The Relationship of the Developing Inner Ear, Subarcuate Fossa and Paraflocculus in the Rat

THEODORE D. McCLURE AND GARMAN H. DARON
Department of Anatomical Sciences, University of Oklahoma Medical Center, Oklahoma City, Oklahoma 73104

ABSTRACT A study of the development of the subarcuate fossa and its relationships to the semicircular canals and to the paraflocculus was made in the rat. Specimens ranging from 12-day embryos through 31 days after birth and adults were used for dissection and microscopic studies.

Two distinct steps are identified in the development of the fossa. First preceded by the differentiation of the semicircular canals, a primitive subarcuate fossa, which is completely filled with loose vascularized connective tissue, develops in the periotic capsule. Second, the primitive dura mater of the posterior cranial fossa evaginates into the area of the primitive fossa displacing the loose connective tissue contained therein, to form a laterally projecting cavity from the posterior cranial fossa, the definitive subarcuate fossa. Thus, the primitive subarcuate fossa appears passively as a product of the pattern of development of the periotic capsule.

The paraflocculus of the cerebellum does not appear to influence the development of the definitive subarcuate fossa since it secondarily occupies the area of the fossa. The pedunculated nature of the paraflocculus is associated with, and probably results from, the diameter of the ostium of the fossa being smaller than its greatest width.

A comparison is made of the development of the subarcuate fossa within the periotic capsule in the rat and man. In the adult rat a definitive subarcuate fossa is present, while in adult man only a rudimentary counterpart exists.

In many mammalian species, the definitive subarcuate fossa is recognized as an outpocketing of the posterior cranial fossa into the temporal bone. The ostium of the fossa lies medial to the anterior semicircular canal and dorsal and lateral to the internal acoustic meatus. From its ostium, the fossa passes lateralward through the arch of the anterior semicircular canal and is housed in the canalicular portion of the periotic capsule of the temporal bone. In addition, the fossa is lined with dura mater and accommodates a lobe of the cerebellum. In the rat, this lobe of the cerebellum is the paraflocculus (Larsell, '52). These basic relationships have been reported for many species of adult mammals (Girard and Didier, '21; Greene, '35; deBeer, '37; Bensley, '48; Straus, '60; Hoyte, '61; Hromada, '65b). However, in other mammalian species, the subarcuate fossa is greatly reduced or nonexistent (Girard and Didier, '21; Kuhn, '41; Sisson and Grossway, '53; Delattre and Renart, '59; Straus, '60; Hromada, '65a). In adult man the subarcuate fossa is described as a rudimentary structure exhibiting an indistinct depression or an irregular slit of varying depth to which the dura mater is firmly attached (Girard and Didier, '21; Kuhn, '41; Bošković, '58; Hromada, '65b). Descriptions of the fossa in human fetuses have been reported by Kernan ('16), Macklin ('21), Girard and Didier ('21), Martin and Anson ('38), Bošković ('58) and Hromada ('65a).

The subarcuate fossa has been described in the chondrocranium in isolated age groups of some non-primates (Fischer, '01; Mead, '09; Terry, '17; Fawcett, '17, '18, '21, '22; deBeer, '29; Roux, '47; Frick and Heckman, '55; Kanan, '61–'62).

This study was undertaken to portray the development of the subarcuate fossa in the periotic capsule of the rat. In addition, the relationships of the fossa to the semicircular canals and to the paraflocculus are presented.

MATERIALS AND METHODS

The ages of the King-Holtzman strain of rats utilized were as follows: (1) prenatal (embryonic) specimens ranging from 12 to 20 days (litters from 12, 14, 16, 18 and 20-days); (2) postnatal specimens ranging from 1 to 31 days; and (3) adult specimens of varying age. The age of the embryonic specimens was determined by daily examination of vaginal smears and pregnancy was dated from the first observation of spermatazoa in the smears. No attempt was made to determine the exact time of copulation or of fertilization. In collecting the embryonic specimens, pregnant females were sacrificed, and the horns of the uterus were removed and placed in 0.9% saline solution. Each embryo was dissected from its extra-embryonic structures, the crown-rump length (CRL) measured, and then immersed in Bouin's fluid. Postnatal rats were sacrificed by decapitation. The superior portion of the calvarium was removed before the head was fixed in Bouin's fluid or formaldehyde.

After 24-hour fixation the embryonic and postnatal specimens were dehydrated in alcohol, cleared in xylene, and embedded in paraffin. Serial sections were cut at 10 μ; they were stained with Ehrlich's or Harris' hematoxylin and counterstained with eosin (H & E). The plane of section for embryos was transverse in relation to the cervical region. The heads of the postnatal specimens were sectioned in a plane horizontal to the base of the skull. For study of the adult head, the rats were decapitated and gross dissections were performed on both skeletal and fresh materials.

OBSERVATIONS

The following format will be utilized in the description of the development of the subarcuate fossa and its relationship to the paraflocculus and semicircular canals. First, a description will be made of these relationships in the adult and this will be followed by presentation of the development of these same relationships in a succession of embryonic and postnatal stages.

Adult specimens

For clarification of terminology, it should be noted that the temporal bone in man is represented in the rat as three separate bones, *viz.*, (1) the squamosal; (2) the periotic capsule; and (3) the tympanic bulla (Greene, '35). The dorsal aspect of the periotic capsule is characterized by a sharp crest of bone which marks the separation of the middle and posterior cranial fossae and delimits its dorsoanterior surface from its posterior surface. This is comparable to the superior crest of the petrous portion of the temporal bone in man (Bast and Anson, '49). Ventral to the dorsal crest and lateral to the internal acoustic meatus on the lateral portion of the posterior surface of the periotic capsule, is a prominent ostium opening into a large, laterally directed fossa, the definitive subarcuate fossa (figs. 2, 3).

