

## **The development of mammalian dural venous sinuses with especial reference to the post-glenoid vein**

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The intracranial venous outflow of mammals drains into both the internal and external jugular veins and the relative role of these two veins varies between different adult mammals as well as at different phases of embryonic and foetal life. In general, the primary head vein (consisting of *venae capitis medialis* and *lateralis* and their tributaries) gives rise to the dural venous sinuses which drain into the anterior cardinal vein (the future internal jugular vein). The external jugular veins appear as the face and jaws develop but, at all times, the two venous systems freely communicate with each other. Morphologically, as shown by Sutton (1888), both the dural venous sinuses and the external jugular venous system are extracranial in so far as they are situated outside the *dura mater*. The chondrocranium and the dermocranium, however, develop in between the dural venous sinuses and the external jugular vein system (Butler, 1957). Thus, in the adult mammal, the bony skull wall separates the two venous systems, and therefore the dural venous sinuses are topographically intracranial whereas the external jugular venous system is extracranial. Furthermore the development of the skull localizes the connexions between the dural venous sinuses and the external jugular venous system to the various fontanelles and neuro-vascular foramina to form the emissary veins. The post-glenoid vein is one of the more important and controversial emissary veins since its presence or absence has been used in attempts to establish mammalian phylogenetic relationships (van Gelderen, 1925; Boyd, 1930).

Rathke (1838) stated that the primary venous drainage of the embryonic brain was through the external jugular vein which left the skull through a foramen situated between the tympanic ring and the temporo-mandibular joint. Later a new vein, the internal jugular, grew cranialwards out of the external jugular and entered the skull through the jugular foramen and formed the internal jugular vein. Only in man and apes did this new route receive all the intracranial venous outflow and the primary route was retained in other mammals to a varying degree. Luschka (1862) agreed with this view and named the cranial exit of the external jugular vein, in the embryonic skull, the 'foramen jugulare spurium' and in 1867 described its occasional occurrence in the postnatal human skull. Confusion has resulted from the application of the term 'foramen jugulare spurium' to the capsulo-parietal fissure (Macklin, 1914, 1921) or to the superior occipito-capsular fissure (de Beer, 1937; Padget, 1957) of the developing skull. As was shown (Butler, 1957) the emissary veins that develop in the occipito-capsular fissure become the mastoid emissary veins in man.

Further confusion was caused by Hochstetter (1906) who stated that the *vena capitis lateralis* left the skull between nerves v and vii and this led Streeter (1915, 1918) to regard the foramen jugulare spurium of the adult skull as 'the exit of a

decadent vena capitis lateralis'. Yet Salzer (1895) had clearly shown, by his investigations of the development of the dural venous sinuses of man and several mammals, that the post-glenoid vein developed as a secondary connexion between the transverse sinus and the external jugular vein and co-existed with the vena capitis lateralis. Also, Grosser (1901) clearly confirmed this in bat embryos. Boyd (1930) questioned Streeter's interpretation of the post-glenoid vein as a persistent vena capitis lateralis but offered no alternative explanation. Butler showed that in the rat (1953) and in man (1957) the post-glenoid vein is not a persistent vena capitis lateralis although they are related developmentally. Apart from the author's preliminary note (1953) there is no published account of the development of the post-glenoid vein and the following account is based on the examination of rat embryos supplemented by observations on other mammals, both embryonic and adult.

#### MATERIALS AND METHODS

Forty-three rat embryos and foetuses ranging from 1.6 mm crown-rump (C.R.) length to full term were examined. In 24 specimens the cardiovascular system had

#### ABBREVIATIONS TO FIGURES 1-11

##### *Veins*

<i>ACV</i>	anterior cardinal vein	<i>PRE</i>	pro-otic emissary vein
<i>ANC</i>	anterior cerebral vein	<i>PRO</i>	pro-otic vein(s)
<i>BAS</i>	basilar venous plexus	<i>PRV</i>	posterior rhombencephalic vein
<i>CS</i>	cavernous sinus	<i>PS</i>	petrosquamous sinus
<i>DA</i>	dorsal anastomotic vein	<i>PT</i>	post-torcular sinus
<i>EJV</i>	external jugular vein	<i>PV</i>	post-trigeminal vein
<i>FV</i>	facial vein	<i>SIG</i>	sigmoid sinus
<i>IJV</i>	internal jugular vein	<i>SOA</i>	supra-otic anastomotic vein
<i>IP</i>	inferior petrosal sinus	<i>SP</i>	superior petrosal sinus
<i>LCV</i>	lateral cerebral vein	<i>SS</i>	superior sagittal sinus
<i>ME</i>	mastoid emissary veins	<i>TH</i>	torcular Herophili (confluence of the sinuses)
<i>MV</i>	maxillary vein	<i>TS</i>	transverse sinus
<i>OS</i>	occipital sinus	<i>VCL</i>	vena capitis lateralis
<i>OV</i>	ophthalmic vein	<i>VCM</i>	vena capitis medialis
<i>Pe.V.</i>	peri-trigeminal vein	<i>VV</i>	vertebral vein
<i>PG</i>	postglenoid vein		
<i>PIV</i>	pituitary vein		

##### *Other structures*

<i>b.a.</i>	basilar artery	<i>o.p.c.</i>	orbito-parietal commissure
<i>c.ep.</i>	cavum epiptericum	<i>o.v.</i>	otic vesicle
<i>c.p.</i>	crista parotica	<i>p.</i>	pituitary gland
<i>e.</i>	optic vesicle	<i>p.o.p.</i>	para-occipital process
<i>h.</i>	hyoid cartilage	<i>p.t.</i>	petrous temporal bone
<i>i.a.m.</i>	internal auditory meatus	<i>s.p.f.</i>	spheno-parietal fontanelle
<i>i.c.a.</i>	internal carotid artery	<i>sq.t.</i>	squamous temporal bone
<i>j.p.</i>	jugular process	<i>t.f.</i>	tentorial fold
<i>m.b.</i>	mid-brain	<i>t.y.</i>	tympenic ring
<i>m.c.</i>	Meckel's cartilage	<i>v</i>	trigeminal nerve
<i>o.c.</i>	otic capsule	<i>vii</i>	facial nerve
<i>o.c.f.</i>	occipito-capsular fissure	<i>ix</i>	glossopharyngeal nerve
<i>occ.</i>	ala occipitalis	<i>x</i>	vagus nerve
<i>o.p.</i>	orbital plate	<i>xii</i>	hypoglossal nerve

been injected with India ink. Twenty rabbit embryos and foetuses, ranging from 5.0 mm C.R. length to full term, and 8 pig embryos, ranging from 6.0 to 30.0 mm C.R. length, were also examined. In several instances graphic reconstructions of the head veins and developing skull were made. The adult pattern of the dural venous sinuses and emissary veins were examined in the rat, rabbit, dog, hedgehog and man.

## OBSERVATIONS

*A. Development of the head veins of the rat*

As far as possible the terminology employed will be the same as that used by the author in his description of the head veins of man (Butler, 1957) and, in order to facilitate comparison, all reconstructions and diagrams are left lateral views.

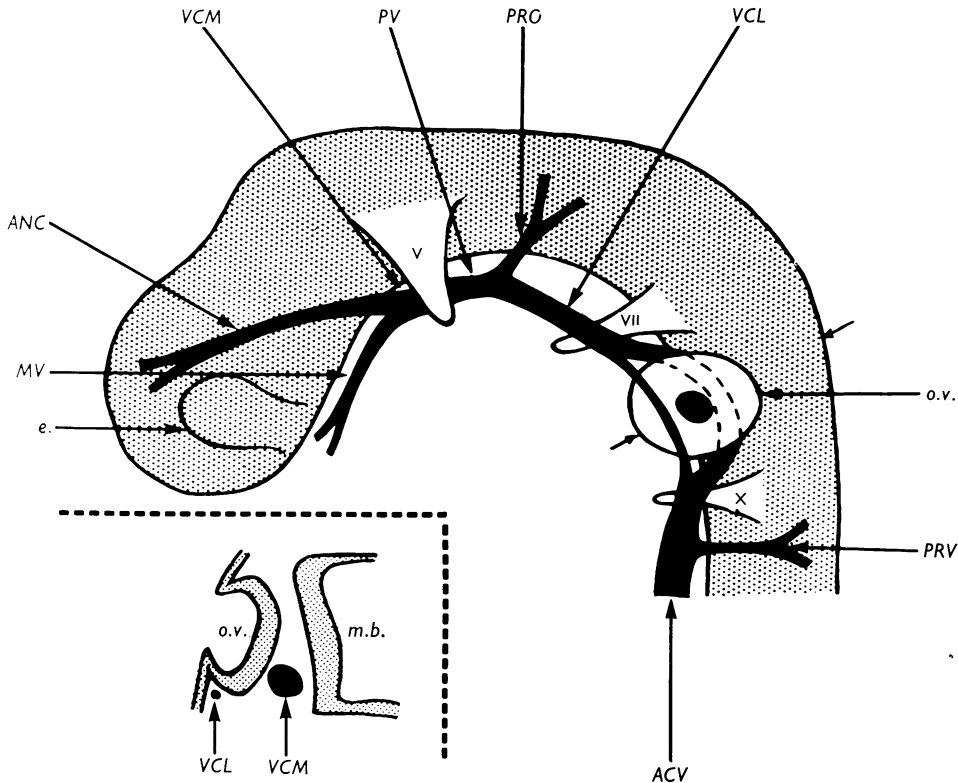


Fig. 1. Left lateral reconstruction of the head veins of 1.6 mm C.R. length rat embryo. Inset shows transverse section of the otic region at level indicated by the unlabelled arrows on main figure. The meaning of abbreviations for Figs. 1-11 is given above.

