

THE DEVELOPMENT OF THE SECOND BRANCHIAL ARCH (REICHERT'S CARTILAGE), FACIAL CANAL AND ASSOCIATED STRUCTURES IN MAN¹

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INTRODUCTION

THE present article reports, primarily, observations on the development of the facial canal, with special reference to the second arch of the primitive branchial skeleton and to the nature of the tissue enveloped by the canal in the course of its closure. Secondly, the study is concerned with concurrent steps in morphogenesis taken by the auditory ossicles (with their muscles and ligaments), the otic capsule, the pyramid for transmission of the stapedial tendon and the semicanal which houses the tensor tympani. Related to all of the above-named elements is the mucoperiosteal membrane, which, in its spread, invests the auditory ossicles and the muscles and nerves on the tympanic wall of the otic capsule.

Complexity in the process of development of the facial canal is owing chiefly to the fact that the otic capsule, which contributes largely to the wall of the canal, is a composite structure—being formed from as many as fourteen originally separate ossification centers. In terms of morphogenesis of the facial canal, this circumstance means that the capsular wall cannot develop at the same

rate throughout its length; rather, it means that disparity in stage is inevitable, since parietal structure in the area of an ossification center will differ from that of a zone which is located between centers (where cartilage has not yet been replaced by bone). Similarly, within the capsule itself, the process of ossification does not proceed everywhere at the same pace—that of the cochlear division speeding to maturity while that of the canalicular part is retarded.

Like the otic capsule, the auditory ossicles develop from cartilage models, the primordial form of each suggesting, on a small scale, the shape of the particular ear-bone in the adult.² However, differing from the capsule, the auditory ossicles appear initially as partial or complete derivatives of the first and second branchial arches (Meckel's cartilage and Reichert's cartilage, respectively).

In a somewhat comparable way, Reichert's cartilage contributes to the formation of the facial canal by serving, for a time, as a constituent of the tympanic wall—further to complicate the developmental history of this channel for transmission of the facial nerve.

Altogether, the formation of the facial canal and the production of the auditory ossicles represent remarkable instances of phylogenetic salvage, in which skeletal elements of a respiratory apparatus, serviceable to aquatic and amphibious creatures, are remodelled to meet the anatomical and physiological needs of primates of the highest order.

Another phase of this process of remodelling in the branchial skeleton con-

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²Pertinent articles already have been cited in an earlier issue of this journal (vol. 29, no. 1, 1955, pp. 21-36), and in the Annals of Otology, Rhinology and Laryngology (vol. 64, no. 3, 1955, pp. 802-824).

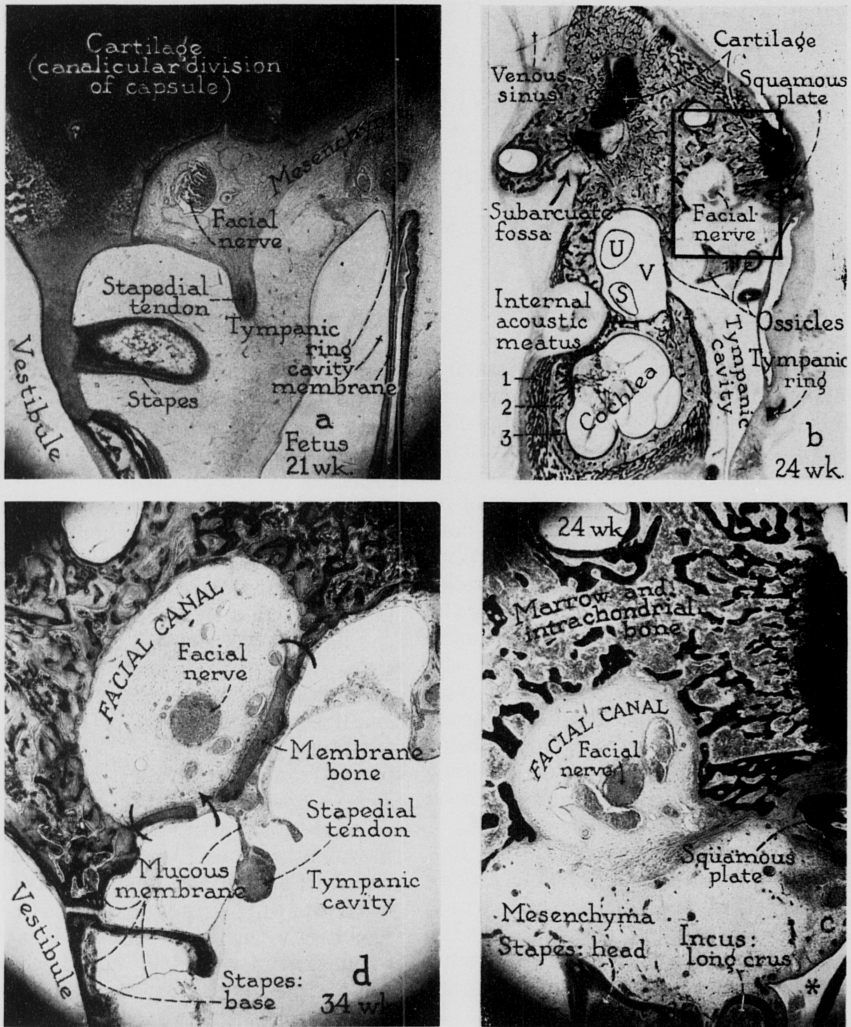


Fig. 1. Five stages in the development of the facial canal and associated structures at a level superior (cranial) to that of the upper attachment of Reichert's cartilage, from midterm to early infancy. Photomicrographs from transversely sectioned otic capsules. Figs. 1b, $\times 3$; others, $\times 10$.

Fig. 1a, fetus of 183 mm., crown-rump length (21 weeks); Wisconsin series 21 (slide 30, line 2, section 2). Fig. 1b and 1c, fetus of 215 mm. (24 wks.); Wis. ser. 62 (sl. 30, line 1, sect. 1); Fig. 1c is a photomicrograph of the rectangular area blocked in Fig. 1b. Fig. 1d, fetus of 310 mm. (34+ wks.); Wis. ser. 68 (sl. 47, line 1 sect. 1). Fig. 1e, newborn (4-day premature); Wis. ser. 124 (sl. 19, line 1, sect. 4). Fig. 1f, infant aged 3 years, 4 months; Wis. ser. 82 (sl. 21, line 1, sect. 1). Abbreviations: B, bone, N, nerve (facial); S, saccule; U, utricle; V, vestibule.

Fig. 1a. In the 21-week fetus, although ossification centers, already fused, form an otic capsule of adult dimensions, local zones of cartilage still persist in the area of the semicircular canals. The mesenchymal tissue in the sulcus which houses the facial nerve is already highly vascular. The tympanic mucous membrane is applied to the ectodermal plate which forms the internal (medial) wall of the external acoustic meatus (at the reader's right); it has not yet been carried medialward to invest the stapes (at the reader's left).

Figs. 1b and 1c. Approximately 3 weeks later, in the fetus of 24 weeks, the primordial facial "canal" is still an open channel, the incomplete wall of which is formed by bone of the middle layer (not of the outer, periosteal layer) of the otic capsule. The canal contains mesenchymal tissue, the facial nerve and rami of the stylomastoid branch of the posterior auricular artery.