The fossa and its ostium have the following relationships to the semicircular canals. The ostium, which is oval in shape, is circumscribed by the bony labryinth of the anterior semicircular canal. From its ostium the fossa extends lateralward beneath the arch of this canal into the substance of the periotic capsule. The posterior bony wall of the fossa contains the posterior semicircular canal with the fossa bulging slightly into the center of this canal. The fossa extends beyond the lateral edge of the lateral semicircular canal which is located in the bony floor or ventral boundary of the fossa. The fossa is smooth in contour and nearly spherical in shape with its greatest diameter being larger than that of its ostium. A schematic representation of these relationships of the subarcuate fossa to the semicircular canals is presented in figure 1.

Externally, the laterally extending fossa is separated from the surface of the skull by a thin bony lamina of the periotic capsule. This lamina is convex on its external surface and is situated dorsal and posterior to the external acoustic meatus, dorsal to the posterior extent of the tympanic bulla, and posterior to a prominent crest of bone which constitutes the junction of the oc-

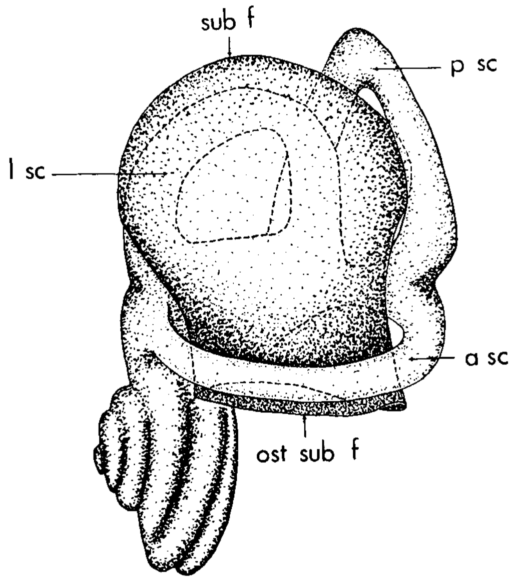


Fig. 1 A diagrammatic representation of the relationships of the subarcuate fossa to the semicircular canals of the right periotic capsule in the adult rat. a sc, anterior semicircular canal; l sc, lateral semicircular canal; ost sub f, ostium of subarcuate fossa; p sc, posterior semicircular canal; sub f, subarcuate fossa.

cipital and post-tympanic hook of squamosal bone.

The dura mater traverses the ostium and lines the entire fossa to the walls of which it is firmly affixed. The paraflocculus traverses the ostium and fills the fossa. It exhibits a proximal constricted portion and an expanded distal portion (fig. 4). This pedunculated appearance of the paraflocculus is associated with the smaller size of the ostium in contrast to the greater diameter of the fossa.

Embryonic specimens

The 12-day embryo (CRL, 5.8 mm) presents the initial differentiation of mesenchymal cells adjacent to the otocyst, the presumptive periotic capsule. The cells between the otocyst and the lateral surface of the rhombencephalon are loosely arranged and highly vascularized while those between the otocyst and the ectoderm are more compact and sparsely vascularized (fig. 5). The otocyst is ellipsoid and has a dorsally directed finger-like process, the endolymphatic duct, extending from its dorsomedial border. There is no apparent differentiation of the semicircular canals.

The dorsolateral aspect of the otocyst at 14 days (CRL, 10.1 mm) is characterized by flange-like extensions which are the primordia of the semicircular canals. Epithelial tissue in the center of the primordium of the anterior semicircular canal has been re-absorbed, establishing the basic adult structural pattern of this canal (fig. 6). Due to dorsal and lateral growth of the vestibular portion of the otocyst the endolymphatic duct is situated ventrally. The proximal portion of the endolymphatic duct courses dorsally just medial to the anlage of the common crus. The mesenchymal cells of the primitive periotic capsule are concentrated to varying degrees, but the exact borders of the capsule are difficult to identify (fig. 6). There is a narrow region of loose vascularized mesenchyme, the presumptive meninges, between the condensed, sparsely vascularized periotic capsular mesenchyme and the marginal layer of the rhombencephalon.

At 16 days (CRL, 16.4 mm) the vestibular portion of the otocyst exhibits three distinct semicircular canals which have developed from the flange-like primordia. The greater portion of the periotic capsule surrounding the otocyst is precartilaginous. The designation, precartilaginous, agrees with the description of Bremer and Weatherford ('41). Extending lateralward from the middle one-third of the medial surface of the periotic capsule is a cavity in the precartilaginous periotic capsule which is filled with loose, vascularized mesenchyme. This cavity is the primordium of the subarcuate fossa and will be designated as the primitive subarcuate fossa (fig. 7). The ostium of the primitive fossa is oval in outline and nearly parallel with the anterior semicircular canal. From its ostium the fossa passes through the arch of this semicircular canal and into the substance of the capsule, but its boundaries are indistinctly differentiated from the precartilage. The posterior semicircular canal is situated in the posterior wall of the fossa. The lateral semicircular canal lies within the floor of the fossa. At the posteroventral portion of the fossa and passing through the arch of the posterior semicircular canal, the precartilaginous wall is perforated by a cord of loose, vascularized connective tissue. This cord is a continuation of the connective tissue filling the primitive fossa and the connective tissue in the region of the sigmoid sinus. Vascular elements traversing this area join the sigmoid sinus. The primitive dura mater traverses the ostium of the primitive fossa, but does not extend laterally into its substance (fig. 7).