*Stage 1. Embryos of 1.6-3.0 mm C.R. length (Fig. 1)*

The maxillary (*MV*), anterior cerebral (*ANC*) and pituitary veins unite just cranial to ganglion *v* to form the vena capitis medialis (*VCM*), which runs medial

to the ganglion and, at its caudal end, turns lateralwards towards the surface of the embryo. (Note: because of its deep situation the pituitary vein is not shown in the left lateral reconstructions of head veins.) Thus, the laterally directed part of the vena capitis medialis lies between the ganglia of v and vii and will be called the post-trigeminal vein (*PV*) (Butler, 1957). A large pro-otic vein (*PRO*) runs ventralwards across the lateral surface of the hind brain, between the ganglia of v and vii, to join the dorsal aspect of the post-trigeminal vein. The post-trigeminal vein then continues caudalwards, lateral to the acoustico-facial ganglion, as the vena capitis

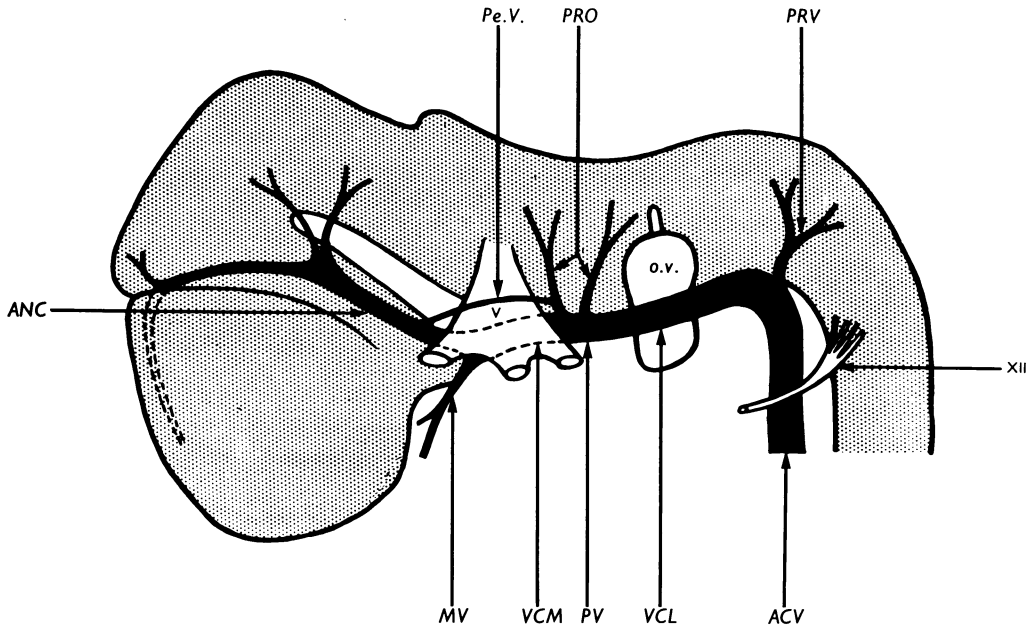


Fig. 2. Left lateral reconstruction of the head veins of a 7.0 mm C.R. length rat embryo.

lateralis (*VCL*). The otic vesicle has not yet separated and there is still an open otic pit (*o.v.*) attached to the surface ectoderm. At the cranial margin of the otic pit the vena capitis lateralis divides unequally into two channels which run through the otic region and reunite at the caudal margin of the pit. The smaller, laterally situated channel runs in the groove between the ventral margin of the otic pit and the surface ectoderm (see inset, Fig. 1). This vein is regarded as the para-otic segment of the vena capitis lateralis. The larger, medially situated channel runs between the floor of the otic pit and the brain and is regarded as the para-otic segment of the vena capitis medialis. The single channel, formed by the reunion at the caudal margin of the otic pit, lies lateral to the ganglia ix and x and is the post-otic continuation of the vena capitis lateralis. By the end of this stage the otic vesicle has completely separated and, as it sinks inwards towards the brain surface, the para-otic segment of the vena capitis medialis becomes obliterated. As this occurs the para-otic segment of the vena capitis lateralis increases in size. Immediately caudal to the ganglia ix and x a large posterior rhombencephalic vein (*PRV*) joins the dorsal

aspect of the vena capitis lateralis. The latter vein continues caudalwards, passing medial to nerve XII, to continue as the anterior cardinal vein (*ACV*).

*Stage 2. Embryos of 4.5–7.0 mm C.R. length (Fig. 2)*

As before, the vena capitis medialis is formed by the union of anterior cerebral, maxillary and pituitary veins but now the point of union lies medial to ganglion v. Caudal to ganglion v the vena capitis medialis turns sharply towards the surface of the embryo as the post-trigeminal vein and it now receives two pro-otic veins, an anterior and posterior. A moderately large vein, the peri-trigeminal vein (*Pe.V.*), lies between the lateral surface of the root of ganglion v and the surface ectoderm. It connects the anterior cerebral vein to the termination of the anterior pro-otic vein and may be regarded as a para-trigeminal extension of the vena capitis lateralis. Together with the vena capitis medialis and the terminal part of the anterior cerebral vein it forms a peri-trigeminal venous ring. The post-trigeminal vein continues caudally, as vena capitis lateralis, passing lateral to the acoustico-facial ganglion and the separated otic vesicle. The para-otic segment of the vena capitis medialis has completely disappeared. Immediately caudal to ganglion x the posterior rhombencephalic vein enters the dorsal surface of the vena capitis lateralis which now bends through 90° as a result of the formation of the cervical flexure. Vena capitis lateralis then passes medial to nerve XII to become the anterior cardinal vein. At this stage the head veins of the rat embryo are almost identical with those of the 14.0 mm C.R. length human embryo (Butler, 1957). The mesenchyme around the brain shows, as yet, no signs of the formation of the dura mater but many small veins drain its contained capillary plexus into the lateral aspect of the various segments of the primary head vein (i.e. vena capitis medialis, post-trigeminal vein and vena capitis lateralis) since there is no external jugular vein. These small lateral tributaries of the primary head vein are the precursors of the various emissary veins.

*Stage 3. Embryos of 10.0 mm C.R. length (Fig. 3)*

The primary head vein is constituted as before but its tributaries are larger and more complex. The commencements of the anterior cerebral veins, lying between the expanding cerebral hemispheres, are beginning to coalesce to form the plexiform superior sagittal sinus (*SS*). Just anterior to the pineal body the right and left anterior cerebral veins diverge to run ventralwards across the lateral surfaces of the mid-brain and they follow the curve of the caudal margins of the cerebral hemispheres. They then pass medial to ganglion v to enter vena capitis medialis. During their course they receive several mesencephalic tributaries into their dorsal aspect and, just before passing medial to ganglion v, each receives a large lateral cerebral vein (*LCV*). Tributary veins from the roof of the mid-brain enter the V formed by the diverging anterior cerebral veins and these will later form the post-torcular sinus (*PT*), which is the equivalent of the occipital sinus of man. The plexus formed by the union of the anterior cerebral veins, superior sagittal and post-torcular sinus is the forerunner of the confluence of the sinuses or the torcular Herophili (*TH*). The peri-trigeminal vein has now reached its maximum size and is almost as large as the vena capitis lateralis. At its caudal end it is joined by the anterior pro-otic vein just before entering the junction of the post-trigeminal vein and vena capitis

lateralis. The vena capitis lateralis runs caudalwards across the lateral surface of the otic capsule (*o.c.*) in company with the post-ganglionic part of nerve VII and the stapedia artery. Just caudal to the otic capsule it receives the large posterior rhombencephalic vein and passes medial to nerve XII to continue as the anterior cardinal vein which, from now on, may be called the internal jugular vein (*IJV*). It will be seen later that the posterior rhombencephalic vein becomes the occipital sinus of the rat and other mammals and this corresponds to the marginal sinus of man.

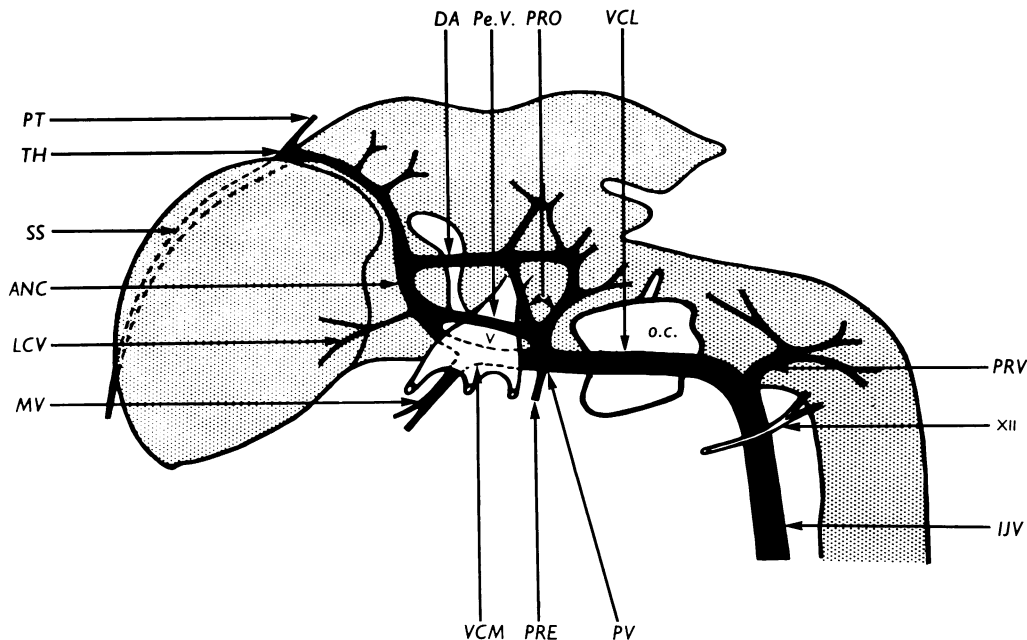


Fig. 3. Left lateral reconstruction of the head veins of a 10.0 mm c.r. length rat embryo.