Fig. 1d. Within a period of 10 weeks, at the fetal age of 34 weeks, the sulcus present in the earlier stage has become, at this level, an almost completely enclosed canal (area of incomplete fusion traversed by arrow). On the lateral aspect, recently added membrane bone now forms the wall of the canal (in approximately one-third of its circumference between the semilunar markers). The canal is of far greater capacity than would be required for mere transmission of the nerve and the abundant vessels. The tympanic mucous membrane has reached adult extent at this level, investing the stapes and covering the medial wall of the middle-ear cavity.

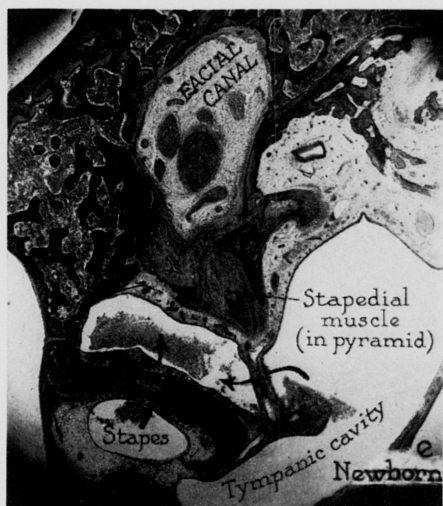


Fig. 1e. In the newborn the facial canal is complete, as is, likewise, the pyramid for transmission of the stapedial tendon. Extensions of the tympanic space pass around the stapedial ligament and the crura of the stapes (as indicated by arrows).

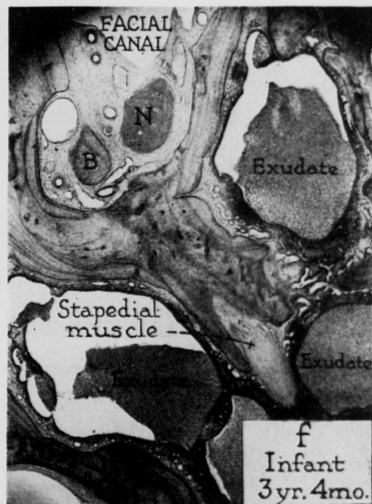


Fig. 1f. The facial canal in the infant, now formed in part of periosteal bone, contains the nerve and numerous blood-vessels.

cerns the utilization of Meckel's cartilage. An account of this step in salvage is now in preparation.

MATERIALS AND METHODS

This report is based upon a study of many of the series of sections in the otological collection at the University of Wisconsin. Reconstructions were prepared from fetal series of 161 mm. and 310 mm. (crown-rump length). The following stages are represented by photomicrographs: fetuses of 48 mm., 161 mm., 183 mm., 215 mm., 310 mm. and term; a newborn infant (4-day premature); infants of 10 weeks, of 6 months, and of 3 years, 4 months. With the following exceptions, the photomicrographs were taken at a magnification of 21 diameters: Figs. 1b and 3a at approximately 6 diameters; Fig. 4a at 38 diameters. The facial nerve and stapedial muscle have been outlined in ink (as an aid to identification) in Figs. 2c to 2f, 3b and 4c.

The reconstructions were prepared at a magnification of 20 diameters, drawn by the artist without reduction. The reconstructions demonstrate, at large scale, the full-length relationship of the branchial arches and their derivatives to the

otic capsule, the facial nerve and other topographically important structures (fig. 5 and fig. 6); they represent two crucial stages in development, namely, the 19-week (161-mm.) and the 34-week (310-mm.).

The photomicrographs are arranged in plates (fig. 1 to fig. 4) to account for stages in development of the same structures at four levels, in craniocaudal succession. The first set (figs. 1a to 1f) represents a level above that of the superior attachment of Reichert's cartilage (see encircled numeral 1 in fig. 5). The photomicrographs in the second group (figs. 2a to 2f) pass through this upper attachment (at numeral 2 in fig. 5), while those of the last group (figs. 4a to 4d) portray the anatomy at the point of lower attachment (at the encircled numeral 4 in fig. 5). The intermediate area (between sites of fusion) is represented by the third set of pictures (figs. 3a to 3d, at or near the point designated by the encircled 3 in fig. 5).

It should be noted that the term "Reichert's cartilage" (or bar) is not synonymous with "second branchial arch." Reichert's bar is cartilaginous throughout its length; the same is not true of the second branchial arch, which includes

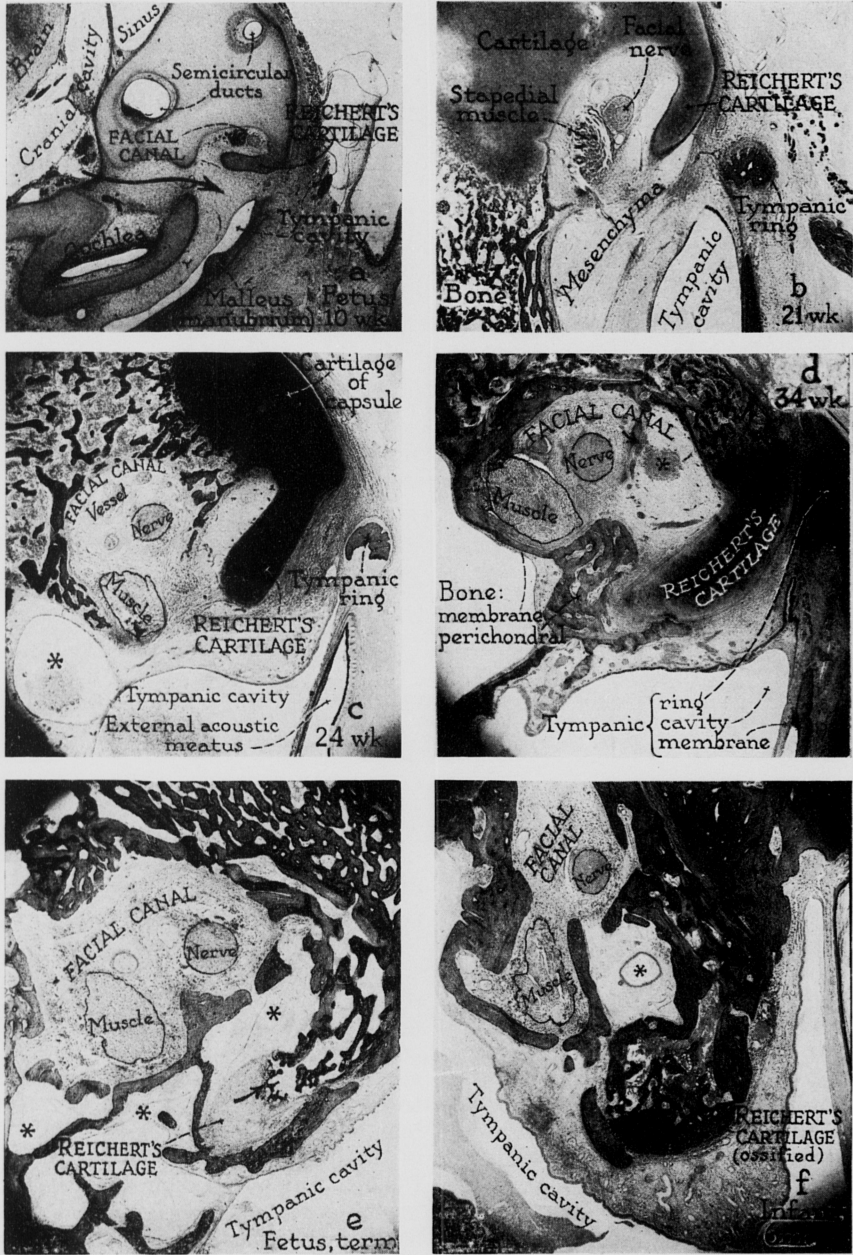


Fig. 2. Development of the facial canal and related structures, continued. From the tenth week of fetal life to the sixth month of infancy; at the level of the superior attachment of Reichert's cartilage. Photomicrographs, $\times 10$.