In the 18-day embryo (CRL, 23.3 mm) the periotic capsule is composed of cartilage and is clearly distinguishable from the adjacent tissues due to its uniform structure and sharply demarcated margins (fig. 8). Two distinct divisions of the periotic capsule can be recognized, viz., the cochlear and canalicular portions. The canalicular portion of this cartilaginous capsule exhibits two regions of undifferentiated, vascularized connective tissue, viz., the area around the various portions of the membranous labyrinth, which portends the development of the perilymphatic space, and the area of the primitive subarcuate fossa. The fossa, from its oval ostium, passes through the arch of the anterior semicircular canal and into the canalicular portion of the periotic capsule. Its posterior border contains the posterior semicircular canal. The fossa lies dorsal to the lateral semicircular canal and extends slightly beyond its lateral extent. A cord of vascularized connective tissue perforates the posteroventral portion of the wall of the fossa and passes through the arch of the posterior semicircular canal. The dura mater extends slightly lateralward into the primitive fossa at its ostium to form the first indication of the definitive subarcuate fossa (fig. 8). The developing cerebellum is adjacent to this indentation of dura mater, but it does not project into the area.

At 20 days (CRL, 39.1 mm) the relationships, degree of differentiation of the periotic capsule, the primitive subarcuate fossa, and the definitive subarcuate fossa exhibit little change from those in the previously described 18-day embryo.

Postnatal specimens

At one day after birth the primitive subarcuate fossa is greatly reduced in size due to the encroachment of the dura mater resulting in the continued enlargement of the subarcuate fossa. The relationships of the fossa to the semicircular canals are the same as those previously described. The dura mater is applied closely to the walls of the ostium, but does not extend to the lateral boundaries of the primitive fossa. The space between the dural lamina and the boundaries of the primitive fossa is occupied by connective tissue (fig. 9). A small area of endochondral ossification is demonstrated at the ventral border of the ostium. This ossification process is similar to that described in man (Bast, '29). Although the subarcuate fossa is rather extensive, its area is occupied by a very loose network of delicate vascularized connective tissue. At this stage in development, the paraflocculus has no direct relationship with the definitive fossa (fig. 9).

At two days after birth the differentiation and relationship of the subarcuate fossa to the semicircular canals within the substance of the canalicular portion of the periotic capsule is similar to the condition in the one-day postnatal specimens.

At three days after birth the ventral half of the ostium of the fossa is composed of endochondral bone. In addition, there are two small regions of endochondral bone, one lateral to the posterior semicircular canal and the other lateral to the lateral semicircular canal. The dura mater is directly apposed to the walls of the fossa where bone is located. For the first time, the paraflocculus occupies some of the available space of the subarcuate fossa (fig. 10).

At four days after birth the paraflocculus is increased greatly in size and extends laterally into the depths of the dura-lined sac; however, it does not completely fill the available space.

At five days after birth the area of endochondral bone in the periotic capsule includes the ventral half of the ostium of the subarcuate fossa and the proximal half of the arch of the lateral semicircular canal. The paraflocculus at the ostium of the fossa is somewhat constricted, forming the definitive pedunculated appearance of the adult.

At eight days after birth the dura mater is closely applied to all of the boundaries of the fossa, thereby eliminating the remaining portion of the primitive subarcuate fossa (fig. 11). A small area of fibrous, vascularized connective tissue occupies the posteroventral portion of the fossa. The cartilage at the lateral portion of the posterior semicircular canal exhibits the initial formation of endochondral bone.

At 14 days after birth the borders of the fossa are composed of trabeculated bone, except for a small area at the posteroventral portion of the fossa. This area is located at the center of the arch of the posterior semicircular canal.

At 31 days after birth the relationships of the fossa to the semicircular canals are the same as previously described. The dura mater lines the inside of the fossa. The paraflocculus occupies more of the available space of the dural sac (fig. 12). A thin lamina of bone is present peripheral to the dura mater forming the wall of the fossa. The area of vascularized fibrous connective tissue is not present at this stage, this region being occupied by bone.

DISCUSSION

Many successive changes occur in the periotic capsule during the development of the subarcuate fossa and before the definitive fossa and its relationship are attained. The development of the membranous labyrinth in the rat has been described by Adelmann ('25) and Guggenheim ('31). These accounts of development in the rat are basically the same as described for the human fetus (Streeter, '06, '07; Wilson, '14; Ingalls, '20; Bartelmez, '22; Anson, '34; Anson and Black, '34; Bast et al., '47; O'Rahilly, '63). Since this study is concerned primarily with development of the subarcuate fossa within the periotic capsule and only incidentally with the membranous labyrinth, it is beyond the scope of this study to present the development of the membranous labyrinth. However, in the 16-day rat embryo the semicircular canals are described in their adult relationships.

Development of the periotic capsule involves changes in the mesenchymal tissue surrounding the membranous labyrinth. The earliest anlage of the capsule consists of a condensation of the mesenchyme adjacent to the lateral wall of the ellipsoid otic vesicle as seen in the 12-day rat embryo and reported in the human fetus (Streeter, '17). This mesenchymal condensation is nearly devoid of vascular elements, a result comparable to that reported for the human fetus (Streeter, '18).

In the 18-day embryo the periotic capsule is cartilaginous and two distinct divisions can be recognized. Bast ('44) reported that in man when the periotic capsule becomes cartilaginous, two divisions can also be recognized. Various investigators have described two divisions of the periotic capsule in other species of mammals (Fischer, '01; Mead, '09; Terry, '17; Fawcett, '17, '18, '21; deBeer, '29; Roux, '47; Frick and Heckman, '55; Kanan, '61, '62).