A new dorsally situated vein, the dorsal anastomotic vein (*DA*), connects the anterior cerebral vein to the pro-otic vein. This marks the first step in the formation of the more dorsally situated lateral sinus (formed from the transverse and sigmoid sinuses) which will become the main venous channel to replace the vena capitis lateralis.

The dura mater and chondrocranium are now developing in the mesenchyme around the sides and base of the brain and it can be seen that the venae capitis lateralis and medialis are outside the developing dura mater, i.e. they are morphologically extracranial. The terminal part of the vena capitis lateralis emerges through the lower and medial end of the occipito-capsular fissure (the future jugular foramen) to become the internal jugular vein. The vena capitis lateralis runs across the lateral surface of the developing otic capsule. The subectodermal mesenchyme, whose venous drainage is now mainly into the developing external jugular vein, will presently give rise to the several elements of the dermocranium. Where there are gaps in the chondrocranium, the various fontanelles and the neuro-vascular for-

amina, there are venous connexions of increasing size between the internal and external jugular venous systems. These are the emissary veins and, already, certain of them have become prominent. The post-trigeminal vein runs lateralwards between ganglia v and vii and then turns caudalwards as the vena capitis lateralis and the genu of this vein lies opposite the caudal end of the sphenoparietal fontanelle. At this genu a group of pro-otic emissary veins (*PRE*) connect it to a temporal tributary of the external jugular vein. Other emissary veins are seen in the superior part of the occipito-capsular fissure and around all the cranial nerves.

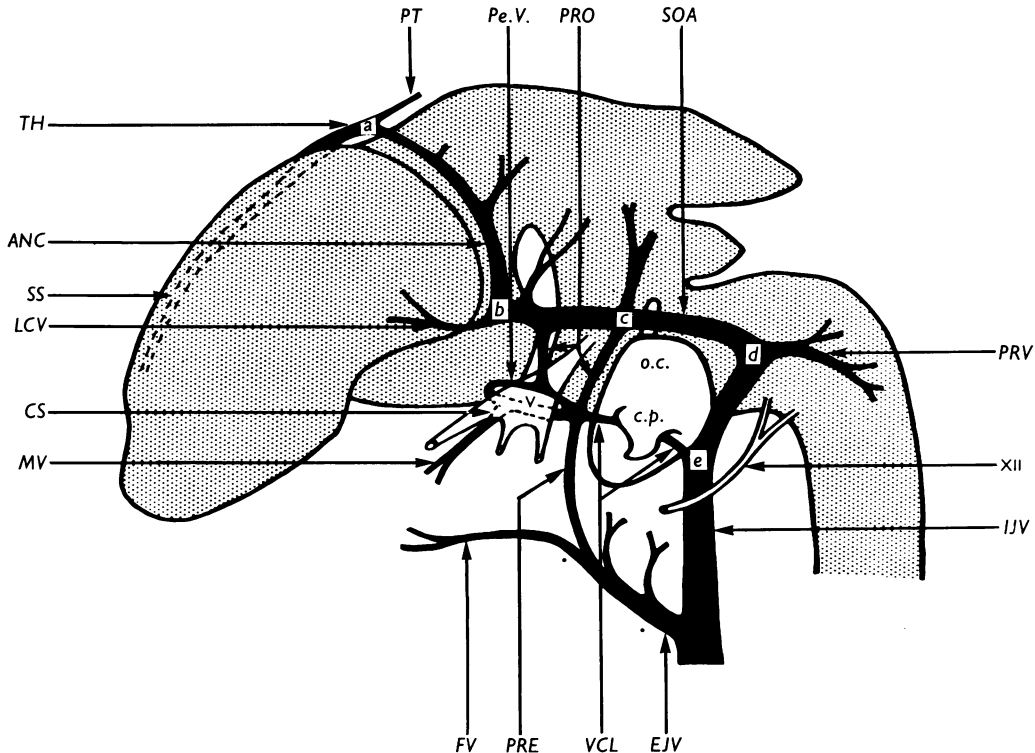


Fig. 4. Left lateral reconstruction of the head veins of an 11.0 mm C.R. length rat embryo. *a-b-c* is the transverse sinus, *c-d-e* is the sigmoid sinus.

#### Stage 4. Embryos of 11.0 mm C.R. length (Fig. 4)

The major feature of this stage is the appearance of the supra-otic anastomotic vein (*SOA*) which connects the pro-otic veins to the posterior rhombencephalic vein and so completes the formation of the lateral sinus. At the same time the terminal part of the anterior cerebral vein, from the entry of the lateral cerebral vein to its junction with the vena capitis medialis, disappears. The completed lateral sinus consists of (1) the transverse sinus formed by the anterior cerebral vein from the torcular to the entry of the lateral cerebral vein (Fig. 4*a, b*) and the new dorsal anastomotic vein between the anterior cerebral vein and the pro-otic veins (*b, c*), and (2) the sigmoid sinus formed from the supra-otic anastomotic vein (*c, d*) and the

posterior rhombencephalic vein from the entry of the supra-otic anastomotic vein to its union with the internal jugular vein (*d*, *e*). Thus the lateral sinus of the rat is formed from the same venous elements as is that of man except that the order of appearance of the dorsal anastomotic and supra-otic veins is reversed (Butler, 1957). The first part of the lateral sinus in the rat is the equivalent of the transverse sinus of man although its direction is vertical to the skull base rather than horizontal because of the difference in the amount of backward growth of the cerebral hemisphere. It runs in the tentorial fold between the caudal pole of the cerebral hemisphere and the cerebellum. The plane of the tentorial fold, and hence the direction of the transverse sinus, is dependent on the growth of the cerebral hemisphere, which continuously changes during development (cf. Figs. 3, 4, 6 and 8). Likewise, the adult position of the tentorial fold depends upon the degree of backward growth of the cerebral hemisphere, which reaches its maximum in man and the higher primates, who have therefore a horizontally directed transverse sinus.

As a result of the diversion of the venous drainage from the cerebral hemispheres by the lateral sinus the only tributaries of the reduced vena capitis medialis (now recognizable as the cavernous sinus, *CS*) are the pituitary and maxillary veins. The latter, which is now recognizable as the inferior ophthalmic vein, receives a large superior ophthalmic vein. The ophthalmic veins have many connexions with the facial tributaries of the external jugular vein across the orbital margin and as they increase in size there is further reduction of the inflow into the diminishing vena capitis medialis.

The more anterior and smaller of the two pro-otic veins has migrated forwards, to run along the root of ganglion *v*, and it now connects the transverse sinus to the peri-trigeminal venous ring; it is the superior petrosal sinus. Through the peri-trigeminal venous ring it is connected to the cavernous sinus both in front of and behind ganglion *v*. The pro-otic emissary veins, together with the distal part of the posterior pro-otic vein, now form a single large channel connecting the junction of the transverse and sigmoid sinuses directly to the external jugular vein.

The chondrocranium is well developed and the relationship of the various veins to it, the dura mater and the extra-dural spaces are clearly seen (Fig. 5). The pro-otic and peri-trigeminal veins and the vena capitis medialis are grouped around ganglion *v* in the cavum epiptericum [an extracranial space situated laterally to the side wall of the orbitotemporal region of the chondrocranium; it contains the ganglia of *v* and *vii*, the stapedia artery and the cavernous sinus (de Beer, 1957)]. The posterior pro-otic vein is close to the anterior surface of the otic capsule, and its continuation, the pro-otic emissary vein, emerges from the cavum epiptericum at the caudal end of the sphenoparietal fontanelle beneath the orbitoparietal cartilage. Cranially, ganglion *v* lies in front of the emissary vein and its mandibular division intervenes between the vein and the ala temporalis (greater wing of the sphenoid). On emerging from the fontanelle the emissary vein continues lateralwards across the anterior surface of the proximal end of Meckel's cartilage to form a temporal tributary of the external jugular vein.

Opposite the geniculate ganglion the post-trigeminal vein turns caudalwards to leave the cavum epiptericum as the vena capitis lateralis and enters the facial groove beneath the crista parotica. In the facial groove it lies supero-lateral to the post-



ganglionic part of nerve VII and the stapedia artery lies ventro-medial to the nerve and vein. At the caudal end of the facial groove the nerve and vein part company and the latter turns medialwards to enter the lower end of the occipito-capsular fissure, where it joins the sigmoid sinus to form the internal jugular vein. At this stage the membrane bones of the dermocranium have not begun to develop.