Fig. 2a, fetus of 48 mm., (10 wks.); Wis. ser. 202 (sl. 18, line 1, sect. 4). Fig. 2b, fetus of 183 mm. (21 wks.); Wis. ser. 21 (sl. 20, line 1, sect. 2). Fig. 2c, fetus of 215 mm. (24 wks.); Wis. ser. 62 (sl. 21, line 1, sect. 2). Fig. 2d, fetus of 310 mm. (34 wks.); Wis. ser. 68 (sl. 23, line 2, sect. 2). Fig. 2e, term fetus; Wis. ser. 102 (sl. 6, line 1, sect. 3). Fig. 2f, 6-month infant; Wis. ser. 98 (sl. 14, line 1, sect. 2).

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such additional structures as the stapedial muscle and its tendon and (according to the opinion of some investigators) at least part of the stapes. The present authors' concern is with the fetal form and attachments of the proximal (posterior) segment of the arch—that is, the portion which is termed Reichert's cartilage (shown in the reconstructions, fig. 5 and fig. 6); the study, being fundamentally otological, is not concerned with the distal (anterior) portion of the arch, which gives rise to other derivatives.

An article, now in preparation, will deal in a comparable way with Meckel's cartilage (of the first branchial arch).

Either in that report, or in one subsequently prepared for a morphological journal, pertinent literature in the wider field of comparative embryology will be reviewed.

OBSERVATIONS AND DISCUSSION

A. RECONSTRUCTIONS

161-mm. fetus—In the 19-week fetus the skeletal element of the second branchial arch is a cartilaginous structure throughout its extent (fig. 5). At the proximal extremity the arch is continuous with the otic capsule. Descending in a sinuous course, it lies free, then gains a second capsular attachment near the

(Continuation of legend)

Fig. 2a. In the fetus of 10 weeks, Reichert's cartilage, at its cranial attachment, is a histologically unmodified projection from the lateral wall of the canalicular division of the otic capsule. Being incurved, the projection forms approximately one-third of the wall of the incomplete facial "canal," and is situated on the posterior aspect of the tympanomeningeal hiatus (the latter traversed by the curving arrow).

Fig. 2b. Within less than a 3-month period (in the fetus of 21 weeks), although the process of ossification has involved the greater part of the capsule, cartilage persists in the canalicular division, to include the capsular wall of the facial canal and Reichert's cartilage (compare fig. 1a). The incomplete channel contains the facial nerve and stapedial muscle lodged in highly vascular mesenchymal tissue. The tympanic ring is adjacent to the arch (Reichert's cartilage); the mucosal (ectodermal) lining of the tympanic cavity is applied to the ectodermal plate, the latter forming the medial limit of the developing external acoustic meatus.

Fig. 2c. In a fetus three weeks older (that is, in one of 24 weeks), the process of ossification has advanced considerably in the canalicular division of the capsule, converting the wall of the facial canal into bone. The bone is of two types, namely intrachondrial in the depths of the canal, and membrane at the free margins (where the wall is still incomplete). Further growth of membrane bone will separate the contents of the primordial facial canal from Reichert's cartilage—the latter having served provisionally as part of the wall at this level. Nearby, on the tympanic (lateral) surface of the capsule, persistent cartilage is continuous with that of the skeletal part of the branchial arch. The canal transmits the facial nerve, stapedial muscle and blood-vessels of relatively large size. Expansion of the tympanic cavity has carried the mucous membrane medialward to the otic capsule (to the reader's left, at *); laterally the membrane forms the innermost of the three layers of the tympanic membrane (lower right in the photomicrograph). The epidermal tissue of the external acoustic meatus and the subadjacent mesenchyma form the other two layers of the tympanic membrane.

Fig. 2d. Within a 10-week period (in the fetus of 34 weeks), when ossification of the capsule is virtually complete, Reichert's cartilage remains cartilaginous. Bone of the middle layer of the capsule (intrachondrial and endochondral combined), perichondral bone of the outer layer and more recently formed membrane bone all contribute to production of a wall for the facial canal. The tympanic cavity has expanded to such an extent that irregular bays are produced on its capsular wall (the summit of one of these being marked by *). The occurrence of such a sacculation, internal to Reichert's cartilage, marks the beginning of separation, into two areas, of the general space which, in earlier stages, was guarded by the branchial projection (compare fig. 2b). Membrane bone (at arrow) serves to effect this separation, and thereby to contribute to the wall of the definitive canal.

Fig. 2e. In the fetus at term Reichert's cartilage remains in part chondral in this area of cranial attachment to the otic capsule; however, it is undergoing ossification (in the zone at the tip of the arrow). The wall of the facial canal is formed by bone of the three types (compare fig. 2c). Membrane bone, by producing an outer (tympanic) wall for the facial canal, now separates the contents of the canal from Reichert's cartilage. An offset of the tympanic cavity intervenes (at *) between the facial canal and the cartilaginous branchial arch. Other membrane-lined bays occur (indicated by similar device, in the lower left quadrant of the figure).

Fig. 2f. In the young infant cartilage has given way to bone. However, the interrelationship of structures and spaces, established in the 24-week stage (fig. 2c), remains essentially unchanged. In succession from superficial to deep, these are: tympanic cavity; Reichert's cartilage; bay of the cavity (at *); and facial canal containing the nerve, blood-vessels and stapedial muscle. The muscle, here approaching the pyramid, courses through a partially segregated channel.

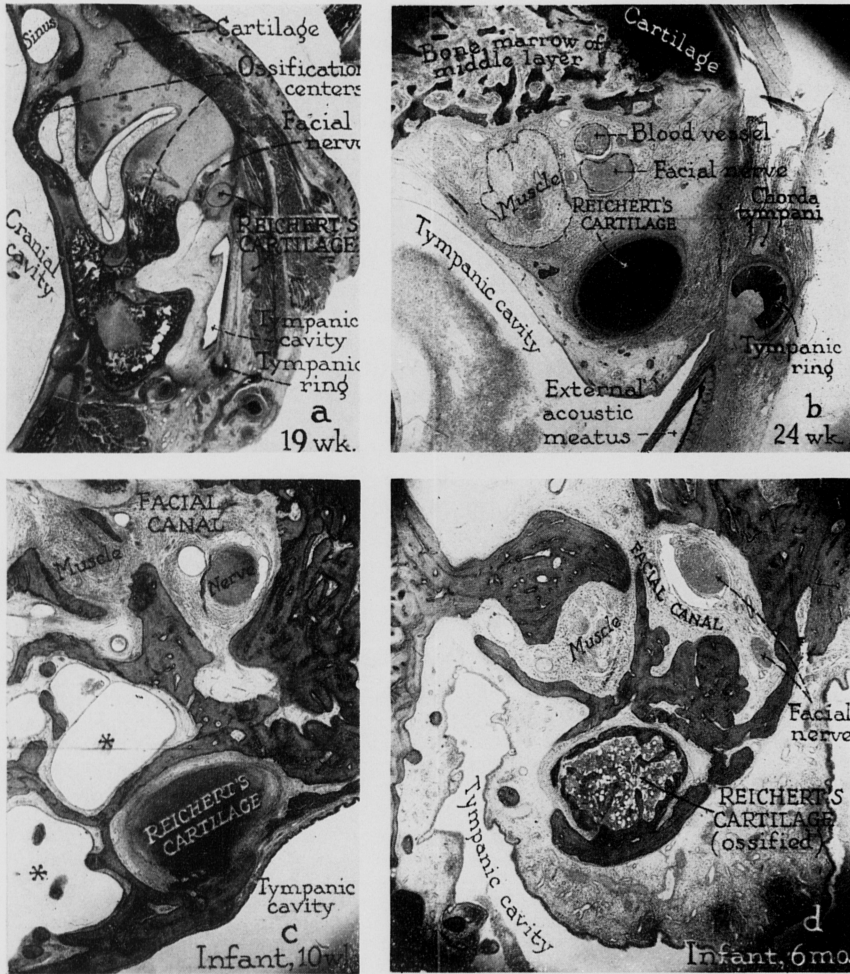


Fig. 3. Development of the facial canal, Reichert's cartilage and other related structures, continued. From the 19-week fetus to the 6-month infant; at a level between the areas of capsular attachments of Reichert's cartilage. Photomicrographs of sections from transverse series. Fig. 3a, $\times 3$; others, $\times 10$.