Bast ('29) observed that in man the earliest visible change in cartilage for preparation of bone formation involves a marked enlargement of cartilage cells, with their nuclei becoming more irregular and pycnotic, and with changes occurring in the cartilage matrix. Subsequently, the overlying perichondrium ruptures and allows osteogenetic buds to enter the altered cartilage. This endochondral ossification process is similar in the rat. The earliest indication of invading osteogenetic buds is recognized in the one-day postnatal rat. As ossification occurs and the individual centers enlarge, they coalesce until the entire capsule becomes involved. Bast ('44) reported that in man the various portions of the membranous labyrinth within the confines of the periotic capsule reach their definitive size before endochondral bone formation begins. This same phenomena was supported by Hoyte ('61) in the rabbit but was not evaluated in the present study.

The subarcuate fossa develops within the canalicular portion of the periotic capsule. In the 16-day rat embryo, the primitive subarcuate fossa is present when the condensed mesenchyme of the primordial periotic capsule differentiates into precartilage. The borders of the fossa are indistinctly defined and the fossa is filled with connective tissue. It appears that the primordium of the subarcuate fossa is a product of the pattern of development of the periotic capsule and that the primitive fossa portends the development of the definitive subarcuate fossa. Therefore, in the rat, development of the subarcuate fossa is passive rather than active. Conversely, in man development of the subarcuate fossa is by an active process (Bast, '32). Bast described the development as a vascular tissue ingrowth from the overlying perichondrium and dura mater into the cartilage mass within the arch circumscribed by the anterior semicircular canal.

The walls of the subarcuate fossa begin to undergo endochondral bone formation before the definitive size of the fossa has been attained but this bone formation does not occur until the dura mater becomes closely applied to its cartilaginous walls. Therefore, ossification of the periotic capsule comprising the walls of the fossa differs from that which is adjacent to the membranous labyrinth where, according to Bast ('29), the latter structure reaches its definitive size before ossification commences.

This work suggests that the vascularized, loose connective tissue in the primitive fossa assists in expansion of the fossa at the expense of the surrounding cartilaginous tissue. This is in agreement with the statement by Bast ('32) that in man the loose connective tissue of the subarcuate fossa is implicated in partial resorption of the cartilaginous capsule allowing for internal expansion of the fossa.

Perforation of the walls of the subarcuate fossa have been reported in only three other species of mammals. Perforation of the floor of the fossa to allow the passage of blood vessels to the exterior of the petrous bone occurs in the water rat (Fawcett, '17). No indication of the region into which these vessels entered or their relationship to the semicircular canals was described. Mead ('09) reported that in the pig several foramina perforate the outer wall of the fossa for passage of small blood vessels to the transverse sinus. The vessels apparently pass through the lateral wall of the fossa, but this was not described. Roux ('47) described two foramina in the posterior ventrolateral portion of the fossa in the musk shrew. These foramina transmitted no blood vessels and were recognized only as a deficiency in the cartilaginous wall. In the 16-day rat embryo, the posteroventral portion of the primitive fossa is perforated by a cord of loose, vascularized connective tissue, which is continuous with connective tissue in the region of the sigmoid sinus. At 31 days after birth, no indication of this vascularized connective tissue cord is present, but it was noted that the definitive subarcuate fossa extends slightly posteriorly through the arch of the posterior semicircular canal. The posterior expansion of the fossa probably forms in the connective tissue cord demonstrated in the region in younger specimens.

Mead ('09) stated that the presence and size of the subarcuate fossa in the pig appears to be partially dependent upon the development of the flocculus (paraflocculus). Since the subarcuate fossa is rather extensive at one day after birth, and the paraflocculus of the cerebellum does not extend laterally into the region of the fossa until three days after birth, the above statement is apparently not correct with reference to the rat. The paraflocculus may in some degree induce evagination of the dura mater to form the subarcuate fossa but it is apparent that the primitive fossa develops prior to and independently of the development of the paraflocculus. The paraflocculus may exert some influence upon the internal dimensions of the fossa after it occupies some of the available space, but this currently is unknown. Hoyte ('61) has shown in the rabbit that after ossification the subarcuate fossa (parafloccular fossa) expands centrifugally by internal resorption and external deposition. DeBeer ('37) stated that the subarcuate fossa closes in many species of mammals because the paraflocculus is vestigial. This cause and effect relationship is supposition and currently cannot be evaluated.

A concavity in the canalicular portion of the periotic capsule, corresponding to the subarcuate fossa of the rat and enclosing a portion of the cerebellum, has been described in several species of mammals including moles, shrews, cats, dogs, hogs, sheep and some primates. Girard and Didier ('21) and Straus ('60) described the fossa in lower and higher primates. They stated that in the New World monkeys, *Cebus, Aloutta,* and *Saimira,* the fossa is broader and deeper than in the Old World monkeys, *Macaca, Papio, Theropithecus, Cereocebus, Circopithecus,* *Erythrocebus*, and *Nasalis*. In all cases the ostium of the fossa is circumscribed by the anterior semicircular canal and the dura-lined fossa extends laterally into the substance of the temporal bone. On the other hand, in some species, notably in man and the anthropoid apes, the temporal bone exhibits only a very slight depression indicative of the subarcuate fossa. This is often small and indistinct, barely warranting the term "fossa." The subarcuate fossa in man is described as an indistinct depression to which the dura mater is firmly attached and into which a small vein passes (Girard and Didier, '21; Kuhn, '41; Bošković, '58; Hromada, '65b).