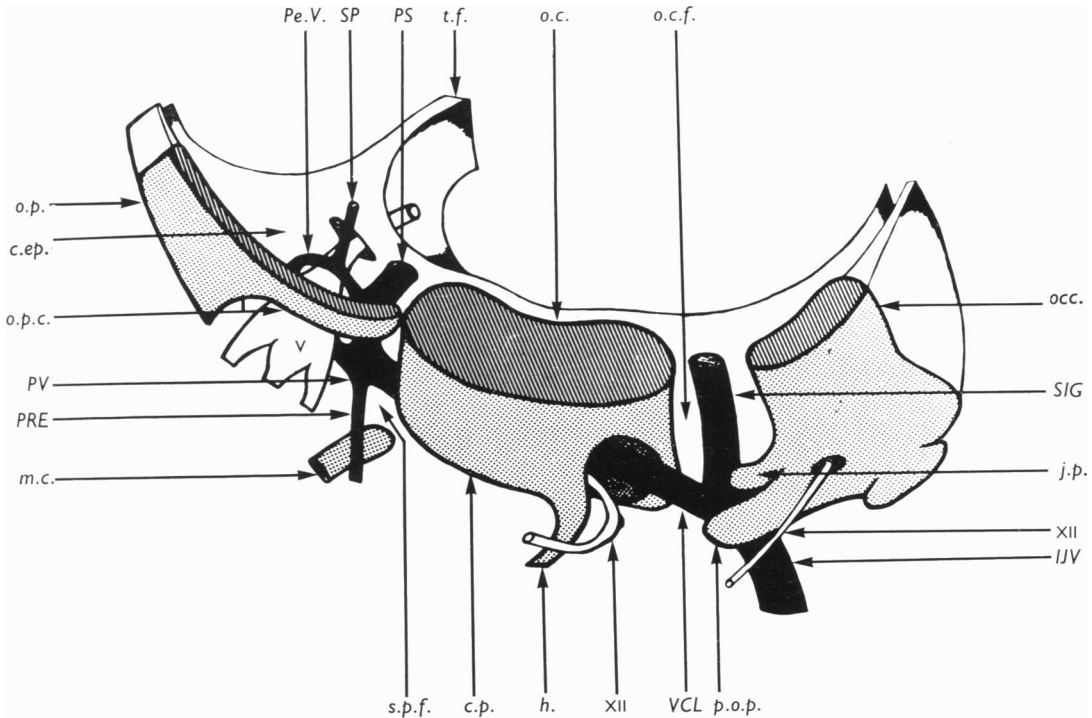


Fig. 5. Left lateral reconstruction of part of the chondrocranium of an 11.0 mm rat embryo showing the relations of the head veins to the cavum epiptericum, spheno-parietal fontanelle, crista parotica and occipito-capsular fissure.

#### Stage 5. Embryos of 15.0 mm C.R. length (Fig. 6)

The main changes in the venous system are:

(1) Disappearance of the post-trigeminal vein so that the superior petrosal sinus (the anterior pro-otic vein) appears as a separate vessel which divides to embrace ganglion V and so enter both the cranial and caudal ends of the now further reduced cavernous sinus (remnant of the vena capitis medialis).

(2) The vena capitis lateralis continues to decrease and, at the same time, the posterior pro-otic vein increases in size. So now, at the apex of the otic capsule, the transverse sinus divides into two large and almost equal vessels: (a) the sigmoid sinus (SIG) which curves around the superior and caudal aspects of the otic capsule to leave the skull by the medial end of the occipito-capsular fissure and becomes the internal jugular vein; (b) the posterior pro-otic vein, which runs down the cranial

margin of the otic capsule and leaves via the sphenoparietal fontanelle as the large pro-otic emissary vein which joins the external jugular vein.

(3) The ophthalmic emissary veins have increased in size and this has led to a further diminution of the cavernous sinus.

(4) The posterior rhombencephalic vein runs on the inner surface of the ala occipitalis approximately parallel to the margin of the foramen magnum but some distance away from it. Therefore it is the occipital sinus which is the equivalent of the marginal sinus of man.

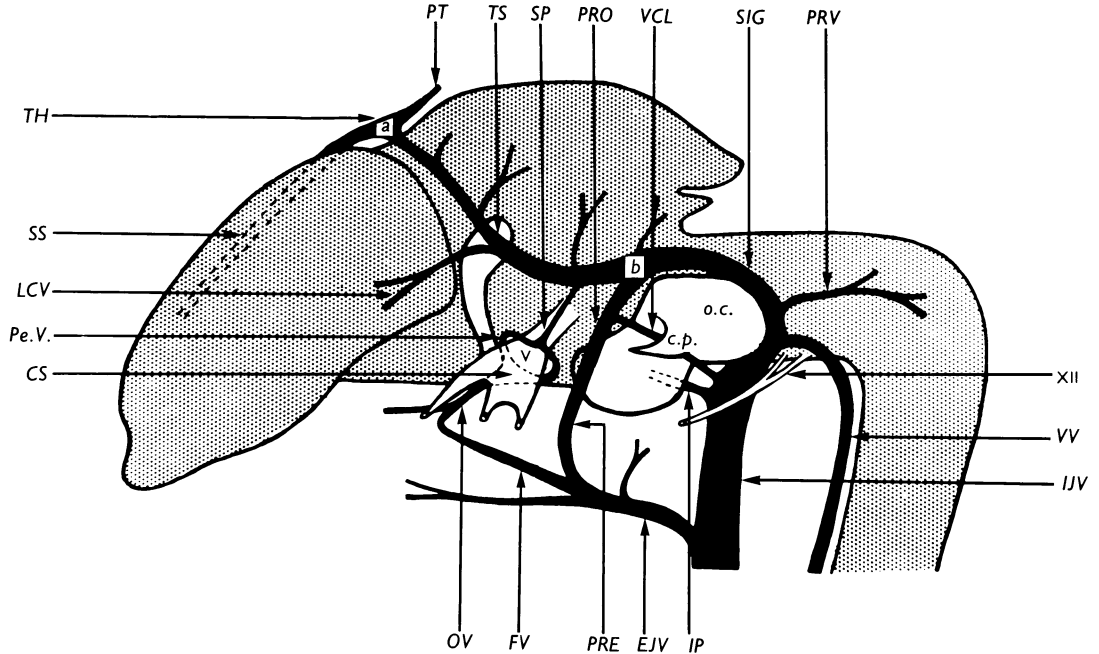


Fig. 6. Left lateral reconstruction of the head veins of a 15.0 mm C.R. length rat embryo. The transverse sinus runs from *a* (the confluence of the sinuses) to *b* at the summit of the otic capsule. Here it divides into the sigmoid sinus, running posterior to the otic capsule, to leave the chondrocranium via the medial end of the occipito-capsular fissure and the pro-otic emissary vein, running anterior to the otic capsule and leaving via the caudal end of the sphenoparietal fontanelle (see Fig. 5). There is still a small vena capitis lateralis running under the crista parotica with the facial nerve. The anterior pro-otic vein runs in the tentorial fold to join the venous ring around the vth nerve ganglion and is the superior petrosal sinus.

(5) A large venous plexus, the basilar plexus, lies on the floor of the chondrocranium between the dura mater and the basi-occiput and basi-sphenoid (Fig. 7). Cranially this plexus surrounds the pituitary gland to form a peri-pituitary plexus which connects with the cavernous sinuses through the pituitary veins. Opposite the inferior end of the occipito-capsular fissures branches of the basilar plexus surround the roots of nerves IX, X and XI and form a plexiform vessel which joins the medial aspect of the termination of the sigmoid sinus. This is the caudal end of the inferior petrosal sinus and eventually it will extend along the lateral margin of the basilar plexus, in the groove between the otic capsule and the basis cranii, to connect the commencement of the internal jugular vein to the cavernous sinus.

As in man, the caudal end of the inferior petrosal sinus appears first. Also the caudal part of the basilar plexus drains by large vertebral veins which cross the xii<sup>th</sup> nerve and enter the foramen magnum to join the large vertebral venous plexus. As the veins of this region become less plexiform the vertebral veins will come to connect with the terminal part of the sigmoid sinus. From this stage onwards these vertebral veins will continue to enlarge and divert more and more of the sigmoid sinus blood into the vertebral venous plexus.

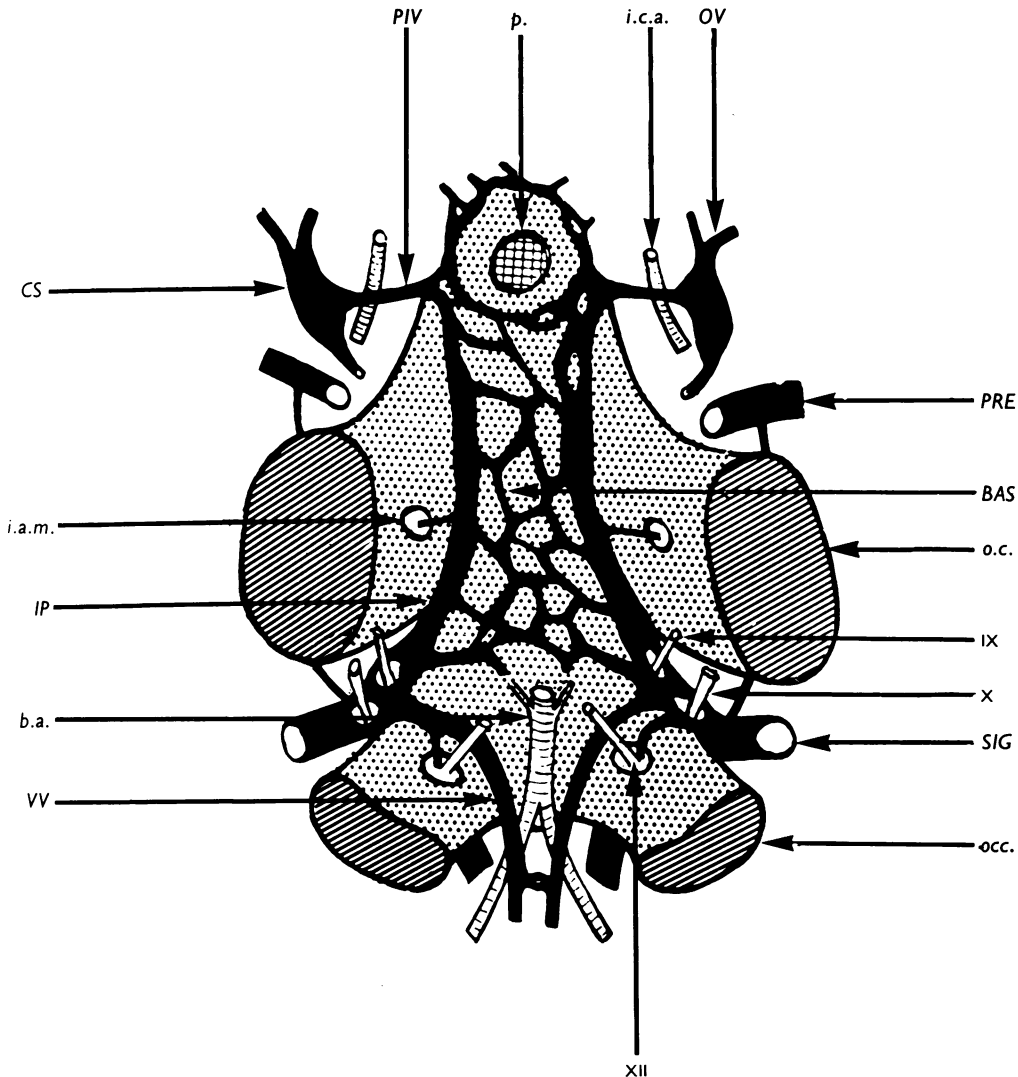


Fig. 7. Reconstruction of part of the base of the chondrocranium of a 15.0 mm c.r. length rat embryo to show the basilar plexus and the formation of the inferior petrosal sinus.

