

15. Epitensoric Position of the Chorda Tympani in Anthropeoidea: a New Synapomorphic Character, with Remarks on the Fissura Glaseri in Primates

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15.1 Introduction

As is well known from human anatomy, the chorda tympani detaches from the facial nerve before its exit from the stylo-mastoid foramen; recurving around the hyoid it enters the tympanic cavity via a small foramen in the facial canal (canaliculus chordae tympani). Then, embedded in an epithelial fold, it passes between the crus longum of the incus and the malleus across the tendon of the tensor tympani muscle. Anteriorly, it is situated at the medial side of the anterior process of the malleus (Folianus) before it exits from the tympanic cavity through the petrotympanic fissure or fissura Glaseri (cf. Warwick and Williams, 1973, figure 286; Henson, 1974, figure 21A; and many other textbooks of human anatomy). The anterior process consists in fact of a small dermal bone called the gonial in the German anatomical literature (Gaupp, 1908, 1911, 1913), which is synonymous with the prearticular of vertebrate paleontology and English comparative anatomy (Williston, 1903; De Beer, 1937).

The chorda tympani nerve transmits fibers from the taste buds and to the salivary glands of the lower jaw. The complicated course of the nerve is tied to the evolutionary history of the mammalian middle ear which was carefully analysed by Gaupp (1913) and Goodrich (1930), to name only the most important early researchers. In fact, the chorda is a posttrematic branch of the facial nerve, which attains its dorsal and recurrent position due to the secondary evolutionary ascent of the mammalian middle ear from the angle of the lower jaw to the basicranium (Allin, 1975, Maier, 1990; Allin and Hopson, 1992).

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The mammalian chorda tympani was first analyzed from a comparative point of view by Bondy (1907). His study was based on histological sections of adult specimens. Although he was mainly interested in the pars flaccida of the tympanic membrane, he also presented many details on the complete course of the chorda tympani in more than 50 species of mammals representing most orders. Among these taxa were several primates, i.e., *Macaca*, *Ateles*, *Hylobates* and *Homo*. He realized that these ‘higher’ primates are all similar in the relationship of the chorda tympani and the tensor tympani muscle, i.e., the nerve passes above this muscle. This is in clear contrast to the majority of mammals from monotremes through marsupials, to ‘insectivores’, bats, rodents, carnivores and cetartiodactyls, where the nerve runs ventral to the muscle. Next to the studied primates only a few other species studied by Bondy showed a dorsal course of the nerve or a course that pierced the muscle tendon: *Myoxus* and *Sciurus* (rodents), *Herpestes* (carnivores), and *Equus* (perissodactyls).

These observations of Bondy (1907) were recognized by a number of authors, namely by Gaupp (1911, 1913) and Goodrich (1930). However, when the latter author wrote: “the relation of its (-m. tensor tympani, W.M.-) ligament to the chorda tympani varies. Usually it reaches the malleus below the nerve; but in *Sciurus* and *Equus* it is pierced by the nerve, and in some (including Man and the Apes) it passes above” (p. 467), he obviously misinterpreted Bondy completely.

Saban (1963) provided valuable information on the relationship between the chorda tympani and the tensor tympani muscle in Primates and he gave detailed drawings of various strepsirhine taxa. In his figure 41 he depicted the middle ear of *Daubentonia* with the chorda tympani passing underneath the insertion of the tensor tympani muscle. He also documented this ventral position of the nerve for other

lemuriforms and loriforms. With respect to *Tarsius*, he remarked on the relationship between the chorda tympani and other structures of the middle ear: “La corde du tympan pénètre dans la cavité tympanique entre l’enclume et le marteau, fait une boucle très serrée autour du muscle du marteau, puis s’engage dans la gouttière malléolaire” (p. 299) (“the chorda tympani enters the cavum tympani between anvil and hammer, forms a sharp loop around the muscle of the hammer and then enters the groove for the anterior process of the malleus”; translation W.M.); although the relationship of the chorda with the tensor tympani is not completely clear from this description, it probably means that the nerve runs underneath the muscle. However, his descriptions are based on macroscopic preparations of adult specimens only, and hence several of the anatomical data he presented seem not completely reliable. In his figures 21 and 83A he depicted a complicated m. tensor tympani in *Tupaia sp.*, while tupaiids are definitively missing that muscle according to all evidence of microscopic anatomy (see below); in his figure 83H he showed a chorda tympani passing below the tensor muscle in *Homo*, while all available evidence testifies that the nerve runs above it. Of platyrrhines he only considered *Ateles* in passing, but his figure 83E seems to show a chorda running above the tensor tympani. Methodologically, Saban (1963) was interested in defining different evolutionary morphotypes of the tensor tympani muscle rather than an interpretation of his data in terms of phylogenetic systematics in the sense of Hennig (1966).

It has long been realized that ontogenetic information is essential for understanding the details of cranial morphology (Gaupp, 1906; Goodrich, 1930; De Beer, 1937; Starck, 1967; MacPhee, 1981; Kuhn and Zeller, 1987; Maier, 1993; Novacek, 1993). Relationships of soft-tissue and skeletal structures are more easily recognized at earlier ontogenetic stages and very often become obscured in adult crania. However, time-consuming preparation and interpretation of histological serial sections is a handicap for broad systematic comparisons. I have been able to build up a fairly comprehensive collection of serial sections of the heads of many primate taxa over the last 30 years, and I am therefore in a fortunate position to investigate the relationship between the chorda tympani nerve and the tensor tympani muscle based on relatively extensive material.

Voit (1909) provided one of the first detailed descriptions of a mammalian fetal skull (chondrocranium) based on histological serial sections. In this study of *Oryctolagus* (rabbit) he also documented the position of the chorda tympani; he noticed the difference from human conditions and provided a drawing that is the basis of Figure 15.1 in this work. Goodrich (1930, figures 488, 489) presented very clear semi-diagrammatic pictures of the ear region of a young specimen of the marsupial *Trichosurus* that also illustrates the positioning of the relevant soft tissue structures including the chorda tympani. However, this is not the place to review the great number of monographic studies on craniogenesis in mammals where remarks on the chorda tympani are found; only the few works of specific relevance to Primates are reviewed:

Starck (1960, p.595, figure 18) stated for the chorda tympani in a fetus of *Pan troglodytes* “Sie verläuft wie bei *Homo* über die Sehne des Musc. tensor tympani...” (“It runs across the tendon of the tensor tympani muscle as in *Homo*”; translation W.M.). In his study of the fetal cranium of *Propithecus sp.*, Starck (1962) did not comment on the relationship of the chorda tympani with the tensor tympani muscle; however, we are able to present observations on the serial sections of the same specimen (see below).

15.2 Materials and Methods

The histological serial sections that have been studied for this paper are listed in Table 15.1. The ontogenetic stages of the sectioned specimens as well as their state of preservation are quite different; brief information on the age or size is given in column 2.

In order to put my data in an appropriate theoretical framework, I also consider briefly the probable outgroups. This is necessary to establish the ancestral morphotypes at different levels in order to define the polarity of character distribution. The Archonta concept was posed by Gregory (1910) on very doubtful morphological arguments; consequently it has been discredited for many decades. Some modern systematic studies, however, have revived the concept (MacPhee and Cartmill, 1986; Simmons, 1993; Novacek, 1990; Wible and Martin, 1993; Murphy et al., 2001; Springer et al., 2005), and some authors even consider Dermoptera as the living sister-group of Primates (Beard, 1993) or even as member of an expanded order Primates (McKenna and Bell, 1997). Bats have been removed from the Archonta by most molecular systematists, leaving only Euarchonta (Scandentia, Dermoptera, and Primates) as a natural group (Waddell et al., 1999; Murphy et al., 2001; Silcox et al., 2005). Surprisingly, Primates and other Euarchonta have recently been united with Glires (rabbits and rodents) in a supraordinal clade Euarchontoglires on molecular data by some authors (Adkins and Honeycutt, 1991; Waddell et al., 1999; Murphy et al., 2001; Sargis, 2002; Bloch and Boyer, 2002; Springer et al., 2005), and therefore a few remarks on Glires may be useful.