The adult rat and man may be considered to present two extremes in regard to the subarcuate fossa. In man, although there is no "real" subarcuate fossa in the adult, developmental processes in this region resemble those occurring in the rat. There is no specific continuous and complete account of the early development of the subarcuate fossa in man. However, Kernan ('16), Macklin ('21) and Martin and Anson ('38) described the subarcuate fossa at a specific age in the human fetus, noting that it was filled with loose vascularized connective tissue. While each of these authors used the term "fossa subarcuata," it is apparent that they were referring to the primitive subarcuate fossa as is present in the rat. None of these authors mentioned a subarcuate fossa in the sense of a dura-lined evagination from the posterior cranial cavity.

Girard and Didier ('21) and Bošković ('58) have described the region of the subarcuate fossa in older human fetuses. Girard and Didier ('21) stated that by the term "fossa subarcuata," they were referring to the region in the developing temporal bone that is filled with vascularized, fibrous tissue. Therefore, their subarcuate fossa is also comparable to the primitive subarcuate fossa in the rat.

Subsequently, the ossification and development of the petrous bone in adult man reduces the subarcuate fossa to a narrow canal. Girard and Didier ('21) designated this canal as the "canal petro cérébelleux." Kuhn ('41) stated that this canal should be called the "tractus subarcuatus." In species of mammals in which there is a "real" subarcuate fossa, Girard and Didier ('21) used the term "enfoncement cérébelleux."

LITERATURE CITED

Aldemann, H. B. 1925 The development of the neural folds and cranial ganglia of the rat. J. Comp. Neur., *89:* 19–171.

Anson, B. J. 1934 The early development of the membranous labyrinth in mammalian embryos, with special reference to the endolymphatic duct and the utriculoendolymphatic duct. Anat. Rec., *59:* 15–25.

Anson, B. J., and W. T. Black, Jr. 1934 The early relation of the auditory vesicle to the ectoderm in human embryos. Anat. Rec., *58:* 127–137.

Bartlemez, G. W. 1922 The origin of the otic and optic primordia in man. J. Comp. Neur., *34:* 201–232.

Bast, T. H. 1929 Osteogenesis of the human periotic capsule. Arch. Otol., *10:* 459–471.

——— 1932 Development of the otic capsule. I. Resorption of the cartilage in the canal portion of the otic capsule in human fetuses and its relation to the growth of the semicircular canals. Arch. Otol., *16:* 19–38.

——— 1944 Perichondrial ossification and fate of the perichondrium with spacial reference to that of the otic capsule. Anat. Rec., *90:* 139–148.

Bast, T. H., and B. J. Anson 1949 The Temporal Bone and the Ear. Charles C Thomas, Springfield, 3–257.

Bast, T. H., B. J. Anson and W. D. Gardner 1947 The developmental course of human auditory vesicle. Anat. Rec., *99:* 55–74.

Bensley, B. A. 1948 Practical Anatomy of the Rabbit. Eighth edition. E. H. Craigie, ed. The Blakiston Co., Philadelphia, 166–195.

Bošković, M. S. 1958 Morfologija, Safržaj I Odnosi Petromastoidnog Kanala Kod Čoveka. Acta med. Iugoslavica, *12:* Suppl. 1:5–43.

Bremer, J. L., and H. L. Weatherford 1941 A Text-Book of Histology. Sixth edition. The Blakiston Co., Philadelphia, 115–125.

deBeer, G. R. 1929 The development of the skull of the shrew. Phil. Trans. Roy. Soc., London, Ser. B., *217:* 411–480.

——— 1937 The Development of the Vertebrate Skull. Clarendon Press, Oxford, 359–405.

DeLattre, A., and R. Renart 1959 L'occlusion de la fossa subarcuata. C. R. Acad. Sci., *249:* 962–963.

Fawcett, E. 1917 The primordial cranium of *Microtus amphibius* (water-rat), as determined by sections and a model of the 25-mm stage. With comparative remarks. J. Anat., *51:* 309–359.

——— 1918 The primordial cranium of *Erinaceus europeas*. J. Anat., *52:* 206–250.

——— 1921 The primordial cranium of *Tatusia novemcincta* as determined by sections and models of the embryos of 12 millimetre and 17 millimetre C. R. length. J. Anat., *55:* 187–217.

——— 1922 The primordial cranium of *Xerus* (Spiny squirrel) at the 17 and 19 millimetres stages. J. Anat., *57:* 221–237.

Fischer, E. 1901 Das primordial-cranium von *Talpa europaea.* Anat. Hefte, *17:* 467–548.

Frick, V. H., and U. Heckman 1955 Ein Beitrag zur Morphogenese des Kaninchenschädels. Acta Anat., *24:* 268–314.

Girard, L., and G. Didier 1921 La fossa subarcuata (Notes d'Anatomie comparée). Bull. Mem. Soc. Anthrop., Paris, Ser. 7, *2:* 44–58.

Greene, E. C. 1935 Anatomy of the rat. Trans. Am. Phil. Soc., *27:* 1–370.

Guggenheim, L. K. 1931 The development of the organ of hearing. Ann. Otol., Rhin., Laryng., *40:* 812–852.

Hoyte, D. A. N. 1961 The postnatal growth of the ear capsule in the rabbit. Am. J. Anat., *108:* 1–16.

Hromada, J. 1965a Comparative and topographical investigation of the fossa subarcuata and its content in man, macaca monkeys and some laboratory animals. I. Fossa subarcuata. Folia Morph., *13:* 275:284.