*Stage 6. Embryos of 16.0–30.0 mm C.R. length (Fig. 8)*

By the time rat embryos are 16.0 mm C.R. length the adult pattern of dural venous sinuses is apparent and, with the development of the membrane bones, the final relationships of the pro-otic emissary vein can be seen to be those of the adult's post-glenoid vein. The final venous changes are:

(1) The caudal limb of the venous ring around ganglion v disappears and the superior petrosal sinus runs forwards in the tentorial fold to cross above the vth ganglion and enter the cranial end of the cavernous sinus in the depths of the *cavum epiptericum*.

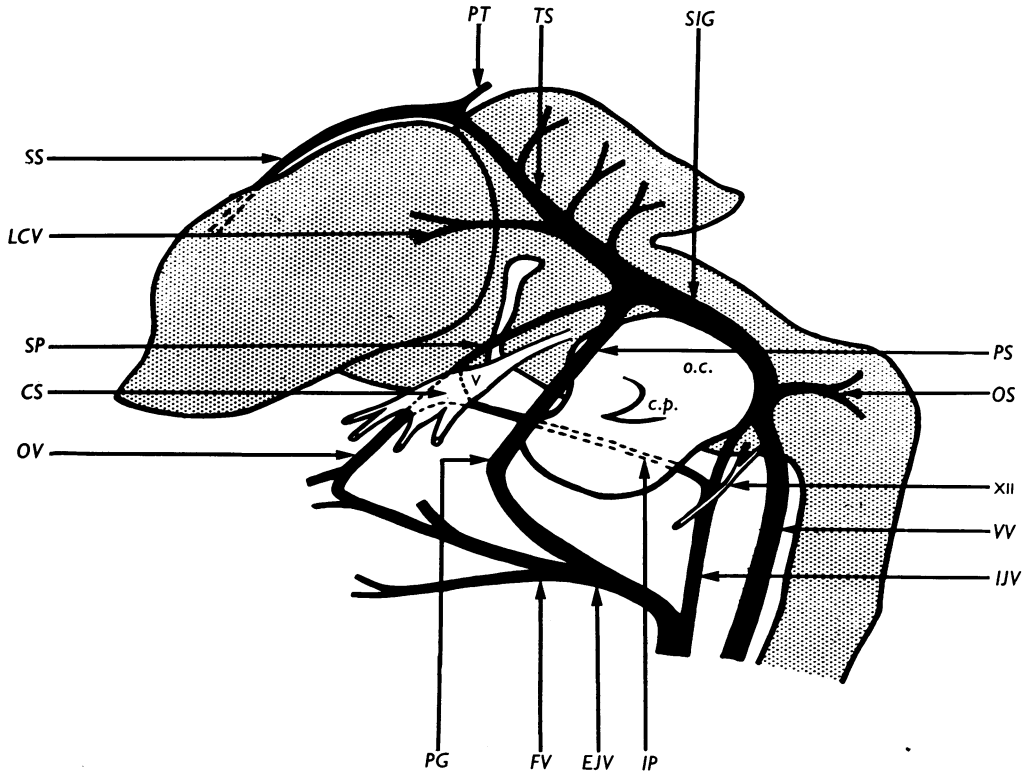


Fig. 8. Left lateral reconstruction of the head veins of a 16.0 mm C.R. length rat embryo. The head veins show the adult pattern and the vena capitis lateralis has disappeared in this particular embryo.

(2) A tiny vena capitis lateralis, running in the facial groove, may be found in the smaller embryos of this group but it has completely disappeared in the larger ones.

(3) The vertebral vein has greatly increased in size and now, beyond the entry of the occipital sinus, it appears as a direct continuation of the sigmoid sinus into the foramen magnum. Consequently the terminal part of the sigmoid sinus is considerably reduced in size and this reduction continues after birth so that, in the adult, the tiny internal jugular vein is formed almost entirely from the inferior petrosal sinus. The latter is now a clearly demarcated channel running along the

petro-basilar groove from the cavernous sinus to the commencement of the internal jugular vein.

(4) The pro-otic and post-glenoid veins have continued to increase in size and, at the apex of the otic capsule, the transverse sinus divides into two equal-sized veins, the post-glenoid and the vertebral.

With the appearance of the dermocranium the final relationships of the dural venous sinuses and emissary veins to the adult skull now become apparent (Fig. 9). Continued growth of the elements of the chondrocranium has caused reduction of

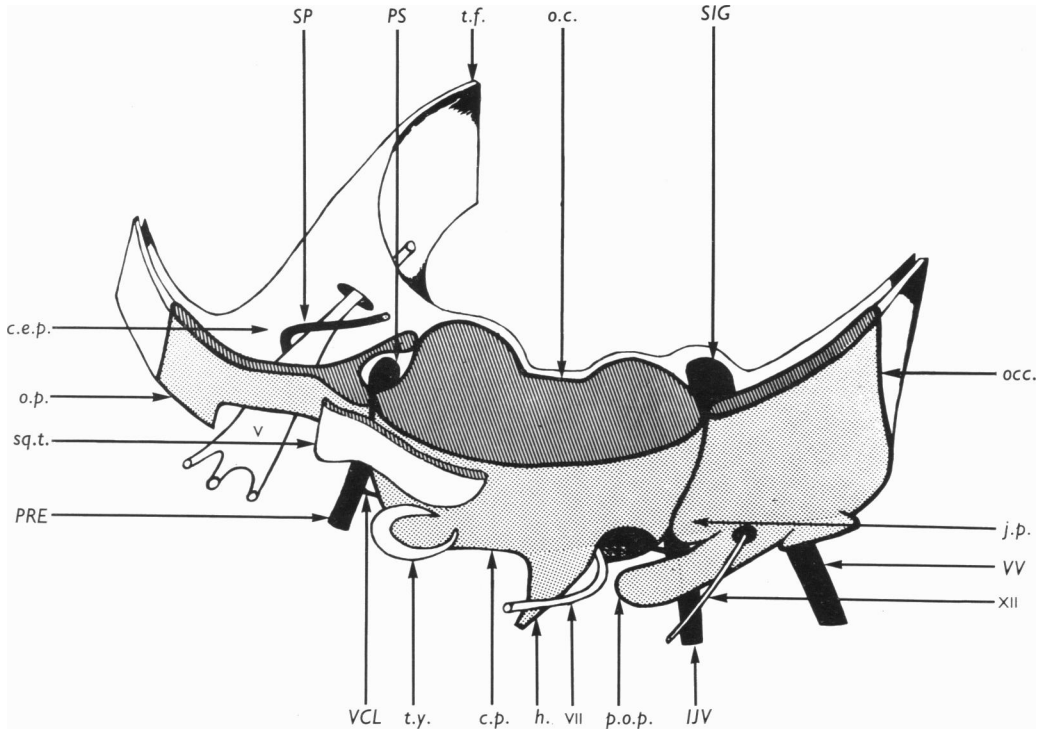


Fig. 9. Left lateral reconstruction of part of the chondrocranium and dermocranium of a 16.0 mm C.R. length rat embryo showing the relationships of the head veins. The occipito-capsular fissure is now closed except for its lower and medial end which remains as the small jugular foramen. The sphenoparietal fontanelle is still widely open and a postero-medially directed flange of cartilage overlies the pro-otic vein (the petro-squamous sinus) and encloses it in a cartilaginous canal of Verga.

the size of the various fissures and fontanelles. Forward growth of the jugular process of the ala occipitalis cuts off the infero-medial end of the occipito-capsular fissure as the tiny jugular foramen and the remaining part of the fissure becomes completely closed. Hence, no mastoid emissary veins are found in the rat. The sphenoparietal fontanelle is smaller and its caudal end, through which passes the pro-otic emissary vein, is overlaid by the superficially situated squamous temporal bone. The proximal end of Meckel's cartilage lies in the middle ear cavity, medial to the tympanic ring, and has become the malleus and incus. Serial sections and

reconstructions clearly indicate that the pro-otic emissary vein is the post-glenoid vein since it emerges from the skull between the squamous temporal bone and tympanic ring, above and behind the fossa for the head of the mandible.

A medially directed flange of cartilage develops on the inner aspect of the caudal margin of the orbito-parietal commissure to form a cartilaginous groove whose margins lie against the cranial surface of the cartilaginous otic capsule to form a canal through which runs the pro-otic vein before it makes its exit via the post-glenoid foramen (Fig. 9). This cartilaginous canal is the parieto-temporal or Verga's canal and so the pro-otic vein is, as in man, the petro-squamous sinus. In the rat the medial cartilaginous flange fails to ossify since no bony canal for the petro-squamous sinus is found in the adult skull.