As to primate systematics I refer to the studies of Szalay (1975b), Cartmill and Kay (1978), Beard and MacPhee (1994), Allard et al. (1996), Soshani et al. (1996), Kay et al. (1997), Ross et al. (1998), and Delperio et al. (2001) as working hypotheses. For taxonomy I refer to Wilson and Reeder (1993).

15.3 Results

15.3.1 GLIRES

In *Oryctolagus* (Lagomorpha) and in the majority of rodents the chorda tympani passes below the insertion of the tensor tympani muscle. This morphotype is documented by a (modified) illustration of Voit (1909) (Figure 15.1). I define this topographic arrangement, which is most probably the plesiomorphic mammalian condition (see discussion), as *hypotensoric*.

TABLE 15.1. List of histological serial sections that have been examined for the relationship between the chorda tympani and the tensor tympani muscle. All sectional series are presently housed at the Department of Zoology, University of Tuebingen. CRL = crown-rump-length. HL = head length.

Species	CRL/stage	Ventral	Intermediate	Dorsal
<i>Oryctolagus cuniculus</i>	41 mm	+	-	-
<i>Ochotona pusilla</i>	34 mm	?	?	?
<i>Rattus norvegicus</i>	Several	+	-	-
<i>Tupaia belangeri</i>	Several	?	?	?
<i>Cynocephalus volans</i>	145 mm	+	-	-
<i>Daubentonia</i>				
<i>madagascariensis</i>	98 mm	+	-	-
<i>Microcebus murinus</i>	Fetal	+	-	-
<i>Lemur catta</i>	Several	+	-	-
<i>Lepilemur mustelinus</i>	54 mm	+	-	-
<i>Propithecus sp.</i>	26 mm HL	+	-	-
<i>Indri indri</i>	66.5 mm	+	-	-
<i>Galagoides demidoff</i>	Neonate	+	-	-
<i>Galago senegalensis</i>	Fetal	+	-	-
<i>Otolemur</i>				
<i>crassicaudatus</i>	Neonate	+	-	-
<i>Loris tardigradus</i>	Neonate	+	-	-
<i>Tarsius bancanus</i>	Neonate	+	-	-
<i>Saimiri sciureus</i>	80 mm	-	-	+
<i>Cebus albifrons</i>	Fetal	-	-	+
<i>Callimico goeldii</i>	62 mm	-	-	+
<i>Callithrix pygmaea</i>	60 mm	-	-	+
<i>Callithrix jacchus</i>	20,31,80 mm	-	-	+
<i>Oedipomidas oedipus</i>	Neonate	-	-	+
<i>Callicebus cupreus</i>	Fetal	-	-	+
<i>Aotus trivirgatus</i>	Fetal	-	-	+
<i>Pithecia monachus</i>	90 mm	-	-	+
<i>Alouatta caraya</i>	36 mm	-	-	+
<i>Ateles geoffroyi</i>	51 mm	-	-	+
<i>Macaca fuscata</i>	58 mm	-	-	+
<i>Papio hamadryas</i>	115 mm	-	-	+
<i>Theropithecus gelada</i>	88 mm	-	-	+
<i>Chlorocebus aethiops</i>	60 mm	-	-	+
<i>Nasalis larvatus</i>	100 mm	-	-	+
<i>Trachypithecus vetulus</i>	Fetal	-	-	+
<i>Hylobates sp.</i>	100 mm	-	-	+
<i>Symphalangus</i>				
<i>syndactylus</i>	Neonate	-	-	+
<i>Gorilla gorilla</i>	Fetal	-	-	+
<i>Pan troglodytes</i>	80 mm	-	-	+
<i>Homo sapiens</i>	Several	-	-	+

In older fetuses of *Oryctolagus*, the anterior portion of the gonial shows a medial process that articulates with the ventral side of the tegmen tympani; for a short distance the chorda is squeezed between gonial and tegmen (goniopetrosal fissure). More rostrally, the chorda reaches the retroarticular space between the medial flange of the ectotympanic and the alisphenoid; hence there exists no petrotympanic fissure (Glaseri) in the sense of human anatomy. The remnant of Meckel's cartilage shows no close contact with any of the bones in its vicinity.

It may be mentioned in passing that *Ochotona* has lost the tensor tympani muscle secondarily, as documented by a serial section in our collection. At least in *Oryctolagus*, the chorda tympani pierces the gonial which constitutes the

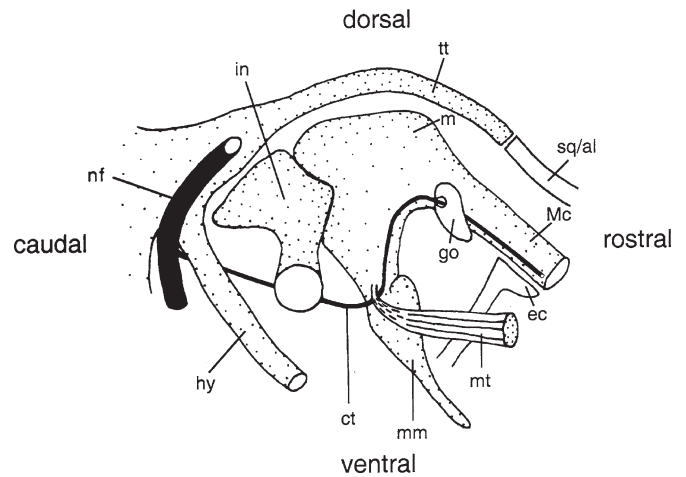


FIGURE 15.1. Diagrammatic drawing of the course of the chorda tympani through a left middle ear viewed from the medial side; the drawing is modified from the study of Voit (1909) on *Oryctolagus cuniculus*. In this species the anterior exit of the tympanic cavity is a fissura squamosotympanica. The following histograms are dorsoventral cross-sections through the insertion of the tensor tympani muscle or through the fissura squamosotympanica. Abbreviations for all figures: al – alisphenoid, as – arteria stapedia, c – capsula otica, ct – chorda tympani, ec – ectotympanicum, GF – Glaserian fissure, go – gonial (prearticular), hy – hyoid, in – incus, m – malleus, Mc – Meckel's cartilage, mm – manubrium mallei, mt – musculus tensor tympani, nf – nervus facialis, sq – squamosum, tt – tegmen tympani.

anterior process of the malleus, and we have good reasons to assume that this also represents a plesiomorphic mammalian condition (cf. Gaupp, 1911). The distribution of this character complex in Glires is presently under study by Ruf, Frahnert and Maier (in press).

15.3.2 Scandentia

Because the tensor tympani muscle is lacking in both *Tupaia* and *Ptilocercus*, its relation with the chorda tympani cannot be judged (Spatz, 1964; Zeller, 1983, 1986). The chorda tympani runs in close contact with the medial side of the gonial, but this ossicle is not pierced by the nerve (Spatz, 1964; Zeller, 1983). I speculate that the reduction of the tensor tympani muscle is due to the large anterior portion of the stapedia artery (Bugge, 1974), which is partly protected by a ventral lamella of the tegmen tympani (Spatz, 1964); this ventral process of the tegmen would prevent a functioning access of the tensor tympani muscle at the base of the manubrium mallei (Figure 15.2A).