Fig. 3a, fetus of 161 mm. (19 wks.); Wis. ser. 13 (sl. 24, line 2, sect. 1). Fig. 3b, fetus of 215 mm. (24 wks.); Wis. ser. 62 (sl. 16, line 1, sect. 1). Fig. 3c, infant of 10 weeks; Wis. ser. 83 (sl. 6, line 1, sect. 2). Fig. 3d, infant of 6 months; Wis. ser. 98 (sl. 6, line 1, sect. 2).

Fig. 3a. In the 19-week fetus, Reichert's cartilage, in its descent toward an inferior attachment, lies between the tympanic ring and the facial nerve.

Fig. 3b. The relationships which occur in the preceding stage are maintained in the fetus of 24 weeks. However, much of the capsular wall which will become part of the facial canal is now formed in bone (primarily of intrachondrial variety, upon which endochondral layers have been deposited). A tympanic wall is represented merely by Reichert's cartilage and by a concentration of connective tissue which will give rise to membrane bone.

Fig. 3c. In the young infant, Reichert's cartilage, having become completely surrounded by bone, is no longer immediately related to the contents of the canal. The definitive facial canal, now a complete channel, transmits the nerve, the stapedial muscle and blood-vessels. The adjacent wall is pneumatized (spaces indicated by *).

Fig. 3d. In the 6-month infant Reichert's cartilage has become ossified; being derived from cartilage, it remains distinct from the membrane bone by which it is encapsulated. The stapedial muscle, near the developing pyramid, is now separated from the facial nerve.

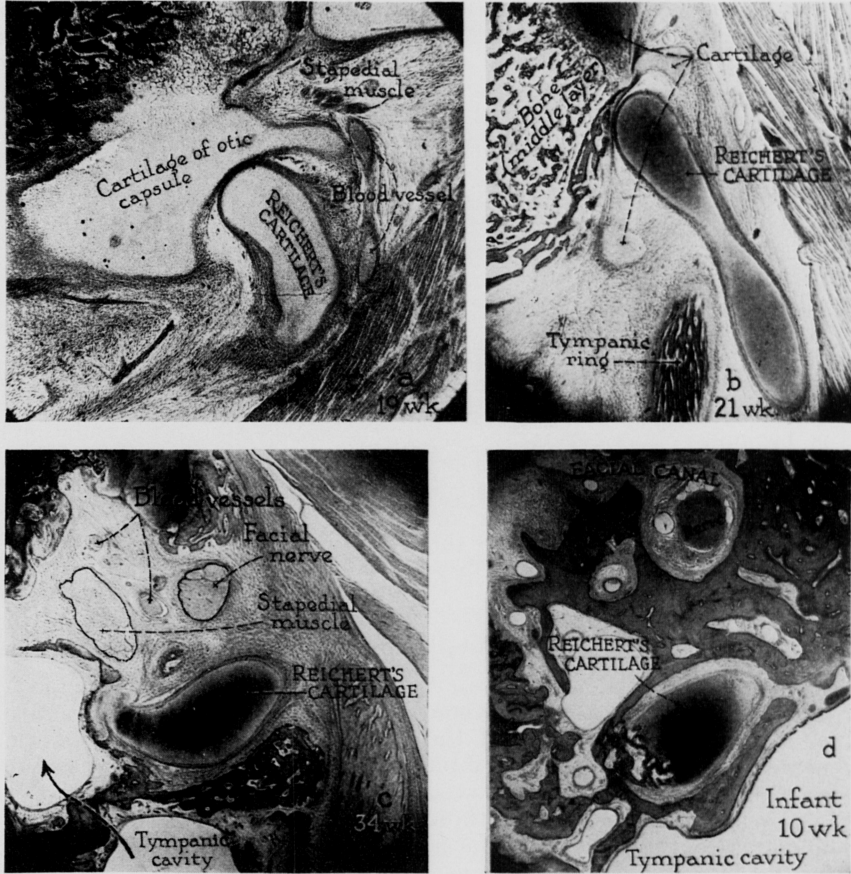


Fig. 4. Development of the facial canal, Reichert's cartilage and associated structures; sets of serial sections concluded. Showing especially the morphogenesis of the cartilage in the area of its later attachment to the otic capsule, from the stage of the 19-week fetus to that of the 10-week infant. Photomicrographs. Fig. 4a, $\times 19$; others, $\times 10$.

Fig. 4a, fetus of 161 mm. (19 wk.); Wis. ser. 13 (sl. 18, line 1, sect. 2). Fig. 4b, fetus of 183 mm. (21 wk.); Wis. ser. 21 (sl. 9, line 2, sect. 1). Fig. 4c, fetus of 310 mm. (34 wk.); Wis. ser. 68 (sl. 14, line 1, sect. 1), Fig. 4d, infant of 10 weeks; Wis. ser. 83 (sl. 2, line 1, sect. 2).

Fig. 4a. In the 19-week fetus Reichert's cartilage is in contact with a portion of the otic capsule which is still cartilaginous.

Fig. 4b. Within a two-week period, in the fetus of 21 weeks, the capsule is largely formed in bone. This change has not yet affected Reichert's cartilage.

Fig. 4c. In the 34-week fetus Reichert's cartilage is being enclosed in membrane bone. Production of such bone is incomplete; as a consequence, the facial "canal" is in a primordial state; the cartilage still forms part of the wall.

Fig. 4d. In the young infant Reichert's cartilage is undergoing ossification; it is now separated from the contents of the definitive facial canal by the newly-formed membrane bone.

point at which it turns downward and outward to appear on the lateral aspect of the tympanic ring. At this stage the facial nerve, stapedial tendon and tensor muscle lie free in mesenchymal tissue; formation of a facial canal is predicted in the occurrence of an elongate ridge marginal to the nerve (at unlabelled arrows in

fig. 5). The otic capsule has been converted into bone except in a seam which extends from the wall of the vestibule in both directions, that is, toward the cochlear and the canalicular divisions of the capsule.³

³Figs. 34 and 41 in T. H. Bast: Contributions to Embryology, Carnegie Publications, vol. 21, pp. 53-82, 1930.

310-mm. fetus — Striking developmental advance is made in the production of features of the tympanic wall of the otic capsule in the interval between nineteenth week and thirty-fourth week of fetal life: a facial canal has been formed; the stapedial tendon is partially enclosed in a pyramidal canal and ledges have appeared along the course of the *m. tensor tympani* as forerunners of a true semicanal (see * in fig. 6a).