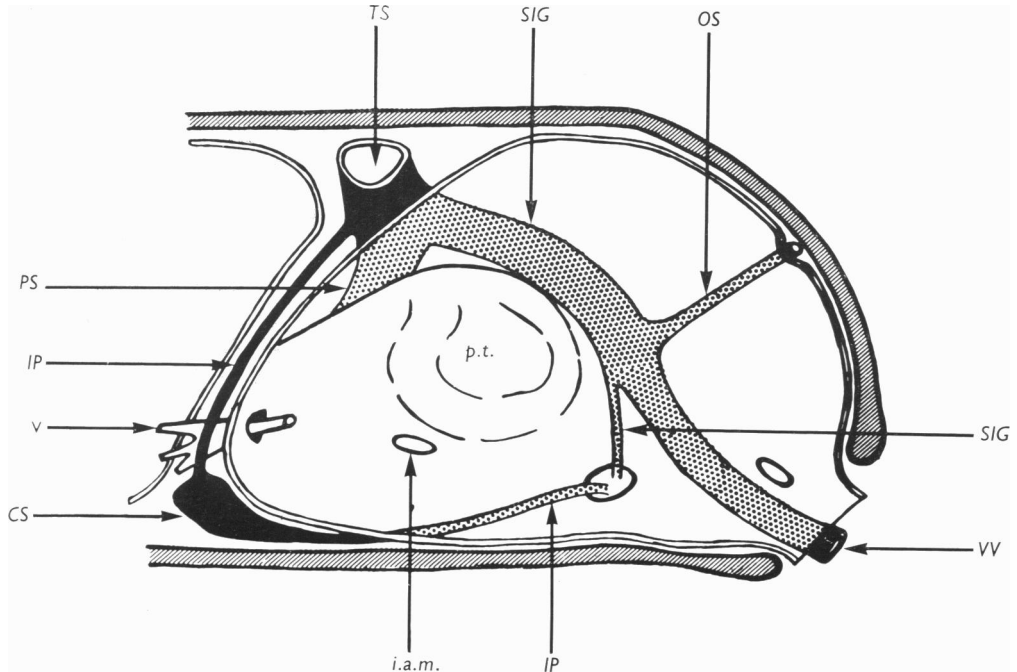


Fig. 10. The arrangement of the dural venous sinuses in the adult rat.

*Adult pattern of dural venous sinuses (Fig. 10)*

At the apex of the petrous temporal bone the transverse sinus divides into three:

(1) The small superior petrosal sinus, which runs forwards into the tentorial fold, crosses the root of ganglion *v* in the roof of Meckel's cave to join the cranial end of the cavernous sinus.

(2) Two very much larger and almost equal-sized channels: (a) the petro-squamous sinus running ventrally and forwards in the petro-squamous groove to emerge through the post-glenoid foramen, and (b) the sigmoid sinus which, after a short course above and behind the petrous temporal bone, receives the occipital sinus. Just beyond this point the sigmoid sinus divides unequally into a very large vertebral

vein and a tiny terminal sigmoid sinus. The former enters the foramen magnum to join the vertebral venous plexus. The latter enters the very small jugular foramen and joins the inferior petrosal sinus to form the diminutive internal jugular vein.

The superior sagittal and inferior petrosal sinuses run a typical course. The cavernous sinus is small, because of the large size of the connexions between the ophthalmic and facial veins, and like that of man it does not contain any obvious trabeculae. There are no mastoid emissary veins.

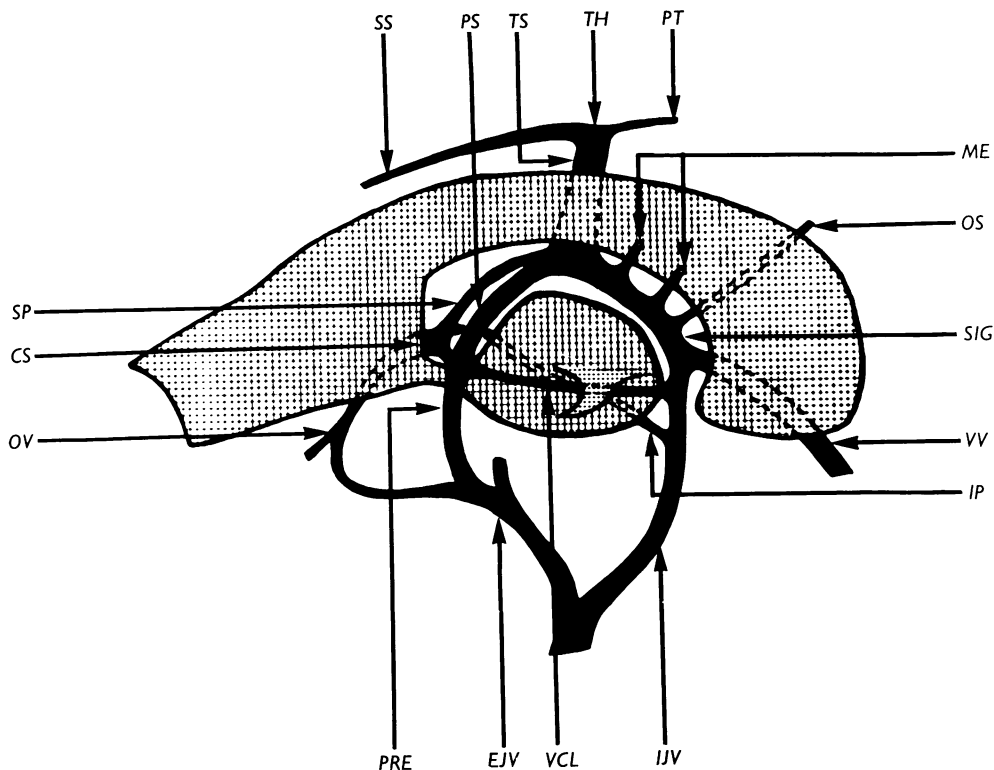


Fig. 11. Schematic representation of the main embryonic head veins and their relationship to certain elements of the chondrocranium. The size of these various veins varies during the development of any particular mammal as do the final patterns seen in adults.

### B. *Some other mammalian embryos*

Rabbit, pig and human embryos display the same general pattern of development of the dural venous sinuses and emissary veins from a primary head vein and its tributaries. Because of similarities in the form of the chondrocranial elements all mammalian embryos have the same basic pattern of fontanelles through which emissary veins may pass and so only specific differences will be noted (Fig. 11).

#### 1. *Rabbit*

A large pro-otic vein, identical in position and relationship to that of the rat, has attained a diameter of 150  $\mu\text{m}$  in the 15.0 mm c.R. length embryo. By the time the

rabbit embryo is some 20.0 mm C.R. length it is reduced to 50.0  $\mu$ m in diameter and has entirely disappeared when the embryo is 30.0 mm C.R. length. The adult rabbit has no post-glenoid vein although minute post-glenoid foramina may be occasionally found. As the embryonic post-glenoid vein disappears large emissary veins develop in the superior part of the occipito-capsular fissure and connect the commencement of the pro-otic vein (petro-squamous sinus) to temporal tributaries of the external jugular vein. Thus the pro-otic vein comes to make its exit through the superior part of the occipito-capsular fissure and not through the sphenoparietal fontanelle. The emissary vein of the superior part of the occipito-capsular fissure is, in fact, a mastoid emissary vein and, in the adult skull, it leaves via an irregular fissure bounded by the occipital and petrous temporal bones. The true identity of this fissure as a mastoid emissary foramen is not immediately evident since it is overlapped by elements of the dermocranium, namely the squamous temporal and parietal bones.

In the full-term foetus the transverse sinus divides at the apex of the petrous temporal bone into two almost equal sized channels:

(1) The mastoid emissary vein, which almost immediately leaves via the mastoid foramen.

(2) The sigmoid sinus, which soon divides into a large vertebral vein and a minute terminal part of the sigmoid sinus. The vertebral vein passes into the foramen magnum and divides into anterior and posterior channels separated by the transverse ligament of the atlas. The anterior channel pierces the atlanto-occipital membrane and emerges on to the anterior surface of the body of the first cervical vertebra. Here the right and left channels unite to form a single median vessel which lies in the groove between the right and left groups of anterior cervical muscles. The median vein then runs caudalwards to enter the thorax, where it deviates to the right and enters the posterior aspect of the junction of the right internal and external jugular veins. The posterior channel joins the vertebral venous plexus.

## 2. *Pig*

A similar series of developmental events were seen in pig embryos and, up to 30.0 mm C.R. length (the oldest embryo examined), there was a petro-squamous sinus and a pro-otic emissary vein although there is no post-glenoid vein in the adult. According to Dennstedt (1904) there may be a small petro-squamous sinus in the adult pig running in a temporal canal. A large mastoid emissary vein and a vertebral vein were present in the 30.0 mm C.R. length embryo.

## 3. *Man*

The same developmental pattern occurs (Butler, 1957) and a small, but transient, post-glenoid emissary vein is found in embryos between 14.0 and 23.0 mm C.R. length. The mastoid emissary veins are prominent in embryos and fetuses and mastoid emissary foramina are almost always found in adult human skulls. Compared to other mammals the vertebral vein is poorly developed.



C. Patterns of dural venous sinuses and emissary veins in some adult mammals (Fig. 12)

Whilst all mammals have the same general pattern of dural venous sinuses and emissary veins the degree of development of the various components varies considerably from species to species.