Doran (1878) had wrongly remarked that in tree shrews "the tensor-tympani tendon is inserted into the root of the manubrium" (p. 441). On the basis of macroscopic dissection, Saban (1963, figures 21 and 83) described and depicted in his *Tupaia* four bundles of a tensor tympani muscle that allegedly insert on a quite distinctive muscular process of the malleus. Because histological serial sections do not show this

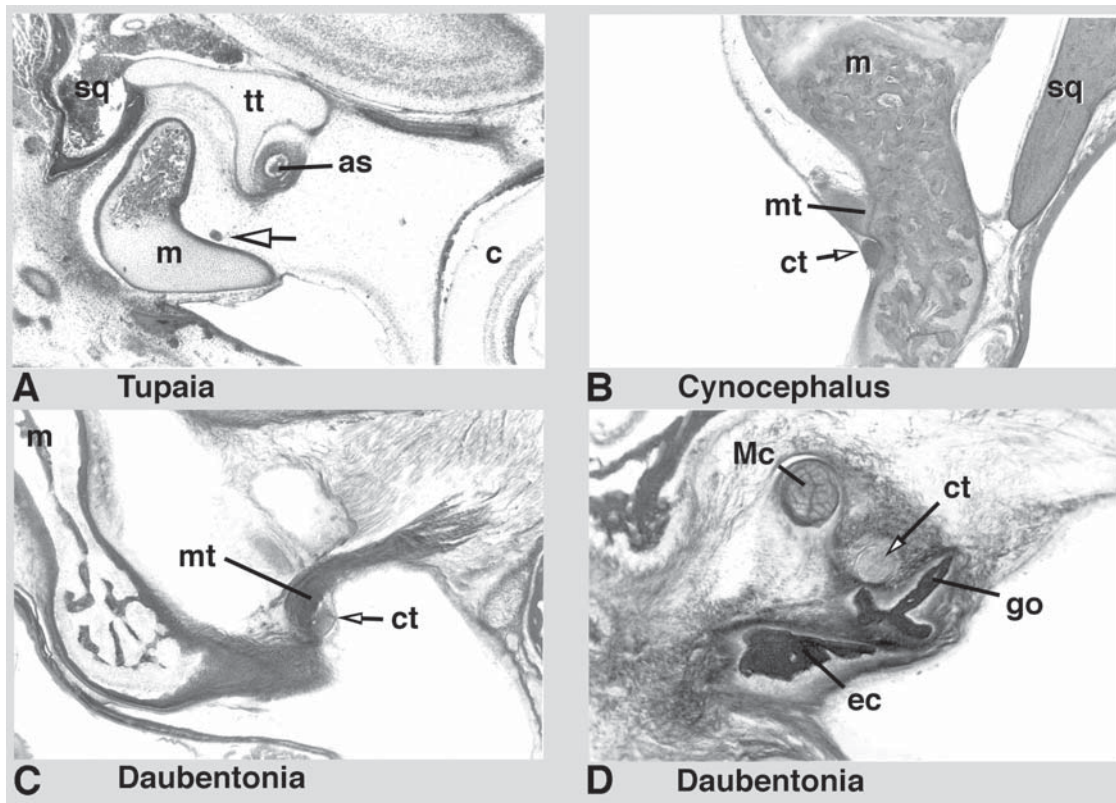


FIGURE 15.2. **A**, *Tupaia glis* (neonate; section 336-2); malleus without the tensor tympani muscle, which is absent; ventral process of the tegmen tympani protects the stapedia artery. **B**, *Cynocephalus volans* (juvenile; section 1290, left side); chorda tympani passes below the insertion of the tensor tympani muscle. **C**, *Daubentonia madagascariensis* (fetal stage; section 171-2); chorda tympani passes below the insertion of the tensor tympani muscle. **D**, *Daubentonia madagascariensis* (same specimen; section 162-2); chorda tympani runs between the gonial and Meckel's cartilage; the gonial is not pierced.

muscle, I suspect that this author misinterpreted the anterior malleolar ligaments as slender muscle slips. MacPhee (1981), knowing this controversy, judged that the presence of a tensor tympani muscle may be variable among the tree shrews, but Zeller (1986) argued that the absence of this muscle, which is also missing in *Ptilocercus*, is a synapomorphy of ptilocercines and tupaiines. The ear ossicles of *Tupaia* are also shown by Fleischer (1973; figure 17); he only noted that a muscular process and a collum mallei are missing. We consider the absence of a tensor tympani as an autapomorphy of the Scandentia.

Tupaia is characterized by a laterally situated but expanded tegmen tympani as well as by a prominent posterior extension of the epitympanic wing of the alisphenoid (Spatz, 1964; MacPhee, 1981). In the adult skull, neither the tegmen tympani nor the epitympanic wing of the petrosal do reach the anterior end of the bulla; instead the alisphenoid forms a considerable part of the anterior roof of the tympanic cavity (Saban, 1963; MacPhee, 1981, figure 29). In my neonate, the chorda tympani appears in the retroarticular space between the protruding gonial and the epitympanic wing of the alisphenoid, close to the

suture with the overlying squamosal. With the formation of the entotympanic bulla, the conditions become more complex at later stages (Saban, 1963; MacPhee, 1981). In sum, *Tupaia* does not possess a fissura petrotympanica or fissura Glaseri sensu stricto.

15.3.3 Dermoptera

In a juvenile *Cynocephalus volans*, the tensor tympani muscle is relatively small, and its thin tendon, which runs in a straight posterior direction, inserts just above the chorda tympani (Figure 15.2B). More rostrally, the chorda tympani is embedded in a longitudinal groove at the medial side of the ossified malleus. This blade-like root of the anterior process of the malleus most likely represents the gonial; however, no perforation of the gonial is observed. Anteriorly, the chorda tympani leaves the cavum tympani squeezed between the ectotympanic and the greatly expanded squamosal – far away from any part of the petrosal, i.e., there is no fissura Glaseri sensu stricto. The ear ossicles of *Cynocephalus* (*Galeopithecus*) are described and compared at length by Doran (1878, p. 442 ff.).

15.3.4 Primates

15.3.4.1 *Strepsirhini*

Daubentonia madagascariensis: The morphology of the chorda tympani in strepsirhine primates is introduced by the example of *Daubentonia*. The arrangement of the chorda tympani looks plesiomorphic in most aspects (cf. Figure 15.2C). It passes on the lateral side of the hyoid and squeezes between the posterior limb of the ectotympanic and the hyoid to reach the dorsolateral wall of the tympanic cavity. It then runs rostrally on the lateral side of the crus longum of the incus, just near its ventral end. The lenticular process of the incus of *Daubentonia* forms a small rostral apophysis, which can also be recognized in Doran (1878; Plate 58, figure 29); it is through the notch formed by this small process (still cartilaginous in our fetal specimen) that the chorda gets guided medially. The chorda is not adjacent to the medial side of the collum of the malleus, but lies more medially in the roof of the primary tympanic cavity. The medially projecting muscular process brings the chorda in close proximity to the malleus below the insertion point of the tensor tympani tendon.

Immediately in front of the tendon, the chorda curves dorsally at right angles to reach the gonial which is already completely fused with the anterior process of the malleus proper. The chorda comes to lie in a groove on the medial side of the gonial, but no perforation occurs. More anteriorly, the dorsal portion of the anterior process is revealed as the cartilaginous element of Meckel, and the nerve is situated between the gonial and the cartilaginous rod (Figure 15.2D). Further forward, the chorda runs along the dorsal side of the gonial, which becomes detached from Meckel's cartilage but is tightly fixed to the anterior limb of the ectotympanic. In front of the gonial, the chorda runs for a short distance between the ectotympanic and the medial process of the squamosal near its suture with the tegmen tympani; therefore in *Daubentonia* the chorda tympani does not exit from the tympanic cavity by a petrotympanic fissure or fissura Glaseri sensu stricto but between the squamosal on the one side and the gonial or ectotympanic respectively on the other (Figure 15.8B). Still more rostrally, the chorda passes laterally between the ectotympanic and the cartilage of Meckel to eventually join the lingual nerve. The cartilage of Meckel is embedded in a groove at the medioventral edge of the squamosal.

Microcebus murinus: The anatomy of the middle ear of the fetal and adult ear region of the mouse lemur have been carefully described by Saban (1963) and MacPhee (1981). In our fetal specimen, the chorda tympani enters the tympanic cavity between the ectotympanic and the posttympanic process of the squamosal. It then runs almost transversely to the medial side of the malleus, where it passes under the tendon of the tensor tympani muscle (Figure 15.3A) before ascending to the gonial; however, the nerve does not come near this bony element and does not perforate it.

Lepilemur mustelinus: The chorda tympani is relatively thin in the weasel lemur. The nerve enters the tympanic cavity across the upper end of the posterior crus of the ectotympanic; it passes underneath the tensor tympani muscle, but at some distance from the insertion (Figure 15.3B). It bends dorsally in front of the muscle but does not come close to the gonial, and only gradually approaches the medial side of Meckel's cartilage. The chorda enters the retroarticular space of the lower jaw through a gap between the ectotympanic and squamosal, i.e., definitely not through a petrotympanic fissure.