As will be established by the use of sections (figs. 1d and 2d), the facial canal at this stage has reached the halfway mark in its development: while virtually a closed channel, a plate of membrane bone is beginning to separate the facial nerve and related structures from Reichert's cartilage. In other words, the primordial relationships are being replaced by those which characterize the definitive canal.

B. SECTIONS

1. Level of Genuiculate Ganglion

In the area between the transverse level of the genuiculate ganglion of the facial nerve and that of the semicanal for the tensor tympani, features are observed which, in some instances, match those that characterize the developing facial canal in the territory of Reichert's cartilage, and in other instances differ considerably therefrom. These similarities and differences deserve introductory review.

48-mm. fetus—In the 10-week fetus the cartilaginous otic capsule is but slightly indented along the course of the facial nerve. As will be described, the site of the future facial canal is still indicated by a mere sulcus in that portion of the otic capsule which, located in the territory between ossification centers, remains cartilaginous in the 21-week fetus (fig. 1a). Despite the immaturity of the otic capsule in the 48-mm. stage, the forerunners of the adult wall of the facial canal are present: internally the cartilaginous otic capsule, in which will appear chronologically intrachondrial, endochondral and perichondral bone; externally, mesenchymal tissue, which, already appearing somewhat concentrated on the tympanic side of the facial nerve,

will later be converted into membrane bone. The mature character of the contained tissue is predicted in the presence of relatively large blood vessels circumferential to the nerve.

183-mm. fetus—In the general area just described, a true facial canal already has been formed in the 21-week fetus; on the internal (capsular) aspect the bone is of perichondral type, whereas on the external (tympanic) aspect the wall is composed of membrane bone. The increase in perichondral bone is gradual, from the level of the vestibular fenestra (oval window) toward that of the semicanal for the *m. tensor tympani*. Encapsulation is progressive, in the upward direction, until the level of the greater superficial petrosal nerve is reached; there the canal is open again. However, where membrane bone will be produced later (to form an external wall), the mesenchymal tissue is becoming markedly fibrous—a condition immediately antecedent to conversion into membrane bone.

215-mm. fetus—In the fetus of 24 weeks the developmental conditions are similar to those existing in the preceding (183-mm.) stage: closure of the facial canal is complete at the level of the genuiculate ganglion, while closure is partial at still more cranial and at caudal levels. Throughout the length of the canal the tissue through which the nerve courses is highly vascular.

310-mm. fetus—The facial canal has attained an adult appearance in the 34-week fetus. Even at the level of the stapes the canal not only is complete but also is composed of mature bone; here perichondral bone has formed a complete lining for the canal, covering the endochondral bone on the capsular aspect and membrane bone on the tympanic aspect (in contrast, see fig. 1c). Although the canal decreases in size as the level of the genuiculate ganglion is approached, its tissue is still vascular.

Term fetus—In one of the specimens of a full-term fetus examined by the authors, a defect occurs in the wall of the facial canal at a level just superior to that of the pyramid on the cochlear (anterior) surface of the latter. It is likely

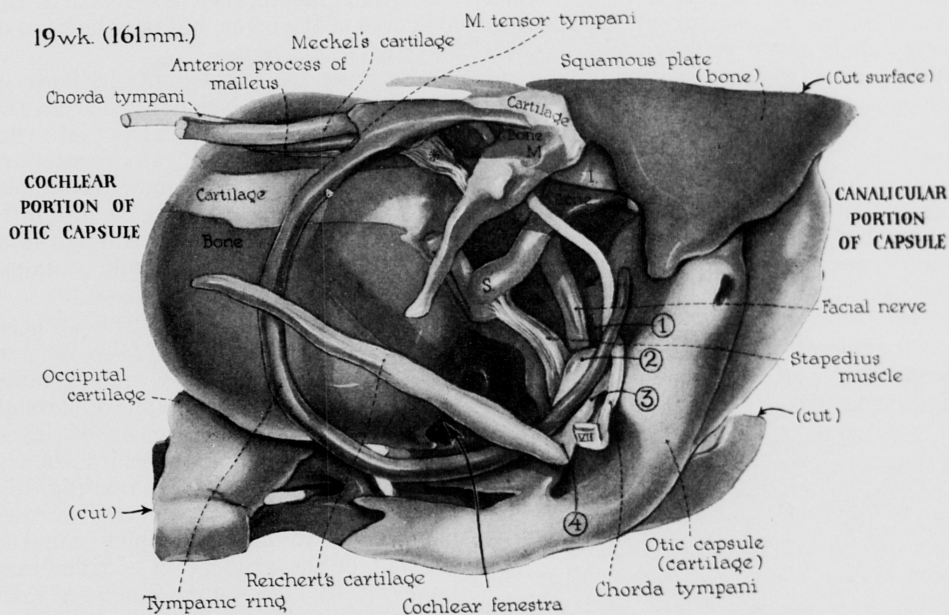


Fig. 5. Drawing of a reconstruction of the otic capsule and related structures, including Reichert's cartilage, in a fetus of 161 mm. (19 wks.). Viewed from the lateral side. Anteriorly and posteriorly the lines of natural continuity with the chondrocranium are indicated by the arrows with the parenthesized label "cut." The comparable part of the squamous plate is similarly designated. Wis. ser. 13, left. $\times 6$. Abbreviations: M, malleus; I, incus; S, stapes.

Photomicrographs of sections in this otological series appear as Figs. 3a and 4a.

Reichert's cartilage, shown through its full extent, first lies internal, then below and external to the posterior segment of the body of the tympanic ring. It is attached to the otic capsule as indicated by the encircled numerals 2 and 4. At this developmental stage, the tensor tympani (at *) lies free in mesenchymal tissue, as do the stapedial muscle, facial nerve and chorda tympani. The formation of a facial canal is foreshadowed in the presence of low elevations (at unlabelled arrows) which border the facial nerve at the level of the stapes.

The otic capsule has been converted into bone except in an area which extends in both directions from the vestibular fenestra (oval window), between Ossification Centers No. 1 and No. 8, and over the posterior reaches of the semicircular canals. Bone has appeared in each of the auditory ossicles. The tympanic ring, fully formed in bone, will soon enclose nine-tenths of a circle.

that such deficiencies are not uncommon. When present, the facial nerve would be left exposed to the middle ear, and, consequently, to involvement from an *otitis media*.

2. Level Cranial to Branchial Arch

161-mm. fetus—The facial nerve and the stapedial muscle are completely extracapsular in the area superior to the cranial attachment of Reichert's cartilage (fig. 5, at 1). The chorda tympani and tensor muscle are similarly free.

At this crucial stage in development, the process of ossification of the otic capsule is approaching completion;³ cartilage, however, has not been replaced in an arrow area anterior to the vestibular

(oval) window and, continuous therewith, over the distal reaches of the arcs of the semicircular ducts (fig. 5). The capsule is still a bulbous shell for the otic-duct system; while continuous with other parts of the chondrocranium, it is, as mentioned, but little affected by the presence of neural and muscular structures which, now lying free in the mesenchymal tissue on the tympanic aspect of the capsule, subsequently will be housed in osseous channels.

183-mm. fetus—In the 21-week (mid-term) specimen, some cartilage persists in the fenestral and canalicular portions of the otic capsule;⁴ its presence is espe-

⁴Loc. cit., Fig. 35 and Fig. 42.

cially striking in the area of the facial nerve where at the site of the canal a mere sulcus occurs on the tympanic wall of the capsule (fig. 1a). Even at this early stage the tissue in which the facial nerve is lodged has assumed a fibrous nature and has become prominently vascularized. These two features establish the position of the future canal and the character of its content. Otherwise the tissue between the mucosal epithelium and the capsular perichondrium is a loosely-textured mesenchyma.