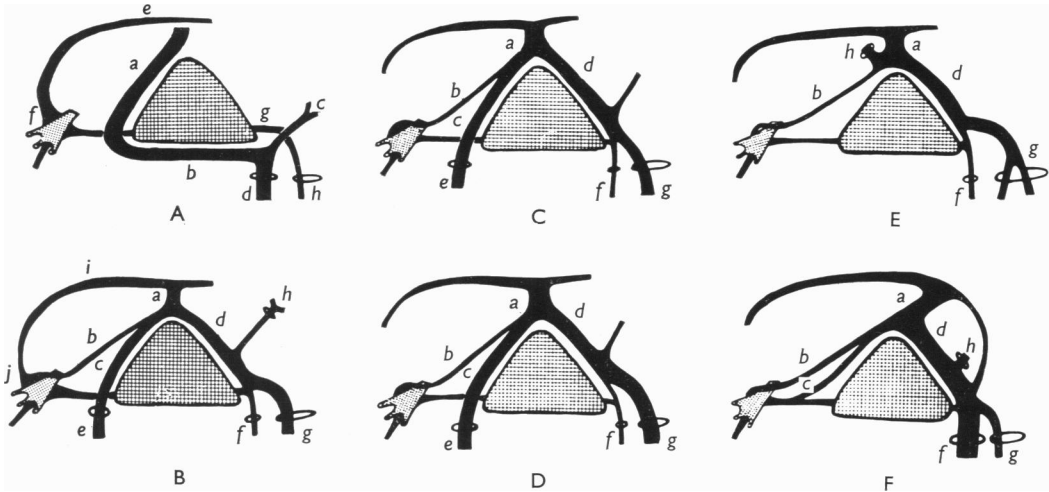


Fig. 12. Diagrams showing the adult pattern of dural venous sinuses in a selection of mammals. Their relationships to the petrous temporal bone (former otic capsule) and the vth nerve are shown. Emissary veins, including the internal jugular, are ringed.

A. *Monotremes*. The petrosquamous sinus (*a*) runs down the anterior face of the petrous temporal bone and then runs through the facial canal, as the persistent vena capitis lateralis (*b*), and emerges through the stylomastoid foramen. It receives the occipital sinus (*c*) and forms the internal jugular vein (*d*). The cranial end of the superior sagittal sinus (*e*) joins the cavernous sinus (*f*) and there is no sigmoid sinus. The inferior petrosal sinus (*g*) continues caudally as the vertebral vein (*h*). (From Hochstetter, 1896.)

B. *Hedgehog*. The transverse sinus (*a*) divides into superior petrosal sinus (*b*), petrosquamous sinus (*c*) and sigmoid sinus (*d*). The petrosquamous sinus emerges as the post-glenoid emissary vein (*e*). The internal jugular vein (*f*) is small and the vertebral vein (*g*) forms the main continuation of the sigmoid sinus. The occipital sinus (*h*) perforates the occipital bone as a large emissary vein. As in Monotremes, the cranial end of the superior sagittal sinus (*i*) joins the cavernous sinus (*j*).

C and D. *Dog and rat*. The transverse sinus (*a*) divides into superior petrosal sinus (*b*), petrosquamous sinus (*c*) and sigmoid sinus (*d*). The petrosquamous sinus emerges as a large post-glenoid emissary vein (*e*). The internal jugular vein (*f*) is small and the vertebral vein (*g*) forms the main continuation of the sigmoid sinus. Despite wide phylogenetic differences these two mammals have a very similar pattern of dural venous sinuses and emissary veins.

E and F. *Rabbit and man*. The transverse sinus (*a*) divides into superior petrosal sinus (*b*), petrosquamous sinus (*c*) and sigmoid sinus (*d*). There is normally no post-glenoid emissary vein in the adult but it is always present in the embryo. The internal jugular vein (*f*) is small in the rabbit and large in man, mainly because of the difference in size of the vertebral vein (*g*). Both have a large mastoid emissary vein (*h*). Despite wide phylogenetic differences there are many similarities in the pattern of dural venous sinuses and emissary veins.

### 1. *Hedgehog* (Fig. 12B)

At the apex of the petrous temporal bone the transverse sinus divides into:

(i) The superior petrosal sinus, which runs forward in the tentorial fold and crosses ganglion v to join the cavernous sinus.

(ii) The petro-squamous sinus, which passes under a bridge of bone, forming the canal of Verga, and emerges from the post-glenoid foramen to join the external jugular vein.

(iii) The sigmoid sinus, which runs behind the petrous temporal bone and receives the occipital sinus. It then divides into a vertebral vein and a terminal sigmoid sinus which joins the inferior petrosal sinus to form the moderately large internal jugular vein.

The occipital sinus perforates the dorsal aspect of the occipital bone close to the midline as a large occipital emissary vein. Caudally, the superior sagittal sinus communicates with the torcular but, cranially, it runs into a groove on the superior surface of the cribriform plate of the ethmoid bone and then joins the cavernous sinuses.

### 2. *Dog* (Fig. 12C)

The transverse sinus divides into:

(i) The superior petrosal sinus, which runs a normal course.

(ii) The large petro-squamous sinus, which makes its exit via the post-glenoid foramen.

(iii) The sigmoid sinus, which soon divides into a large vertebral vein and a small terminal sigmoid sinus which joins the inferior petrosal sinus to form the small internal jugular vein. The vertebral vein passes under a bridge of bone on the inner surface of the occipital bone, just above the occipital condyle, and is called the sinus condyloideus.

### D. *Anomalous emissary veins*

Little, if anything, is known concerning anomalies of the emissary veins of adult mammals except in man. Ten examples of partial or complete absence of the human sigmoid sinus have been recorded (Wood, 1939) and I have seen four more. It is commonplace to find considerable inequality of the jugular foramina in human skulls and this anomaly is probably more frequent than is realized. In many instances reduction or absence of the sigmoid sinus is accompanied by the presence of an abnormally large mastoid emissary foramen which may be as much as 7.0 mm in diameter. Boyd (1930) stated that the human mastoid emissary foramina are usually about 1.0 mm in diameter, 10.0% are over 2.0 mm and only rarely do they reach 4.0–5.0 mm. Reduction of the sigmoid sinus may be unilateral or bilateral and is associated with a reduced internal jugular vein and a small jugular foramen. When the sigmoid sinus is absent the internal jugular vein is formed solely from the inferior petrosal sinus and only that part of the jugular foramen that conveys the inferior petrosal sinus and nerves ix, x and xi is present. A small post-glenoid foramen occurs in slightly under 1.0% of human skulls (Boyd, 1930) and this is in accord with the small size and transitory appearance of the pro-otic emissary veins in the human embryo and foetus.

## DISCUSSION

The earliest stage of development of the head veins of the rat shows, as do all other vertebrate embryos examined [reptiles (Grosser & Bretzina, 1895), birds (Hughes, 1934), bats (Grosser, 1901), pig (Sabin, 1917) and man (Mall, 1904; Streeter, 1918; Markowski, 1922; Butler, 1957; Padget, 1957)], the same basic pattern of a primary head vein which continues caudalwards as the anterior cardinal (future internal jugular) vein. With one exception its tributaries (pituitary, anterior cerebral, pro-otic, posterior rhombencephalic and maxillary) drain the developing brain. The anterior cerebral, pro-otic and posterior rhombencephalic veins correspond to the anterior, middle and posterior cerebral veins of Streeter (1918) and the anterior, middle and posterior dural stems of Padget (1957). The only ventral tributary is the maxillary vein [primitive maxillary vein of Padget (1957)], which drains the region of the developing eye and emerging maxillary process. In the very early stages there is no external jugular vein and, in the present investigation, it was not clearly recognizable until the embryos were 11.0 mm C.R. length. It was almost certainly present before this and Padget (1957) recognized its forerunner in man, the ventral pharyngeal vein, in embryos of 5.0 mm C.R. length. As pointed out by Padget (1957), the subdivision of the primary head vein into vena capitis medialis and lateralis segments is confusing, but examination of very young mammalian embryos shows that the very first venous drainage of the brain is by a venous channel lying in close contact with its lateral surface. As the cranial nerves and ganglia develop there is a tendency to form venous rings around them, particularly v, ix, x, xi and xii. Also, the position of the primary venous channel is affected markedly by the development of the otic region. Since the commencement of the primary head vein, formed by the union of maxillary, anterior cerebral and pituitary veins, lies medial to the vth ganglion it can be called the vena capitis medialis. As shown, it eventually becomes the cavernous sinus. That part of the primary head vein which runs between the otic pit and the lateral aspect of the brain has also been called vena capitis medialis and it clearly represents part of the primary venous channel draining the brain. It is, however, soon forced out of existence by the sinking in of the otic vesicle and replaced by a major channel which lies lateral to the otic vesicle and, later, to the otic capsule. Because of its importance in the further development of the head veins and in order to emphasize its relationship to the otic capsule it is regarded as essential to call it vena capitis lateralis. The peri-trigeminal vein, which lies lateral to the vth ganglion, is in line with the para-otic part of vena capitis lateralis and may be regarded as homologous with it. Caudal to the otic capsule the precise relation of the terminal part of the primary head vein to the ixth, xth and xith nerves depends upon the degree of venous ring formation, which varies during development and from one embryo to another. However, it consistently passes medial to the xiiith nerve to become the anterior cardinal vein and this crossing point may be regarded as marking the termination of the primary head vein.