Lemur catta: The ring-tailed lemur shows a relationship between chorda tympani and tensor tympani muscle that closely resembles that in *Lepilemur*; however, the chorda seems to contain more fibres (Figure 15.3C). It only gradually approaches the anteriormost portion of the gonial but always remains at some distance from it. Finally it reaches the retroarticular space together with the cartilage of Meckel between the ectotympanic and the alisphenoid. Later on in ontogeny, the morphology of this region in Lemuriformes is complicated by the formation of a petrosal bulla and by the inclusion of the ectotympanic ring (cf. MacPhee, 1977, 1981); therefore, this region is not strictly comparable with that of anthropoids.

Propithecus sp. and *Indri indri*: The chorda tympani in the sifaka corresponds largely to that in other Lemuriformes; however, it passes underneath the tensor tympani muscle close to its insertion at the malleus (Figure 15.3D). Our fetus of *Indri indri* is not very well preserved, but the sectional series clearly shows that the chorda tympani runs below the tendon of the tensor tympani muscle. In *Propithecus sp.* the tegmen tympani reaches far forward (Starck, 1962; Figures 15.2 and 15.3), but at the anterior end of the ectotympanic ring the tegmen has ended and the chorda tympani together with the cartilage of Meckel are dorsally covered by a narrow medial wing of the squamosal.

Galago senegalensis, *Galagoides demidoff*, *Otolemur crassicaudatus*: The relatively young fetus of *Galago senegalensis* shows a tensor tympani muscle that runs almost transversely from the lower side of the epitympanic wing of the petrosal to insert at the muscular process of the malleus; the chorda tympani crosses the muscle on its ventral side, but at some distance from the insertion point. In a somewhat older specimen of *Galagoides demidoff*, the nerve also passes underneath the tensor tympani muscle somewhat medial to its insertion (Figure 15.4A). In both galagos the chorda tympani pierces the gonial, a character state not otherwise encountered in primates!

In the neonatal *Otolemur crassicaudatus*, the chorda tympani runs almost transversely and curves around the lower side of the tendon of the tensor tympani (Figure 15.4B). Although the penetration hole is not directly shown in our sectional series, the nerve runs inside the gonial more anteriorly. Saban (1963; figure 83C) postulated a special lorisiform-type of the tensor tympani muscle; his figure shows the chorda tympani passing below the muscle insertion.

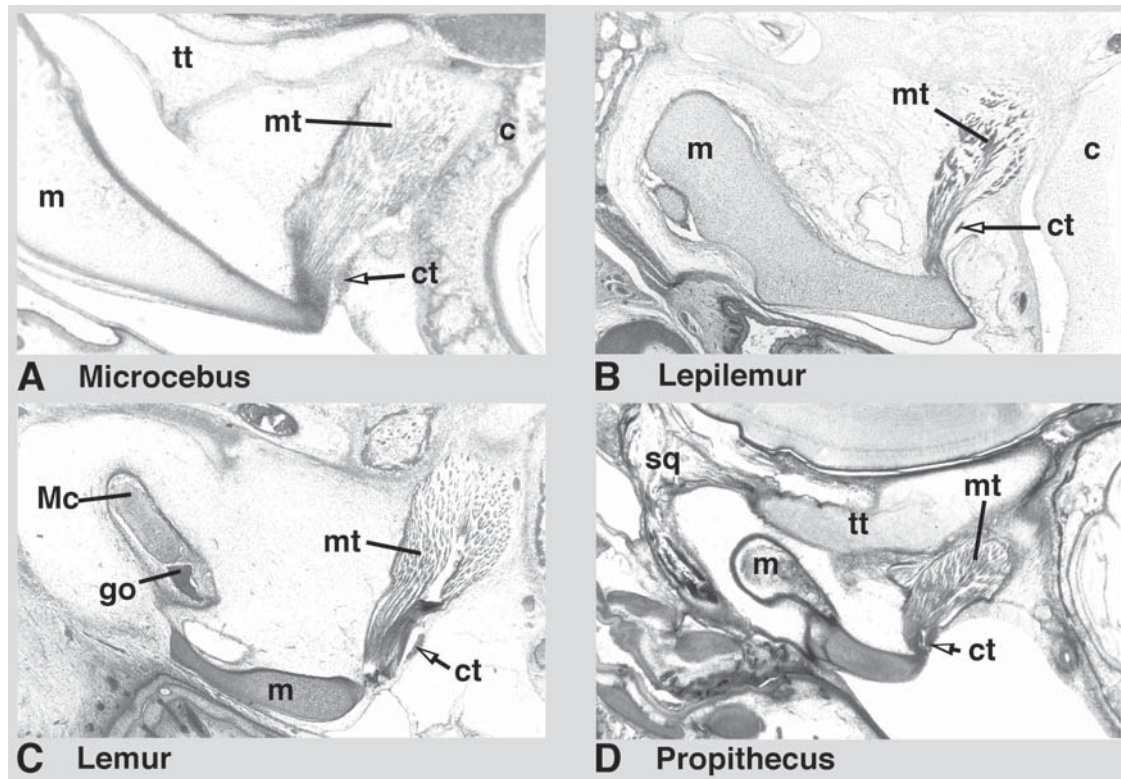


FIGURE 15.3. **A**, *Microcebus murinus* (fetal stage; section 107-1-3); chorda tympani passes below the tensor tympani tendon close to its insertion. **B**, *Lepilemur mustelinus* (fetal stage; section 99-2-4); thin chorda tympani passes below the tensor tympani muscle at some distance from its insertion. **C**, *Lemur catta* (fetal stage; section 278-2-1); chorda tympani passes below the tensor tympani muscle somewhat medial to its insertion. **D**, *Propithecus* sp. (fetal stage; section 161-2); chorda tympani passes below the tensor tympani muscle close to its insertion at the malleus.

Loris tardigradus: In a neonatal slender loris the chorda tympani enters the tympanic cavity between the ectotympanic and the squamosal, then runs almost transversely to pass below the tensor tympani – muscle (Figure 15.4C). The nerve sharply bends around the strong tendon and steeply ascends in front of it. The tensor tympani muscle runs in a posterior-anterior direction, and the nerve passage is not close to its insertion at the malleus. Quite different from galagids, the anterior part does not come close to the anterior process or gonial respectively, and in this feature it resembles some lemuriforms.

15.3.4.2 Haplorhini

Tarsiiformes

Tarsius bancanus: In a serial section of a newborn *T. bancanus* it can be clearly seen that the chorda tympani passes below the tendon of the tensor tympani muscle, i.e., it is of the primitive hypotensoric morphotype (Figure 15.4D). Because this head was sectioned sagittally, it proved to be impossible to follow the chorda posteriorly and anteriorly.

The ear region of adult *Tarsius* sp. was carefully described by Saban (1963). As to the tensor tympani muscle he stated: “De type lémuriforme, il se compose d’un étroit ruban

musculaire logé dans le toit de la caisse du tympan. Devant la fenêtre ovale, les fibres, ceinturé par la corde du tympan se redressent pour se fixer par un tendon sur le manche du marteau” (p. 296) (“Being of the lemuriform type, it is composed of a straight muscle slip fit into the roof of the cavum tympani. In front of the oval window its fibres, embraced by the chorda tympani, take a new direction to insert by a tendon at the neck of the malleus”; translation W.M.). His figure 83 D shows that the chorda tympani passes underneath the insertion of the tensor tympani muscle; consequently he classified it with the lemuriform type (p. 321).

Anthropoidea

Platyrrhini, Saimiri sciureus: The chorda tympani detaches from the facial nerve, then turns around the proximal end of the hyoid cartilage and runs along the ventral margin of the squamosal into the middle ear. The area of detachment is covered by the posterior limb of the ectotympanic ring. The nerve turns medially and slightly dorsally in front of the crus longum of the incus. The chorda passes well above the tensor tympani muscle and runs in the middle of the epitympanic recess (Figure 15.5A). I call this condition, which is almost certainly derived, *epitensoric* (see discussion).

