinus
ir	inferior ramus of stapedial artery
mf	metotic fissure
mica	medial internal carotid artery
mv	medial vein
pbcc	posterior basicapsular commissure
pica	promontory artery (lateral internal carotid artery)
pp	parachordal plate
pr	promontorium of petrosal
pt	pterygoid
rc	Reichert's cartilage
sa	stapedial artery
sq	squamosal
sr	superior ramus of stapedial artery

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