Like the capsule, the stapes is still composed partly of cartilage as are malleus and incus.⁵

215-mm. fetus—Within a period of 3 weeks in a 24-week specimen, profound changes have taken place in the structure of the otic capsule. Although remnants of cartilage are still to be found in the area of the subarcuate fossa and on the outer wall of the capsule deep to the squamous plate (figs. 1b and 1c), ossification in the cochlear division of the capsule has resulted in the production of bone of the three typical layers (fig. 1b at 1, 2 and 3). In the canalicular division of the otic capsule the formation of endochondral bone in the middle layer is tardy, as is also (and even more strikingly) the production of an outer (periosteal) layer (fig. 1b). This means that the wall of the facial "canal" is composed of intrachondrial bone throughout its capsular portion. Where bone is wanting (on the tympanic one-third of the circumference) the mesenchymal tissue has become concentrated (fig. 1b). This change predicts formation of membrane bone (compare fig. 2c).

The facial canal contains relatively large blood-vessels which almost surround the facial nerve (fig. 1c). The mesenchymal tissue is continuous with, but distinguishable from, the primitive marrow of the capsule through numerous hiatuses between spicules of intrachondrial bone of the middle layer. Bone of this type forms the wall of the facial canal, which at this stage encloses more than a semicircle.

Mucous membrane has reached the long crus of the incus, but not the head of the stapes (fig. 1b).

The posterior segment of the body of the tympanic ring is separated from the otic capsule by the squamous plate (fig. 1b). Appearing as segregated centers of ossification in the 50-mm. (10-week) fetus, a semicircle of bone is promptly formed. Growth continues through fetal life; fixation to the otic capsule is almost complete in early infancy.⁶

310-mm. fetus—In the 10-week period between the 215-mm. (24-week) and 310-mm. (34-week) stages, endochondral bone has been rapidly produced, through deposition upon the spicules of intrachondrial bone, along two-thirds of the circumference of the facial canal (fig. 1d). The deep sulcus of the preceding stage has become an almost complete canal as a result of the production of membrane bone (fig. 1d, between the semilunar markers); the two plates of bone have not yet fused (fig. 1d, at the fault traversed by the arrow). It is to be noted again that the canal thus formed is far more capacious than would be required for transmission of the nerve and the numerous blood-vessels which are its contents.

With the expansion of the tympanic cavity the once abundant mesenchyma (fig. 1c) has become a thin stratum—in some areas a true submucosal layer (fig. 1d); it lies close to the otic capsule and the outer wall of the facial canal, is carried over the stapedial tendon, draped therefrom to the head of the stapes and invests the latter ossicle (head, crura and tympanic surface of the base).

Newborn—In the infant at birth the facial canal is completely closed. The pyramid for transmission of the stapedius tendon has become part of the anterior wall of the canal on the side toward the auditory ossicles (fig. 1e). At this stage membrane bone (on the tympanic portion of the canal) and spicules of combined intrachondrial and endochondral bone (on the capsular fraction) constitute the wall of the canal. Later, a new contribution will be made by the periosteal

⁵Fig. 11a (of the 161-mm. stage) and Fig. 11b (of the 190-mm. fetus) in S. F. Richany, B. J. Anson and T. H. Bast: Quarterly Bulletin of Northwestern University Medical School (vol. 28, no. 1, 1954, pp. 17-45).

⁶The full account of the development of the tympanic ring was published in the spring 1955 issue of this journal (vol. 29, no. 1, pp. 21-36) and in the September, 1955, issue of the Annals of Otolaryngology and Rhinology (vol. 64, no. 3, pp. 802-824).

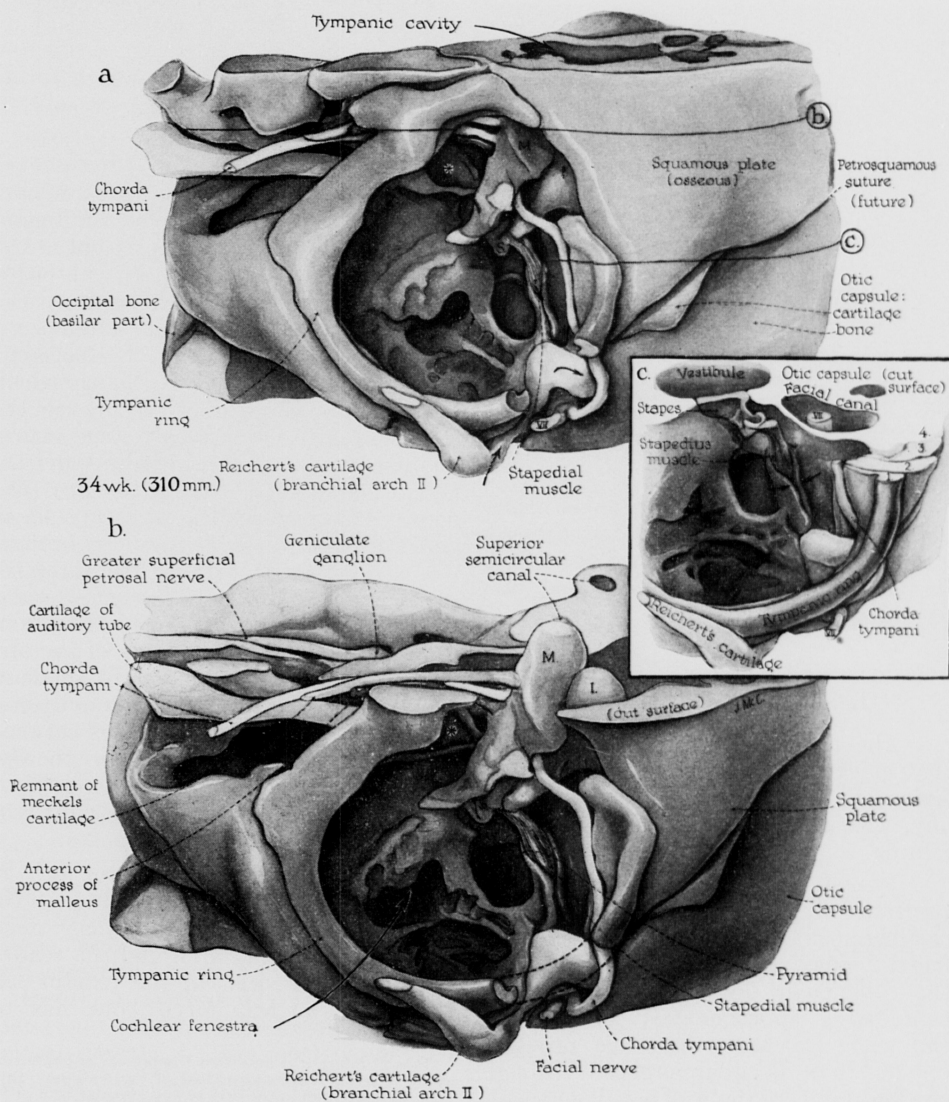


Fig. 6. Drawings of a reconstruction of the otic capsule and related structures in a fetus of 310 mm. (34 wk.). Viewed from a lateral and slightly superior position. Left ear. Wis. ser. 68. Figs. 6a and 6b, $\times 2.7$; Fig. 6c $\times 4$. Abbreviations: M, malleus; I, incus; S, stapes.