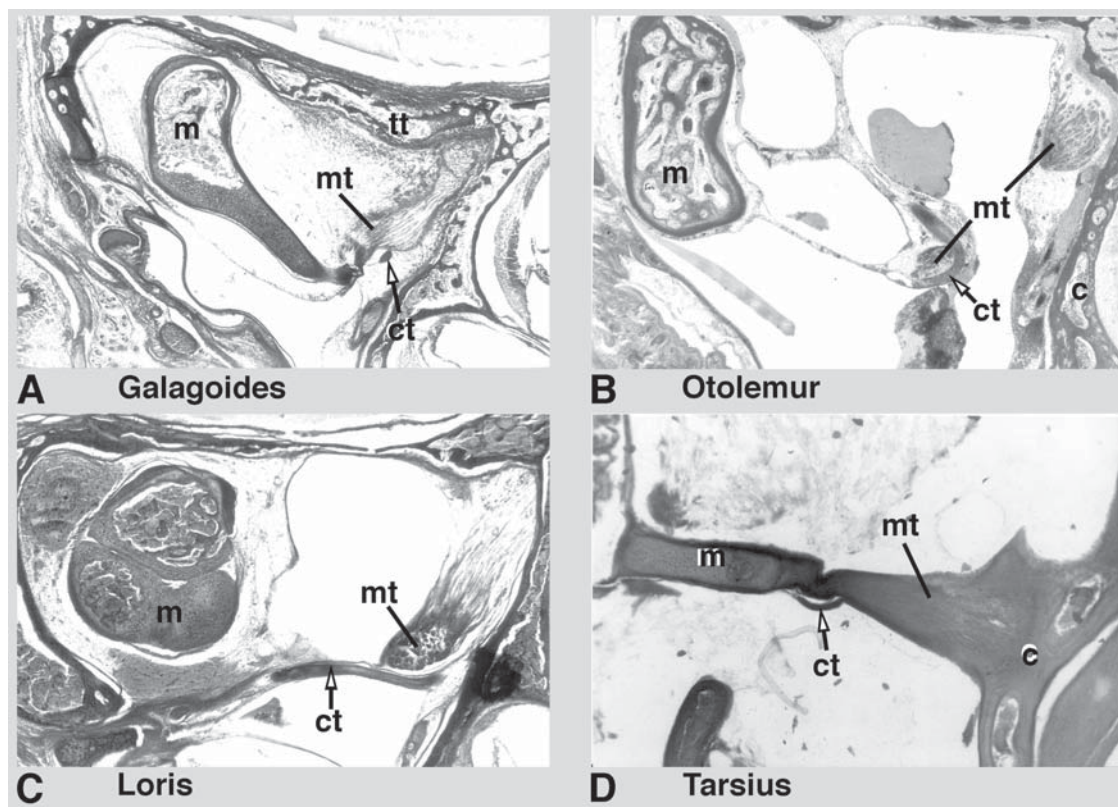


FIGURE 15.4. **A**, *Galagoides demidoff* (neonatal; section 40-2-1); chorda tympani passes below the tensor tympani muscle somewhat medial to its insertion. **B**, *Otolemur crassicaudatus* (neonatal; section 1290); tendon of the tensor tympani runs more longitudinally and the chorda tympani is shown curving underneath the tendon. **C**, *Loris tardigradus* (neonatal; section 133-2-1); chorda tympani runs transversely and turns around the tendon of the tensor tympani muscle. **D**, *Tarsius bancanus* (neonate; section 347-2); chorda tympani passes just below the insertion of the tensor tympani muscle, i.e., it shows a hypotensoric condition.

The tensor tympani muscle in *Saimiri* originates more rostrally and is deflected at right angles by a tendinous loop fixed to a processus cochleariformis before inserting at the processus muscularis of the malleus; this muscle originates in the gap between the cochlear capsule and the tegmen tympani, but it does not reach as far forward as the auditory tube. Rostrally, the chorda tympani is not near the anterior process of the malleus or Meckel's cartilage, but rather runs medially to adjoin the belly of the tensor tympani muscle. Due to the lateral and anterior expansion of the tegmen tympani (as part of the petrosal), the chorda enters the retroarticular space by a gap between the ectotympanic and this part of the petrosal, i.e., by a true petrotympanic fissure (Glaseri).

Cebus albifrons, *Callimico goeldii*, *Ateles geoffroyi*. From a fairly long list of platyrrhine species (see Table 15.1) only a few have been chosen for illustration. Although the topography and size of the tensor tympani muscle seems to vary considerably, the chorda tympani invariably crosses well above its tendon, i.e., it is always epitensoric (Figures 15.5 B–D). The approximation of the nerve to the malleus varies in the different taxa, but it never pierces the anterior process of this ear ossicle.

Catarrhini: Macaca fuscata, Papio hamadryas doguera, Trachypithecus vetulus, Nasalis larvatus. All investigated cercopithecoids, both colobids and cercopithecids, (see Table 15.1) invariably show a chorda tympani passing well above the tensor tympani muscle and at a distance from the malleus. Only in *Trachypithecus* does the nerve lie relatively close to the insertion of the tendon of the tensor muscle (Figures 15.6 A–D). Anteriorly, the chorda tympani does not come close to the gonial, which is quite diminutive. In the fetal macaque the chorda enters the retroarticular space between the anterior end of the tegmen tympani and Meckel's cartilage; only after the resorption of this relatively massive cartilage rod does the ectotympanic secondarily form the ventrolateral margin of the Glaserian fissure. In the baboon, the chorda lies more medially and indeed exits from the tympanic cavity by the gap formed between the tegmen tympani (still being cartilaginous) and the medial lamella of the ectotympanic, i.e., by a true petrotympanic fissure (Figure 15.8B). The same conditions are seen in the *Trachypithecus* specimen.

Symphalangus syndactylus, Gorilla gorilla, Pan troglodytes, Homo sapiens. All studied hominoids have a chorda tympani that runs above the tendon of the tensor tympani muscle, i.e.,

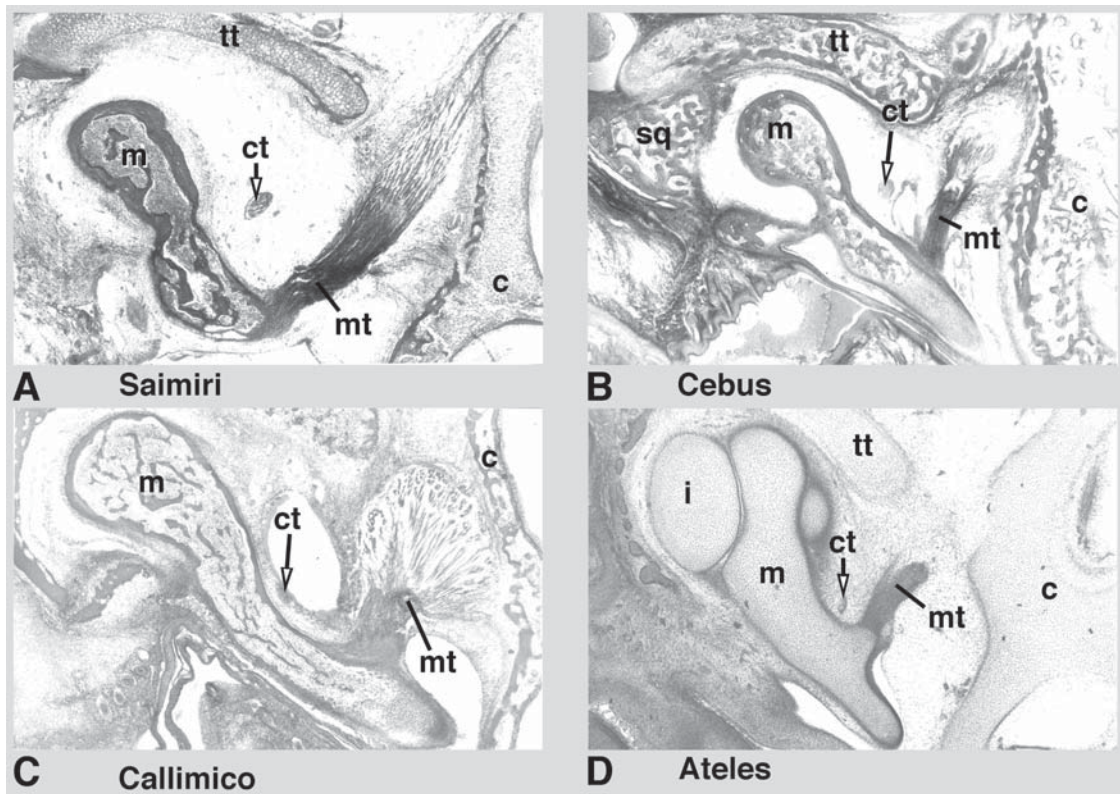


FIGURE 15.5. **A**, *Saimiri sciureus* (fetal stage; section 278-1); chorda tympani crosses above the tensor tympani muscle; it shows no close approximation to the malleus. **B**, *Cebus albifrons* (late fetal stage; section 263); chorda tympani passes above the tensor tympani muscle. **C**, *Callimico goeldii* (late fetal stage; section 131-21); chorda tympani passes across the tensor tympani muscle; due to pneumatization of the epitympanic recessus, the nerve is brought closer to the malleus. **D**, *Ateles geoffroyi* (young fetal stage; section 79-1-2); chorda tympani runs above the insertion of the tensor tympani muscle.