In all mammals so far investigated, with the exception of the Monotremes, the para-otic part of vena capitis lateralis disappears during embryonic life and is replaced by a new channel situated dorsal to the otic capsule. The para-otic part of vena capitis lateralis, together with the accompanying post-ganglionic part of the

facial nerve and the stapedia artery, becomes overhung by the crista parotica (the future tegmen tympani) and so comes to run in the roof of the middle ear cavity. The precise reasons why this vein should commonly disappear are not clear, particularly since it persists as a main drainage channel in reptiles (Grosser & Brezina, 1895) and Monotremes (Hochstetter, 1906). In all mammals (except Monotremes) a lateral sinus, formed from the new channel dorsal to the otic capsule, replaces vena capitis lateralis and it connects the anterior cerebral, pro-otic and posterior rhombencephalic veins. With the appearance of this new channel the terminal part of the anterior cerebral vein disappears and consequently the superior sagittal sinus now drains into the lateral sinus. The terminal parts of the anterior and posterior pro-otic veins, however, persist to form adult dural venous sinuses. The smaller anterior pro-otic vein migrates forwards to run in the tentorial fold and joins the peri-trigeminal vein which, with the vena capitis medialis, forms the venous ring around the vth ganglion. It becomes the superior petrosal sinus, and since the caudal limb of the venous ring usually disappears the sinus runs above the ganglion to terminate in the cavernous sinus in front of it. Coates (1934) investigated the relationship of the superior petrosal sinus to the root of ganglion v in 31 human cadavers: 30 sinuses passed above the root of the ganglion, 12 below it and 13 both above and below. Similar variations most probably occur in other mammals.

The larger posterior pro-otic vein becomes the petro-squamous sinus and it joins the peri-trigeminal vein opposite the pro-otic emissary veins. This was clearly shown in human embryos by Markowski (1911, 1922), but Streeter (1915, 1918) wrongly interpreted this vein as the superior petrosal sinus. As shown in the human embryo (Butler, 1957) and confirmed in this investigation, the posterior pro-otic vein is, without doubt, the forerunner of the petro-squamous sinus. The superior petrosal sinus runs in the tentorial fold along its line of attachment to the petrous temporal bone and is closely related to the root of the vth ganglion and this is precisely the position of the anterior pro-otic vein. The posterior pro-otic vein lies in the angle between the antero-lateral surface of the otic capsule and the orbito-parietal commissure (Figs. 5, 9) and, in rat embryos of 16.0 mm C.R. length onwards, becomes enclosed in a cartilaginous canal of Verga and emerges between the tympanic ring and squamous temporal bones as the post-glenoid vein.

In the embryo rat, as in the human and other mammalian embryos, there is a stage at which the lateral sinus divides at the apex of the otic capsule into two almost equal channels (Figs. 6, 8). The anterior channel, formed from the posterior pro-otic vein, is the petro-squamous sinus, and the posterior channel, formed from the supra-otic anastomosis and the terminal part of the posterior rhombencephalic vein, is the sigmoid sinus. These two channels were named the 'vordere Ast' and 'hintere Ast' of the transverse sinus by Shindo (1915). As a result of the development of the various emissary veins, which connect the dural venous sinuses to the external jugular venous system, the pattern of the dural venous sinuses, particularly in respect of the petro-squamous and sigmoid sinuses, varies from time to time during the development of any particular mammal and differs in various adult mammals. These variations determine the relative roles of the internal and external jugular veins in conveying the venous drainage from the brain. Much attention has been paid, by previous writers, to the so-called vein of the foramen jugulare spurium with regard

to the interrelationship between the internal and external jugular venous systems with almost complete neglect of the other emissary veins. The present investigations indicate that: (a) different gaps in the developing chondrocranium have been called the foramen jugulare spurium, and (b) the diversion of blood from the internal to the external jugular venous systems is not solely dependent on the presence or absence of a vein of the foramen jugulare spurium.

Rathke (1838), despite having reversed the order of development of the internal and external jugular veins, clearly defined the place of exit of the main para-otic emissary vein from the developing mammalian skull, namely between the tympanic ring and the temporo-mandibular joint. This was confirmed by Luschka (1862), who coined the name 'foramen jugulare spurium', and the only foramen that it can be in the adult mammalian skull is the post-glenoid foramen, through which emerges the petro-squamous sinus. Salzer (1895) stated that the foramen jugulare spurium is variable in position in the adult mammalian skull but has its classic site in the dog. It may be above the zygoma (hedgehog), above and behind the ear opening (guinea-pig) or between the zygoma and outer ear (mouse). According to Mead (1909) and Shindo (1915) the occipito-capsular fissure forms the foramen jugulare spurium in the mouse. De Beer (1937) further confused the issue by calling the superior occipito-capsular the foramen jugulare spurium *or* the mastoid foramen.

Where there are gaps in the developing chondrocranium there are potential connexions between the developing dural venous sinuses and the external jugular venous system, and the relative size of such veins varies during the development of any mammal and in adult mammals of different species. The major places at which such emissary veins occur are the orbit, the foramen magnum and the great fissure around the cranial, superior and caudal borders of the otic capsule which includes the occipito-capsular fissure and the spheno-parietal fontanelle (Fig. 11). Connexions between the ophthalmic veins and the facial vein are constantly found and their size influences the size of the cavernous sinus. A vertebral vein (sinus condyloideus), connecting the sigmoid sinus to the vertebral venous plexus, is also a constant feature and frequently forms the main termination of the sigmoid sinus (Fig. 12). The true relationship of the emissary veins to the otic region of the chondrocranium can only be seen in the developing skull prior to, and during, the development of the membrane bones. In the adult skull the manner in which the membrane bones overlie the elements of the chondrocranium may obscure the true relationships of an emissary vein as, for example, the mastoid emissary vein of the rabbit. Here the squamous temporal and parietal bones overlie the fissure between the petrous temporal and occipital bones.

The anterior channel of the lateral sinus is the petro-squamous sinus, and during embryonic life it always communicates with the temporal tributaries of the external jugular vein by a pro-otic emissary vein or veins passing through the spheno-parietal fontanelle (Figs. 5, 9, 11). When the dermocranium develops, this emissary vein comes to lie between the mandibular fossa of the squamous temporal, cranially, and the tympanic ring, caudally. This vein, and this vein only, can be called the vein of the foramen jugulare spurium as defined by Rathke (1838) and Luschka (1862) and it forms the post-glenoid vein of the adult mammal. It appears to be a constant feature of all mammalian embryos but only persists in some adult mammals. But in

some mammalian embryos it may reach quite a large size before finally regressing, e.g. rabbit, pig. Although the vena capitis lateralis plays a part in the development of the post-glenoid vein it cannot be described as a persistent vena capitis lateralis. The post-trigeminal segment of the primary head vein, which joins the vena capitis medialis to the commencement of the vena capitis lateralis, emerges through the posterior end of the sphenoparietal fontanelle but the vena capitis lateralis continues caudalwards under the crista parotica with the facial nerve and the stapedia artery.

Adult Monotremes (*Tachyglossus* and *Ornithorhynchus*) exhibit a most unusual pattern of head veins in that the vena capitis lateralis is present (Hochstetter, 1896, 1906). The petrosquamous sinus runs down the anterior face of the petrous temporal bone and then enters the facial nerve canal at its anterior end and accompanies the facial nerve to the stylo-mastoid foramen; it then joins the internal jugular vein. The anterior end of the superior sagittal sinus connects with the cavernous sinus as is seen in the hedgehog (Fig. 12A).

In addition to these three major emissary veins (ophthalmic, vertebral and post-glenoid) there are numerous other gaps in the developing skull in which potential emissary veins are found and every adult mammal has its own peculiar pattern of interconnexions between the internal and external jugular venous systems. Additionally, the complexities of the development of the head veins leads to the appearance of numerous variations, as is well seen in man, and this is almost certainly true of other mammals. Attempts have been made to use the pattern of the head veins to establish phylogenetic relationships (van Gelderen, 1925; Boyd, 1930) but there has been a tendency to focus attention on the post-glenoid vein and to ignore the other emissary veins which play an equally important part in determining the balance between the internal and external jugular venous systems (Fig. 12). Also, due allowance must be made for the variability of the venous system. The mammalian skull has a complex developmental pattern and, although different species show the same major elements of the chondrocranium and dermocranium, there is considerable variation in detail from one to another. The position of the various fontanelles and neuro-vascular foramina are one obvious factor in determining the position of the emissary veins and there does seem to be a basic pattern common to most mammalian embryos (Fig. 11). These observations, however, can offer no guide to the factors which determine the final pattern seen in any particular mammal. If the pattern of the mammalian head veins is to be used as a guide to phylogenetic relationships then the whole pattern must be considered and not one particular emissary vein. Furthermore, it can only be of real value if it is regarded as one component of the 'total morphological pattern' (Clark, 1959).

#### SUMMARY

In all mammalian embryos the first main venous channel draining the brain into the anterior cardinal vein lies in close contact with the lateral surface of the neural tube. With the development of the cranial nerves and otic vesicle it is replaced by a composite channel whose cranial part lies deep to the vth ganglion (vena capitis medialis, the future cavernous sinus) and a caudal part (vena capitis lateralis)

running lateral to the otic vesicle and capsule. In all mammals, except Monotremes, the vena capitis lateralis disappears during embryonic life and is replaced by the lateral sinus (consisting of transverse and sigmoid parts) which lies dorsal to the otic capsule. The large posterior pro-otic vein of the embryo becomes the petrosquamous sinus, which leaves the chondrocranium via the sphenoparietal fontanelle to join a temporal tributary of the external jugular vein. This is the vein of the foramen jugulare spurium and, when the dermocranium appears, it is seen to make its exit between the squamous temporal bone and the tympanic ring, i.e. it is the post-glenoid vein of the adult mammal. The post-glenoid vein is not a persistent vena capitis lateralis. The interconnexions between the internal and external jugular venous systems are not solely dependent upon the presence or absence of the post-glenoid vein and many other emissary veins are involved. Such emissary veins are potentially present in every gap in the developing skull and their degree of development varies during embryonic life and in different adult mammals. If phylogenetic relationships are to be inferred from the pattern of emissary veins and dural venous sinuses then the total pattern must be considered and not just the post-glenoid vein. Also, due allowance must be made for the variability of the pattern of head veins consequent upon their complicated mode of development.

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