In Fig. 6a and Fig. 6b, removal of a segment of the tympanic ring exposes the area of cranial attachment of Reichert's cartilage to the otic capsule and the portion of the same cartilaginous arch between the points of cranial and caudal attachment (these marked by unlabelled arrows); the transverse lines indicated by the encircled letters "b" and "c" are those to which the reconstruction has been opened in the correspondingly lettered figures (that is, in fig. 6b and fig. 6c). In Fig. 6c, structures are numbered in the order of their depth, from the tympanic ring (at 1) to the otic capsule (at 4). The distal extremity of Reichert's cartilage has been omitted.

Photomicrographs of sections in this otological series appears as Figs. 1d, 2d and 4c.

Fig. 6a. The reconstruction shown entire. The otic capsule has become ossified except in parts of the canalicular division. Ossification of the malleus, incus and stapes is virtually complete. The pyramid for transmission of the stapedial tendon is being formed by the fusion of two osseous ridges; a similar process will result in the production of a simicanal for the tensor tympani (the wall of the channel being indicated by *, here shown without the muscle).

From a point of cranial attachment to the capsule (at the upper arrow). Reichert's cartilage (cut distally) descends in sinuous course deep to the tympanic ring, where a second attachment is made (at the lower arrow); then, turning forward, the cartilage passes superficial to the tympanic ring and on a plane with the latter. In its upper reaches the cartilage forms part of the outer wall of the developing (primordial) facial canal.

stratum in the form of a uniform lining (see succeeding stage, fig. 1f).

The tympanic mucous membrane lines intercommunicating parts of the middle ear, passing around the stapedial tendon and into the obturator foramen (fig. 1e, at arrows).

Infant—The general changes which are first evident in the cochlear division of the otic capsule, in early postnatal years, come finally to involve the region of the facial canal: endochondral bone is produced with great rapidity; marrow is largely replaced by bone. As a result, the otic capsule attains a relatively compact texture (fig. 1f). Actually, the otic capsule in many a newborn infant could be mistaken for that of an adult.

The distribution of the mucous membrane is likewise mature; it has pressed into irregularities on the medial wall of the tympanic cavity, to produce numerous bay-like extensions.

3. Level of Superior Attachment of Reichert's Cartilage

The next area to be considered is that at which the proximal extremity of Reichert's cartilage is continuous, cranially, with the otic capsule (see encircled 2 in fig. 5).

48-mm. fetus—The otic capsule in the fetus of 10 weeks is still completely cartilaginous (fig. 2a). The primordial facial "canal" is a deep sulcus to which the canalicular division of the capsule contributes approximately one-half of the wall; Reichert's cartilage provides one-fourth of its circumference. Through the hiatus where the wall is still deficient, the unmodified mesenchymal tissue is continuous with that which occupies the space between the tympanic mucous membrane and the otic capsule.

The auditory ossicles, like the capsule, still consist wholly of cartilage.

The tympanic cavity is a narrow chink; the epithelial plate which forms its lateral boundary has not yet split to form a meatal space.

183-mm. fetus—In the 21-week fetus ossification has involved the greater part of the otic capsule. However, the region of the canal is cartilaginous, except in the anterior portion (fig. 2b). In the latter area a thin projection of bone, from the ossified part of the capsule, extends toward the free extremity of Reichert's cartilage—a developmental change which initiates the process of closure of the canal.⁷ At this intermediate stage in production of a facial canal, the latter channel is bounded by five histological elements: cartilage of the otic capsule, in which invasive vascular tissue is producing a spongy condition (to allow for expansion of the arcs of the semicircular ducts); Reichert's cartilage; intrachondrial bone of the middle layer of the otic capsule; membrane bone (still small in amount); concentrated mesenchyma, which, passing across the hiatus between Reichert's cartilage and the newly-formed ledge of membrane bone, presently will be converted into osseous tissue of the latter sort (compare fig. 2c).

215-mm. fetus—The fetus of 24 weeks represents a definitive stage in the development of the facial canal, since, while the branchial arch and the related portion of the otic capsule remain cartilaginous, intrachondrial bone has re-

⁷It is of interest to note that the process of ossification at the external (cranial) aperture of the vestibular aqueduct virtually duplicates that of the capsular wall of the facial canal. The developmental steps represented by the 183-mm. and 215-mm. fetuses, among others, are described and figured in the authors' article which appeared in the summer 1951 issue of the Quarterly Bulletin (vol. 25, no. 2, pp. 96-107) and in the Annals of Otolaryngology and Laryngology in the same year (vol. 60, 6o. 4, pp. 1072-1084).

(Continuation of legend for Figure 6.)

Fig. 6b. The reconstruction, with the superior segment removed (at the level marked by the encircled "b" in fig. 6a). The interrelationships of the following structures are revealed: greater superficial petrosal nerve; the remnant of Meckel's cartilage (first branchial arch); the chorda tympani; the stapes incus and malleus with the anterior process of the malleus; the cartilaginous auditory tube; the developing semicanal (at *) for the tensor tympani muscle.

Fig. 6c. The portion of the same reconstruction in the general area of capsular attachment of Reichert's cartilage. The two upper segments have been removed (to the level marked "c" in fig. 6a). Here, on larger scale, are demonstrated the facial canal and the following closely related structures: the tympanic ring (at 1); the squamous plate (at 2); an area of persistent cartilage in the wall of the otic capsule (at 3); and the subjacent ossified part of the capsule (at 4).

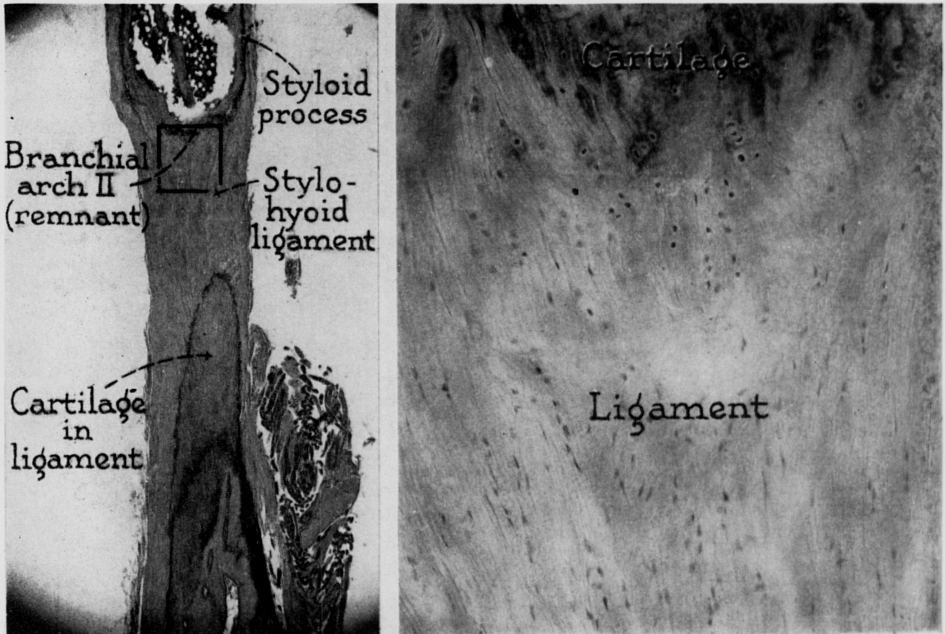


Fig. 7. The adult remnant of Reichert's cartilage, in relation to the styloid process of the temporal bone proximally and to stylohyoid ligament and related structures distally. Photomicrographs of sections prepared from a dissection-room specimen (adult male). Fig. 7a, $\times 16$; Fig. 7b, $\times 165$ (at higher magnification, the area blocked in Fig. 7a).