they are all epitensoric. As compared with the majority of cercopithecoids, the chorda lies closer to the collum mallei and closer to the insertion point of the tensor tympani muscle (Figures 15.7 A–D). It is clear in the *Hylobates* fetus that the chorda leaves the tympanic cavity squeezed between the ectotympanic and the still cartilaginous tegmen tympani, i.e., by a petrotympanic fissure. The chorda has no close relationship with the gonial or cartilage of Meckel in this taxon. In all the hominoids the anterior exit of the chorda tympani is by a petrotympanic fissure, i.e., by a true Glaserian fissure.

15.4 Discussion

The monophyly of the Haplorhini and of the Anthropoidea is well founded (Szalay, 1975b; Ross, 1994; Ross et al., 1998), but the number of supporting morphological characters is not overwhelmingly great (Mickoleit, 2004). Middle ear anatomy has been most relevant for establishing this monophyly (Szalay, 1975a), but it has mostly concentrated on the specific course of the promontory branch of the internal carotid artery. The chorda tympani has not yet been addressed in this

context although some information on this nerve is dispersed in the literature as shown above. To my knowledge, this nerve has never been studied under a strict phylogenetic-systematic aspect. One reason for this neglect may be that this problem cannot be properly addressed on a pure osteological basis but requires histological sections of fetal stages. With a collection of more than 40 serial sections of representatives of most primate families at hand, a comparative study of the microscopic anatomy of this nerve and its relations with other middle ear structures was feasible on a broader scale.

It can be clearly demonstrated that in all anthropoid species the chorda tympani passes across the malleolar insertion of the tensor tympani muscle, i.e., it is epitensoric. In contrast, in all studied strepsirrhines it passes below that insertion, i.e., it is hypotensoric. *Tarsius* is also hypotensoric.

Of course this character distribution raises the question of the ancestral morphotype in order to define the plesiomorphic and apomorphic condition. There exists ample evidence, however, that the hypotensoric state is plesiomorphic for mammals: Bender (1906) and Bondy (1907) have shown that the chorda has a hypotensoric position in monotremes and in a number of marsupials. Zeller (1989) does not explicitly

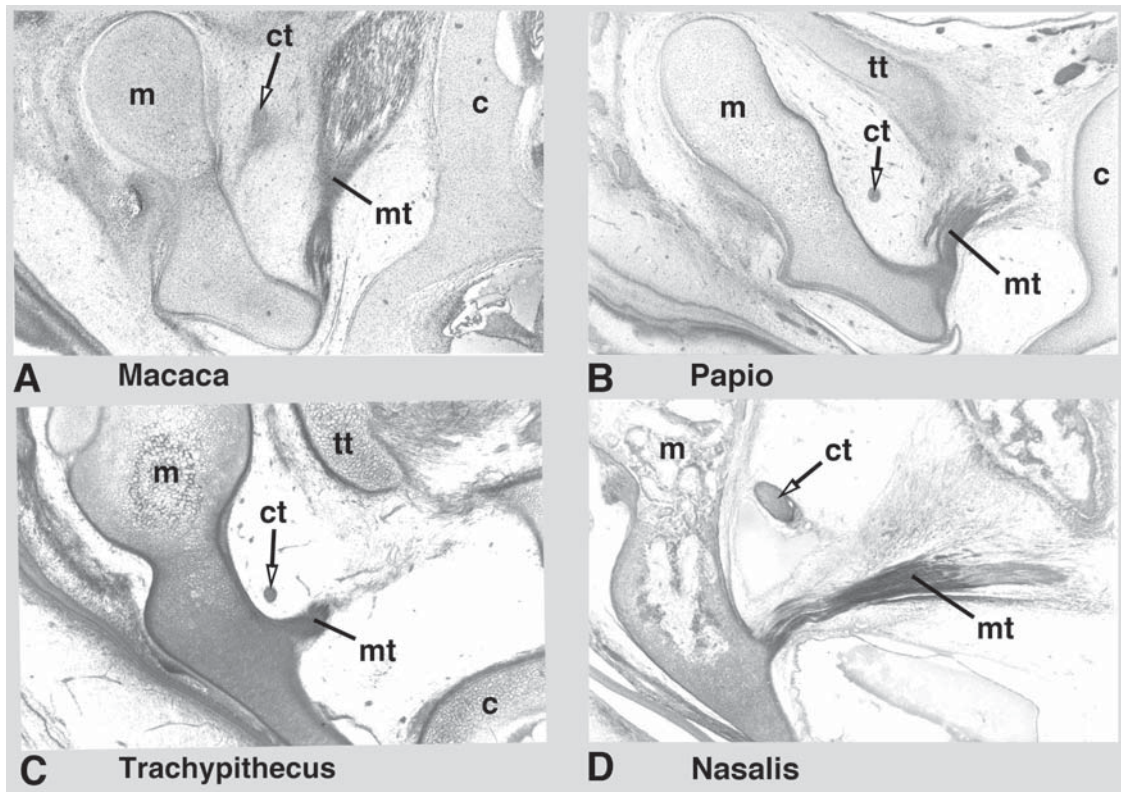


FIGURE 15.6. **A**, *Macaca fuscata* (young fetal stage; section 92-2); chorda tympani crosses way above tensor tympani muscle. **B**, *Papio hamadryas doguera* (young fetal stage; section 107-2); chorda runs well above the tensor tympani muscle. **C**, *Trachypithecus vetulus* (fetal stage; section 179-2-1); chorda tympani passes across the tensor tympani muscle, but in proximity of its insertion. **D**, *Nasalis larvatus* (late fetal stage; section 295-1-1); chorda runs above the tendon of the tensor tympani muscle.

comment on the relationship of the chorda with the tensor tympani in *Ornithorhynchus*, but his figure 47 clearly shows that it passes below that muscle. Cords (1915) for *Perameles* and Toeplitz (1920) for *Didelphis* have stated that the chorda tympani in these marsupials passes below the tendon, and no different information has come forth so far from any other marsupial taxon. Figures 488 and 489 in Goodrich (1930), which also show the ventral position of the chorda tympani, are based on *Trichosurus*. We have checked a number of marsupial taxa, and all have a hypotensoric chorda tympani.

If we accept the cladogram of Murphy et al. (2001) as working hypothesis, basal afrotherians and xenarthrans are of special importance for reconstructing the ancestral morphotype of eutherians. MacPhee (1981, figure 63 a, c) showed that at least in the tenrecs *Hemicentetes* and *Setifer* the chorda tympani passes below the tensor tympani muscle; I can confirm the hypotensoric position of the chorda in *Microgale pusilla*. *Elephantulus myurus* and *Macroscelides proboscideus* of my collection are also hypotensoric. Reinbach (1952, p. 395) described in his most careful study of the fetal skull of *Dasyurus novemcinctus* (xenarthran) the chorda tympani running underneath the tensor tympani muscle. These scattered data together with the evidence from many other

eutherian orders render it most likely that the hypotensoric condition represents the ancestral morphotype of Eutheria and Boreoeutheria.