——— 1965b Comparative and topographical investigation of the fossa subarcuata and its content in man, macaca monkeys and some laboratory animals. II. Contents of fossa subarcuata. Folia Morph., *13:* 285–293.

Ingalls, N. W. 1920 A human embryo at the beginning of segmentation with special reference to the vascular system. Contr. Embry. Carnegie Inst., Wash., *11:* 61–80.

Kanan, C. V. 1961–1962 The study of the development of auditory capsule of the chondrocranium in *Camelus dromedarius* at 5.4 cm C. R. L. stage. Acta Morph. Neerl. Scand., *4:* 63–70.

Kernan, J. D., Jr. 1916 The chondrocranium of a 20 mm human embryo. J. Morph., *27:* 605–645.

Kuhn, H. H. 1941 Das anatomische Verhalten des Hiatus subarcuatus im menschlichen Felsenbein. Inaugural-Dissertation. Frankfurt A. M., Gelnhausen.

Larsell, O. 1952 The morphogenesis and adult pattern of the lobules and fissures of the cerebellum of the white rat. J. Comp. Neur., *97:* 281–356.

Macklin, C. C. 1921 The skull of a human fetus of 43 millimeters greatest length. Contr. Embry. Cara. Inst., Wash., *10:* 57–103.

Martin, J., and B. J. Anson 1938 Otic capsule and membranous labyrinth of the 29 mm. (crown-rump) human embryo. Arch. Otol., *27:* 279–303.

Mead, C. S. 1909 The chondrocranium of an embryo pig, *Sus scrofa.* Am. J. Anat., *9:* 167–209.

O'Rahilly, R. 1963 The early development of the otic vesicle in staged human embryos. J. Embry. Exp. Morph., *11:* 741–755.

Roux, G. H. 1947 The cranial development of certain Ethiopian "Insectivores" and its bearing on the mutual affinities of the group. Acta Zool., *28:* 165–397.

Sisson, S., and J. D. Grossway 1953 The Anatomy of the Domestic Animals. Fourth edition, revised. W. B. Saunders Co., Philadelphia, 56–59, 137, 159, 170, 190–191.

Straus, W. L. 1960 The subarcuate fossa in primates. Anat. Rec., *138:* 93–103.

Streeter, G. L. 1906–1907 On the development of the membranous labyrinth and the acoustic and facial nerves in the human embryo. Am. J. Anat., *6:* 139–165.

——— 1917 The factors involved in the excavation of the cavities in the cartilaginous capsule of the ear of the human embryo. Am. J. Anat., *22:* 1–25.

——— 1918 The histogenesis and growth of the otic capsule and its contained periotic tissue-spaces in the human embryo. Contr. Embry. Carnegie Inst., Wash., *7:* 5–54.

Terry, R. J. 1917 The primordial cranium of the cat. J. Morph., *29:* 281–433.

Wilson, J. T. 1914 Observation upon young human embryos. J. Anat., *48:* 315–351.

PLATES

Abbreviations

a sc, anterior semicircular canal
br, brain
cc, common crus
cer, cerebellum
dur, dura mater
ed, endolymphatic duct
f mag, foramen magnum
i a m, internal acoustic meatus
l sc, lateral semicircular canal
ost sub f, ostium of the subarcuate fossa
oto, otocyst
pfl, paraflocculus
p sc, posterior semicircular canal
p sub f, primitive subarcuate fossa
sub f, subarcuate fossa
ves, vestibule of the membranous labyrinth