Figs. 7a and 7b. In this adult head a remnant of Reichert's cartilage arch persisted in continuity with bone at the tip of the styloid process. Within the substance of the stylohyoid ligament (derived from the same branchial arch), either cartilage or bone may be formed (sometimes in continuity with the os hyoideum).

placed cartilage in the otic capsule and, continuous with these spicules, membrane bone has begun to take part in the process of closure of Reichert's cartilage (fig. 2c). Already an osseous wall is being formed internal to the branchial arch in the area closely related to the facial nerve. This plate of membrane bone, upon completing a wall around the facial nerve, the stapedial muscle and the related blood vessels, will have divided the primordial facial "canal" (of, say, the 21-week fetus) into the definitive canal and a cul de sac situated between the membrane bone and Reichert's cartilage. The latter space will soon become pneumatized (see later stages, figs. 2d to 2f).

Nearby, advancing pneumatization has carried the mucous membrane medialward, to form other bays of this kind (one of them indicated by * in fig. 2c) near the facial canal.

310-mm. fetus—Ten weeks later (in a 34-week specimen), formation of a defini-

tive facial canal has been completed. On the deep aspect, perichondral bone has produced an investment external to the intrachondrial bone of the middle layer; on the superficial aspect, cartilage of the second branchial arch, recently formed membrane bone and perichondral bone combine to bound the canal (fig. 2d). The channel itself is being subdivided by the growth of a partition of membrane bone (fig. 2d, at arrow), to produce a compartment—the true, or definitive, canal—for the facial nerve, stapedial muscle and numerous blood vessels; another compartment, in becoming invaded by mucous membrane, produces one of the many pneumatized bays of the tympanic cavity (fig. 2d, at *).

Term fetus—In the fetus at term the process of ossification has spread from the capsule along the proximal segment of the branchial arch; spicules of combined intrachondrial bone and endochondral bone meet the cartilage of the arch

(fig. 2e, at the tip of the arrow). The facial canal at this level is now formed by bone of the outer and middle layers and by membrane bone. A pocket-like extension of the tympanic cavity (at *) intervenes between Reichert's cartilage externally and the newly-formed tympanic wall of the facial canal internally. At this level the facial nerve is not separated from the stapedial muscle.

Infant of 6 months—The former cartilage is now completely ossified in this area of continuity with the otic capsule. The interrelationships of structures within the facial canal, seen in the primordial, incomplete channel of the 21-week fetus, are, for the most part, retained in the infant and the adult; however, membrane bone forms a partial compartment for the stapedial muscle. The tissue within the canal remains strikingly vascular.

4. Between Attachments of Reichert's Cartilage

The third important level in cranio-caudal succession is that which passes through the branchial arch midway between its two attachments (see encircled 3 in fig. 5). Four stages will be considered.

161-mm. fetus—In this 19-week fetus, between capsular attachments, the Reichert's cartilage is cartilaginous (fig. 3a), as it is at a more proximal point in a specimen slightly older (183-mm. fetus, fig. 2b).

As previously mentioned, the canal for the facial nerve appears only as ridges along the margins of the nerve (fig. 5); as yet there is no comparable precursor of a semicanal (for the tensor tympani).

215-mm. fetus—In the 24-week specimen Reichert's cartilage remains cartilaginous (fig. 3b, in midcourse; fig. 2c, at cranial continuity with the otic capsule). At the former level there is as yet no canal for the facial nerve; in fact, the nerve and the stapedial muscle merely lie close to the capsule, lodged in mesenchymal tissue (fig. 3b). The capsular wall, at the site of the future canal, is composed of intrachondrial bone and residual cartilage.

10-week infant—In the young infant, Reichert's cartilage remains unaltered. However, it has become surrounded by newly-formed bone, and is

separated thereby from the facial nerve (fig. 3c). The facial canal is a complete channel; within the canal the stapedial muscle, approaching the pyramid, is partially separated from the nerve.

6-month infant—In a slightly older specimen the branchial arch has become ossified within its osseous sheath (fig. 3d; compare fig. 2f).

5. Level of Inferior Attachment of Reichert's Cartilage

Last in the succession of crucial levels is that at which Reichert's cartilage is fused with the otic capsule (fig. 5 at encircled 4).

161-mm. fetus—In the 19-week fetus the arch at its lower portion is, like the remainder of the structure, a cartilaginous element (fig. 4a).

183-mm. fetus—The Reichert's cartilage, in the fetus of 21 weeks, is cartilaginous in the area of lower attachment (fig. 4b), as it is at the cranial attachment (fig. 2b).

310-mm. fetus—The arch remains cartilaginous throughout its length in the fetus of 34 weeks (figs. 4c and 6).

The wall of the facial canal is still incomplete.

10-week infant—Even in the infant the Reichert's cartilage remains a chondral structure throughout the portion pictured, except where it is in contact with the osseous sheath; there bone-formation is locally under way (fig. 4d).

CONCLUSIONS

FACIAL CANAL AND NERVE

While the canalicular division of the otic capsule is still cartilaginous, in the fetus of 21 weeks, the future canal for the facial nerve is a shallow, vertical furrow situated just posterior to the vestibular (oval) and cochlear (round) windows.

Within a 3-week period, the "canal" has deepened. The wall is formed by bone of the middle layer; characteristically, and unlike a periosteal (outer) layer, it is composed of scattered spicules of intrachondrial bone, between which the primitive marrow is continuous with the tissue in the facial canal. Even at this early stage, the tissue in which the nerve

and stapedia muscle are lodged, is highly vascularized.

In a fetal specimen 10 weeks older the deepened sulcus has acquired a lateral wall, thus becoming a true canal; endochondral bone has been applied to the intrachondrial spicules, while membrane and periosteal bone complete the wall on the tympanic aspect. In this process, the canal becomes separated from Reichert's cartilage, which in earlier stages constituted an outer boundary.

In the fetus at term, periosteal bone has enveloped Reichert's cartilage. During early infancy Reichert's cartilage, undergoing ossification, becomes fused with the periosteal bone of the capsule.

REICHERT'S CARTILAGE

The skeletal element of the second branchial arch remains cartilaginous throughout its length (even in the late fetus of 34 weeks).

In the fetus at term the branchial arch is ossified only in the proximal segment, where it is continuous cranially with the otic capsule.

Conversion of cartilage into bone is such a slow process that in the 10-week infant ossification has advanced distalward in the branchial arch only to the area of inferior attachment of the arch to the capsule; even in some adults cartilage persists in the stylohyoid ligament

near the tip of the styloid process of the temporal bone.

It is only at the lower level that Reichert's cartilage makes a contribution to the wall of the definitive facial canal, whereas, in fetuses prior to the 24-week state it was an important parietal element.

TYMPANIC MUCOUS MEMBRANE

As one of the results of pneumatization, mucous membrane becomes closely related to the tympanic wall of the facial canal.

In the 10-week fetus the narrow tympanic cavity has extended posterolaterally, almost reaching the posterior limit of the tympanic ring.

During a developmental period of less than 3 months (in the fetus of 24 weeks) the cavity has widened to such a degree that the mucous membrane is applied to the otic capsule.

Within another period of approximately the same length, bays of the tympanic cavity have appeared in the area between Reichert's cartilage and the newly-formed wall of the facial canal. Concurrently, mucous membrane has completely invested the auditory ossicles and has invaded the middle layer of the otic capsule—to initiate the process which, in some specimens, results in extensive pneumatization of the temporal bone.