Glires are more difficult to interpret: *Oryctolagus* (Leporidae) and the majority of rodents are hypotensoric, but a few taxa (*Aplodontia*, all glirids, some sciurids, *Castor*, *Anomalurus*, *Pedetes*) are epitensoric (Ruf, Frahnert and Maier, in press). Of the euarchontans, *Cynocephalus* is hypotensoric whereas in scandentians the tensor tympani muscle is secondarily lost and the chorda cannot be typified. Because all strepsirhine primates are also hypotensoric, it is most parsimonious to conclude that the ancestral morphotypes of Euarchontoglires, Euarchonta, and Primates are hypotensoric as well.

Obviously only a small number of taxa acquired the apomorphic epitensoric condition independently. This character distribution seems to prove that this feature is strongly constrained developmentally and that it is not easily modified. The invariable epitensoric condition in Anthropeida can therefore be considered with confidence to be a valid new synapomorphy for this group. It is interesting that within the haplorhines *Tarsius* has still retained the plesiomorphic state.

The question remains why the course of the chorda tympani is so conservative in most mammals and why it is altered in

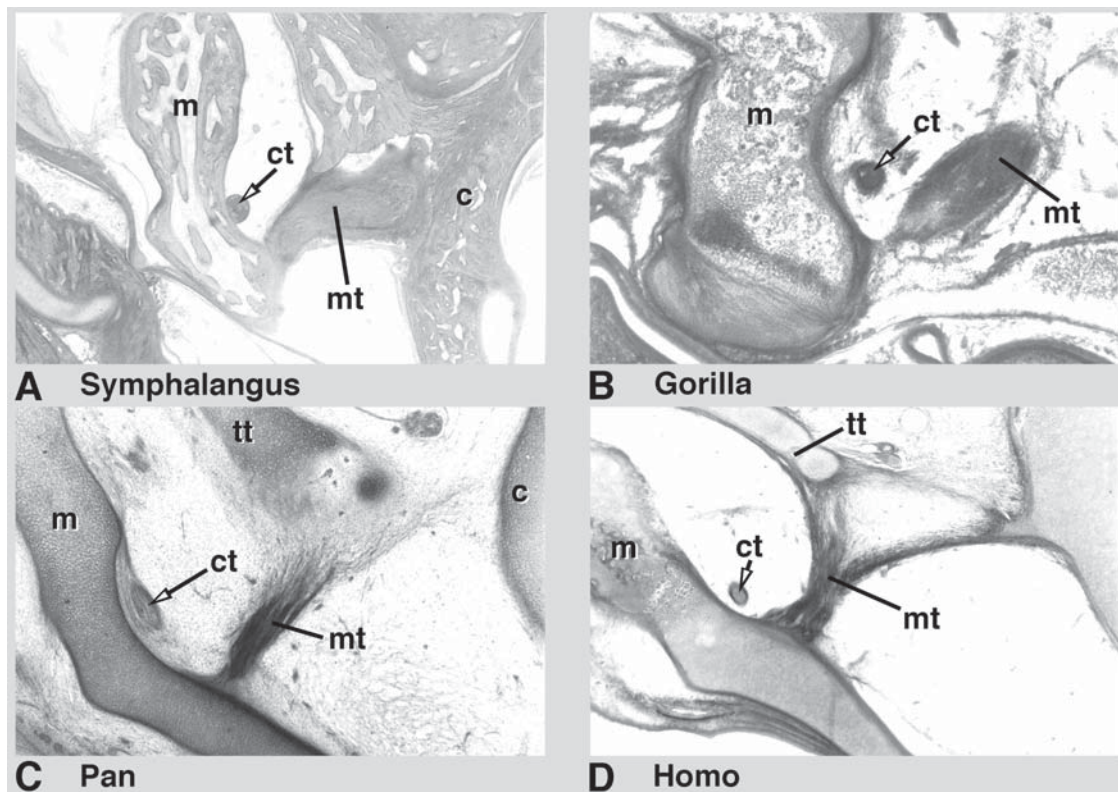


FIGURE 15.7. **A**, *Symphalangus syndactylus* (late fetal stage; section 634); chorda tympani crosses above the insertion of the tensor tympani muscle. **B**, *Gorilla gorilla* (newborn; section 366); chorda tympani passes above the insertion of the tensor tympani muscle. **C**, *Pan troglodytes* (younger fetal stage; section 193-2); the chorda runs above the insertion of the tensor tympani muscle. **D**, *Homo sapiens* (late fetal stage; section 641); chorda tympani passes across the insertion of the tensor tympani muscle.

a few groups. The conservative arrangement of the chorda is the more surprising as it normally makes a remarkable detour ventrally to pass at the underside of the tensor tympani and then ascends again to reach the gonial. This suggests that the relationship of these two heterogeneous structures is established early in ontogeny when the chorda usually shows a more straight course; when the muscle is displaced ventrally later in development, the nerve is trapped by the muscle and has to follow its shift. Anatomists have other well-known examples of such recapitulatory relationships: cervical roots of the accessory nerve, recurrent branch of the vagus nerve, sympathetic and parasympathetic nerves for the heart etc. Very probably, the ventral displacement of the insertion point of the tensor tympani muscle – and with it the chorda – is connected with the evolutionary development of a neck region (collum) of the malleus; Fleischer (1973) has shown that a neck only occurs in functionally derived morphotypes of the malleus.

Why in a few taxa – among them the anthropoids – the chorda tympani has escaped the developmental trap is not yet understood. Perhaps, a heterochronous development of nerve and muscle allows a dorsal transgression of the chorda. Sciurid embryos could probably provide a good model for studying this correlation, because the nerve course not only varies interspecifically (as far as known) in this rodent family

but also intraspecifically in *Sciurus vulgaris*. In some taxa (*Herpestes*, *Equus*) the nerve pierces the muscle tendon thus representing an intermediate stage. At least it could be argued that the epitensoric condition with the straight course of the chorda tympani should be slightly more economic, i.e., selectively advantageous once the ontogenetic constraints are overcome.

There exists another curious structural correlation between the chorda tympani and a bony element of the lower jaw, the gonial or prearticular. Gaupp (1908, 1911, 1913) carefully studied the peculiar relationship of the two structures. He clearly demonstrated that a homologous perforation of an exocranial bony element lying at the medial side of the articular and mandibular cartilage is found in many amphibians, sauropsids and mammals. He used this relationship, together with other arguments, to homologize the bony element and named it the gonial (Gaupp, 1908). He did not know at that time that Williston (1903) had already called this same bone the prearticular in some extant and fossil sauropsids. Formerly the bone had been known under a variety of names which were based on incorrect homologizations with dermal bones of the lower jaw of osteognathostome fish. Meanwhile, the prearticular (gonial) is well known in various extant and fossil fishes (Jarvik, 1980).

Although the term prearticular of Williston (1903) has temporal priority, the concept of the gonial is based on a much broader and much more subtle morphological analysis in Gaupp (1911). Whereas Goodrich (1930, figure 483) still used both terms alternatively, meanwhile the term prearticular dominates, especially in paleontology; the term gonial is only used in German embryology. Starck (1962) discussed the problems of homology and terminology of the gonial at some length.

The perforation of the gonial/prearticular by the chorda tympani varies among mammals. Already in monotremes there exists a difference: *Ornithorhynchus* shows a perforation, *Tachyglossus* does not. Most marsupials also show a perforated gonial as do many eutherians (Gaupp, 1911). It is certainly most unlikely that this peculiar relationship between the chorda tympani and the gonial is established several times independently in osteognathostomes; therefore, this character state is generally supposed to be plesiomorphic. It is of some interest that the perforation of the gonial (prearticular) is found only in galagos (not in lorises) among euarchontans. In strepsirhines the anterior part of the chorda shows varying relationships with the gonial: in some it runs close to the medial side of this bone while in others it remains at some distance; the same holds true for the epi-tensoric anthropoids.