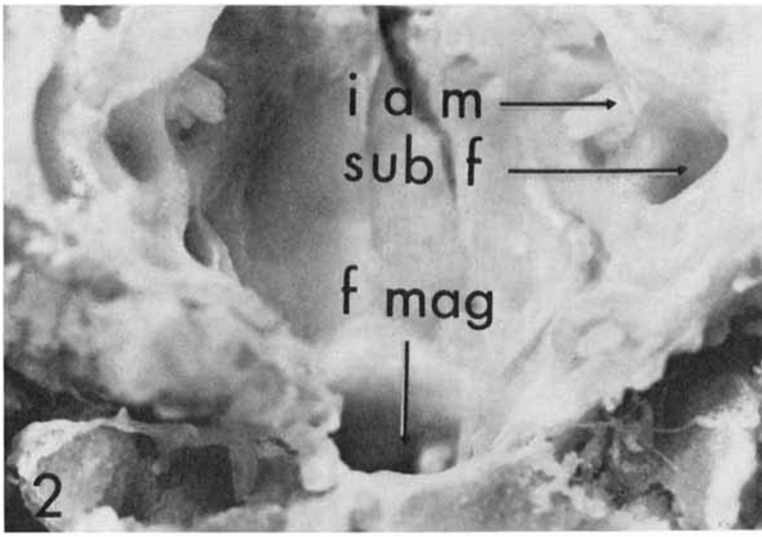
PLATE 1

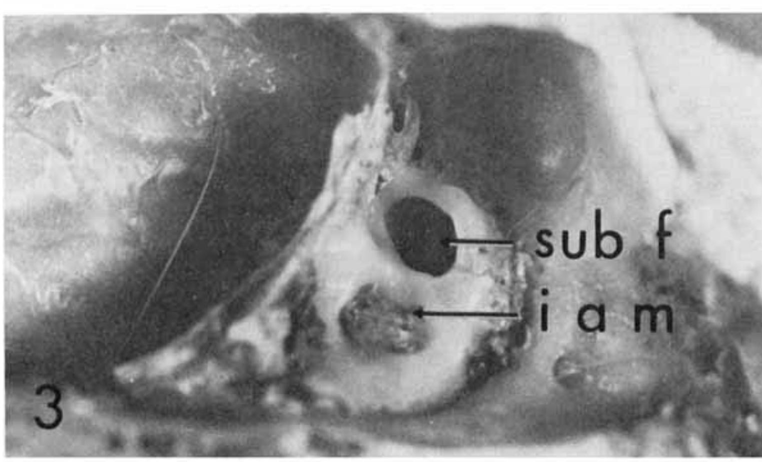
EXPLANATION OF FIGURES

2 A dorsal view of the posterior cranial fossa of the adult rat. × 6.

3 A medial view of the bisected head of the adult rat. × 6.

4 The ventral surface of the brain stem of the adult rat. Notice tl pedunculated appearance of the paraflocculus. × 6.


i a m
sub f
f mag
2


sub f
i a m
3

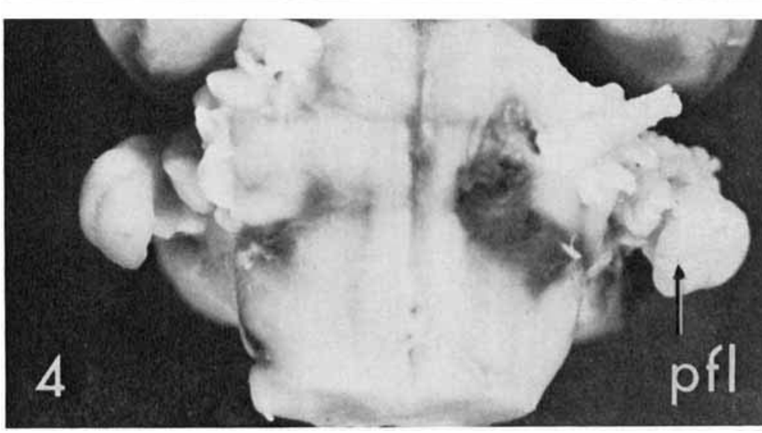

4
pfl

PLATE 2

EXPLANATION OF FIGURES

5 Photomicrograph of a section through the region of the otocyst of the 12-day rat embryo. H. & E. × 60.

6 Photomicrograph of a section through the level of the anterior semicircular canal of the left periotic capsule of the 14-day rat embryo. H. & E. × 60.

7 Photomicrograph of a section through the level of the primitive subarcuate fossa of the left periotic capsule of the 16-day rat embryo. H. & E. × 60.

8 Photomicrograph of a section at the level of the primitive subarcuate fossa in the right periotic capsule of the 18-day rat embryo. Notice the slight evagination of the primitive dura mater into the loose connective tissue of the primitive subarcuate fossa. H. & E. × 60.