J.H. Glaser (1680) described in man a 'hiatus membranæ tympani', "der von späteren Anatomen irriger Weise auf die zwischen der Fossa glenoidalis und dem Meatus auditorius externus osseus befindliche Spalte bezogen wurde (Fissura Glaseri)" (Hyrtl, 1845, p. 53); ("which erroneously by later anatomists was referred to the fissure between the glenoid fossa and the bony meatus externus"; translation W.M.) Despite this misunderstanding the fissure was later on named after him as fissura Glaseri. According to Hyrtl (1873, p. 253) it was J. Henle who recognized that the fissura Glaseri in fact is not situated between the tympanic and squamosal but between the tympanic and the 'tegmen tympani', which in Eutheria is an expansion of the petrosal. The statement of van der Klaauw (1931) that "the fissura Glaseri is at first the aperture for the cartilage of Meckel, which disappears later in development" (p. 164), is misleading; the existence of a cartilage of Meckel was only discovered in the first half of the nineteenth century by Meckel (1815), when embryology had become an important field of research (Russell, 1916; Nyhart, 1995). The first modern textbook of comparative embryology explicitly mentions that in the human embryo the chorda tympani together with the cartilage of Meckel pass through the "Fissura petrotympanica oder (or) Glaseri" (Hertwig, 1888, p. 461). Therefore, the fissura Glaseri sensu stricto is by definition only the gap between the (ecto-) tympanic and the tegmen tympani as it is found in man (see also Gegenbaur, 1892; p. 214). It should be mentioned that the exact position of the anterior exit of the cavum tympani is often not well defined and difficult to study in serial sections of fetuses; moreover, its morphology may change considerably during ontogeny.

It was soon recognized by some authors that the anterior exit of the chorda tympani is often somewhat different from the human condition and may not be fully equivalent in different mammals (van Kampen, 1905; van der Klaauw, 1931; MacPhee, 1981). Other skeletal elements were found framing the gap in various mammals, namely the squamosal and the alisphenoid. For example, monotremes and marsupials have no petrotympanic fissure, because they do not possess a tegmen tympani (contra van Kampen, 1905); in the latter clade, tiny tubercles at the suprafacial commissure or bony crests of the petrosal, which are the result of secondary excavations by pneumatization, have been interpreted as tegmen tympani, but this homology is doubtful and these structures are far away from the 'Glaserian fissure sensu lato'. In a juvenile of *Monodelphis domestica* (head-rump-length 63 mm) the chorda tympani exits just medial to the postglenoid process through the gap between ectotympanic and alisphenoid bulla; this confirms the notion of van der Klaauw (1931, p. 165) on *Notoryctes*. This exit is certainly no fissura Glaseri as defined in man and in anthropoids.

If again we take the cladogram of Murphy et al. (2001) as reference, the anatomical conditions of afrotherians and xenarthrans are of special relevance for the reconstruction of the ancestral morphotype of Eutheria. As far as I am aware, no study of the anterior exit of the chorda tympani exists for primitive taxa close to the basal branching of the eutherians. However, it can be concluded from figures 56 and 57 of MacPhee (1981) that in tenrecs only squamosal and sphenoid wings but no part of the petrosal are near the rostral end of the tympanic cavity. The situation is different in macroscelidids, where the expanded tegmen tympani reaches the rostral end of the ectotympanic and contacts a short squamosal (MacPhee, 1981, figure 44). In my specimen of *Elephantulus*, the chorda enters the retroarticular space by a gap whose dorsal margin is formed by the squamosal and alisphenoid and the lower by the gonial/prearticular.

As to the Glires, it has been mentioned above that in *Oryctolagus* the chorda exits between the ectotympanic and the alisphenoid wing. *Ochotona* is difficult to interpret, because the sidewall of the cranium shows a wide fontanella in the relevant area. In rodent fetuses the region of the anterior exit of the chorda tympani looks special, because parts of the tegmen tympani are shifted outside the primary sidewall of the chondrocranium; moreover, the glenoid fossa is modified, and it seems difficult to compare this region with that of other mammals (Ruf Frahnert and Maier, in press).

The anatomy of *Tupaia* and *Cynocephalus* has been described above; it is evident that in none of them does a fissura Glaseri sensu stricto exist. The same holds true for the studied strepsirhines. *Tarsius* has not yet been studied for this aspect of its anatomy. We can therefore conclude that in the groundplan of Euarchonta and Primates there existed no petrotympanic or Glaserian fissure.

The medial position of the anterior portion of the chorda tympani, the long and broad tegmen tympani as well as the

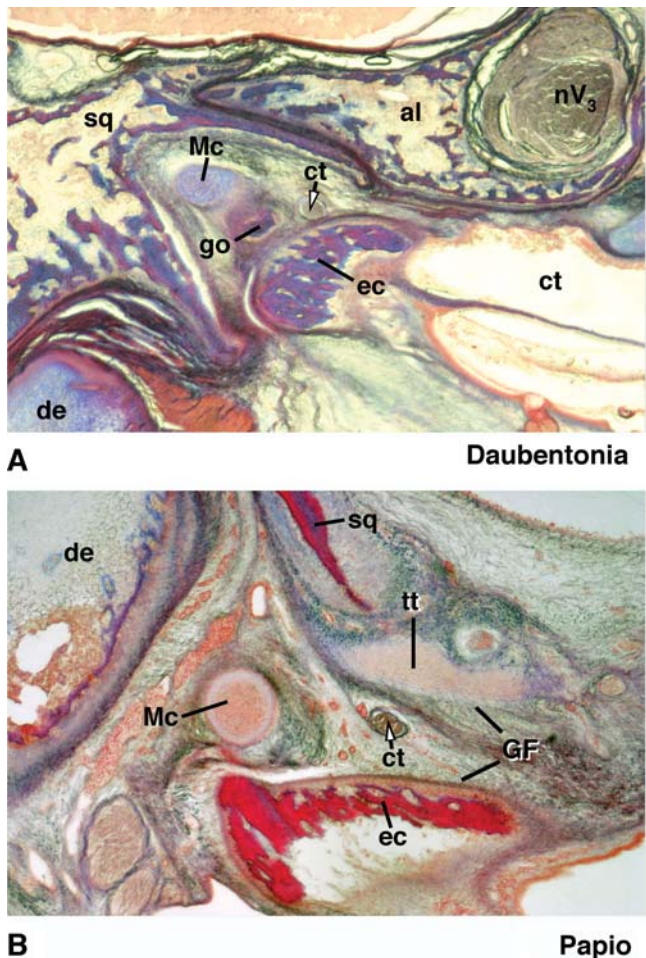


FIGURE 15.8. Dorsoventral cross-section at the fissura Glaseri. **A**, In the strepsirhine *Daubentonia* the chorda exits between the ectotympanic, gonial (prearticular), and squamosal or alisphenoid respectively, i.e., through a fissura Glaseri sensu lato. **B**, In the anthropoid *Papio hamadryas doguera*, the chorda tympani exits anteriorly from the tympanic cavity between the ectotympanic and the tegmen tympani, which is a part of the otic capsule, i.e., through the petrotympanic or fissura Glaseri sensu stricto (GF).

narrow epitympanic wing of the squamosal seem to be conditions for the formation of a true petrotympanic fissure of Glaser. Therefore I presume that this character may well be a further apomorphy of the Anthropoidea (Figure 15.8). In cleaned skulls the contribution of the petrosal by means of the tegmen tympani is not always easy to establish, but CT-sections should be helpful. The diagnosis of the petrotympanic fissure is potentially useful for the study of fossil skulls. Already van Kampen (1905), van der Klaauw (1931) and a few others had recognized the problem of an exact homologization of the Glaserian fissure. MacPhee (1981) suggested to avoid the term petrotympanic fissure and to use 'Glaserian fissure' in a wider sense instead, but this suggestion would mean to ignore a craniological character of possible systematic value.

15.5 Summary

The course of the chorda tympani nerve within the cavum tympani has been studied on the basis of more than 40 histological serial sections representing all major taxa of Primates and some presumed outgroups. It is shown that in all strepsirhines the chorda passes underneath the tensor tympani muscle; this hypotensoric character state, which is plesiomorphic for mammals and for primates, is also found in *Tarsius*. In all Anthropoidea, however, the chorda tympani passes above the tensor tympani muscle; this derived epiten-soric state is considered as new synapomorphy of this clade. There is good evidence that the anterior exit of the chorda tympani from the cavum tympani through a petrotympanic fissure (Glaserian fissure sensu stricto) is also an apomorphic state of anthropoids, which is not yet found in strepsirhines and euarchontan outgroups.

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