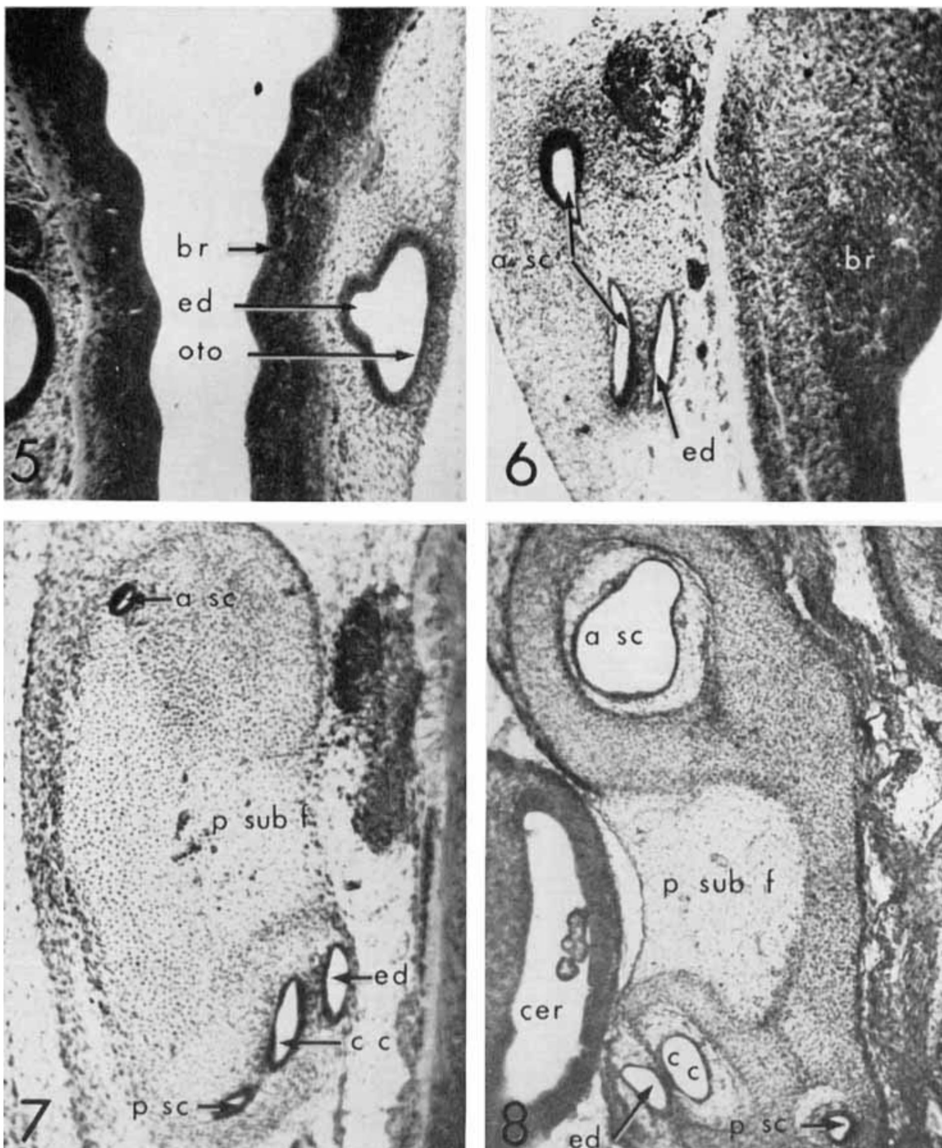

br
ed
oto
5
a sc
br
ed
6
a sc
p sub f
ed
c c
p sc
7
a sc
p sub f
cer
c c
ed
p sc
8

PLATE 3

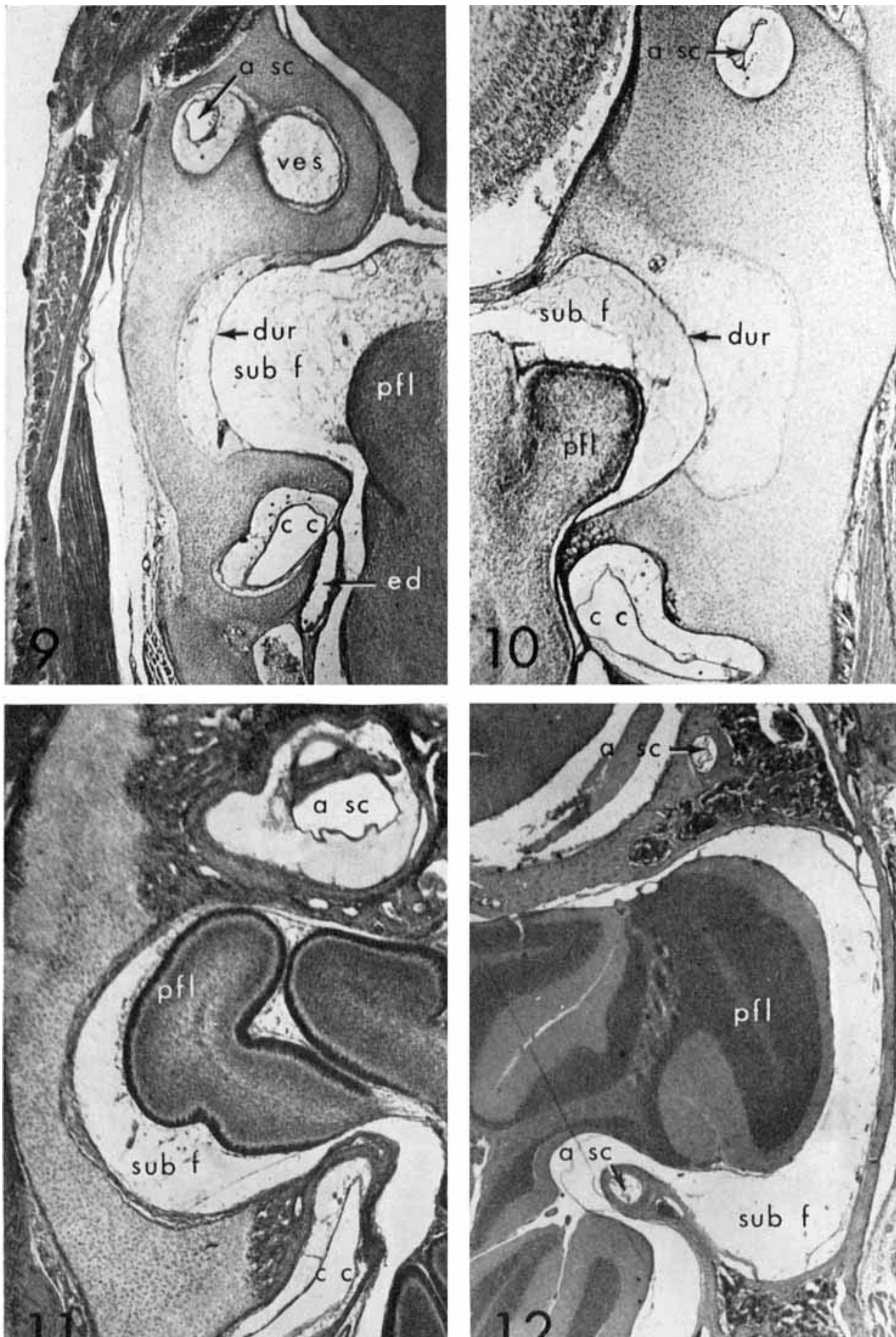
EXPLANATION OF FIGURES

9 Photomicrograph of a section through the subarcuate fossa in the left periotic capsule of the one-day postnatal rat. H. & E. × 30.

10 Photomicrograph of a section through the subarcuate fossa in the right periotic capsule of the three-day postnatal rat. H. & E. × 30.

11 Photomicrograph of a section through the subarcuate fossa of the left periotic capsule of the eight-day postnatal rat. H. &. E. × 30.

12 Photomicrograph of a section through the subarcuate fossa of the right periotic capsule of the 31-day postnatal rat. H. & E. × 25.


a sc
ves
dur
sub f
pfl
c c
ed
9
a sc
sub f
dur
pfl
c c
10
a sc
pfl
sub f
c c
11
a sc
pfl
a sc
sub f
12