Resumen por el autor, Charles C. Macklin.

Nota preliminar sobre el cráneo de un feto humano de 43 mm. de longitud máxima.

El presente trabajo comprende una breve descripción del condrocráneo, esqueleto del arco branquial, vértebras cervicales y huesos de membrana del feto humano núm. 886 de la colección de la Carnegie Institution de Washington, basándose en veintiocho modelos y una reconstrucción de perfil. Las porciones cordal y precordal del tallo central forman un ángulo de 115°. Los centros de preosificación se mencionan. El cartílago supraoccipital esta osificándose excepto en los bordes, de los cuales parten los procesos ascendente y descendente. El autor dá una explicación de la equivocación de Bolk al interpretar esta región. El surco occipitoparietal separa parcialmente la placa parietal de la escama occipital situada debajo. Los arcos neurales de las vértebras occipitales están bastante acusados, existiendo tubérculos yugulares marcados y procesos paracondiloides. El cartílago supracoclear falta. El proceso estiloides está unido con la cápsula por medio de cartílago. El proceso mastoideo es un pequeño nódulo libre. El orificio perilinfático está dividiéndose por los procesos intraperilinfáticos anterior y posterior, que se aproximan. Las alas hipoquiasmáticas son pequeñas. Las comisuras prequiasmáticas son precartilaginosas y los orificios del mismo nombre son relativamente grandes. La comisura alicoclear o língula en vías de desarrollo es completa, pero muy delgada. En la región etmoidal no se encontraron cartílagos paraseptales superiores. El proceso cupular es largo y precartilaginoso. En el meato medio se encuentra un proceso precartilaginoso delgado y largo. El autor ha modelado y descrito el sistema del conducto nasolacrimal del mismo modo que muchas de, las demas estructuras con él relacionadas, tales como el notocordio, nervios principales y ganglios, etc. Se han representado todos los huesos de membrana con excepción del nasal.

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PRELIMINARY NOTE ON THE SKULL OF A HUMAN FETUS OF 43 MM. GREATEST LENGTH

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Studies on the developing skull of man and the lower forms have recently gained an impetus through the appearance of several papers. Among the contributions from American laboratories may be mentioned those of Kernan ('16) and Lewis ('20) on the human skull, Terry ('17) on the cat, and Rice ('20) on the lizard. Although a great amount of work has already been done, yet the science of craniogenesis is only in its infancy. Of particular service has been the wax-plate method of reconstruction, and in recent years the refinement of this method represented in the plaster of Paris technique (Lewis, '15) has become a very valuable aid. It is of interest to pursue the study of the development of the human skull not only for its own sake, but even more on account of its relation to the larger field of the development of the head, and to the still larger domain of evolution, and I offer this preliminary note upon the developing skull of a human fetus already well advanced in the scale of differentiation in the hope that it may prove helpful in advancing our knowledge of cranial morphogenesis.

The Embryological Collection of the Carnegie Institution of Washington presents splendid opportunities for the investigation of almost any problem in human antenatal development, and I was fortunate in being able to avail myself of its privileges. I chose for study human fetus no. 886, of 43 mm. greatest length, because it represents a stage sufficiently near that of the 40-mm. fetus which I described some years ago (Macklin, '14) to provide interesting material for comparison, and yet sufficiently far from my earlier specimen to avoid duplication of the work of research. No. 886 was obtained in perfect condition and was exceptionally well prepared. The sections were cut in the frontal plane at a thickness of 100 μ and the series is practically perfect. The models were done in plaster of Paris, and number twenty-eight. They are faithful reproductions of the original structures.

A model of the entire skull, cervical vertebrae, and cartilaginous branchial arch skeleton was first made at a magnification of ten diameters, and this was used for the grosser studies. The central stem and the right half of the occipital cartilage were also made at the same enlargement. For the examination of the minuter details, special models were made of selected parts, taken from the right side of the skull, and enlarged twenty diameters. In addition to the cartilage, the membrane bones of the right side were modeled, together with the closely related soft parts, as the nerves, vessels, mucous membranes, etc., to be referred to in the description. Profile reconstructions were also made, showing the texture of the frontal and parietal bones, and the relation of the skull to the brain and to the external form.

DESCRIPTION

The skull, in general form, is much like that of the 40-mm. human embryo from the collection of Professor McMurrich, of the University of Toronto, known as 'I^a Toronto,' which I formerly described (Macklin, '14), and which will be referred to in this paper as Ia. No. 886, however, is noticeably less developed than Ia, although the latter is shorter, and this apparent discrepancy is to be explained by the fact that the dimension of Ia was obtained by crown-rump measurement, while in the case of no. 886 it was greatest length.

Development is proceeding most rapidly in the anterior parts, notably in the ethmoidal region, judging from the character of the cartilage and from a comparison of earlier and later stages, as that of Lewis ('20), embryo no. 460, of 21 mm., and Ia.

Indications of future ossification centers

The cartilage is mostly mature, and it is practically a continuous mass. In ten regions (four paired and two unpaired) it is undergoing the change preliminary to ossification, although in no case is there actual bone formation present. This change in the cartilage is most marked in the case of the center for the supraoccipital cartilage, which is single and involves the entire thickness of the plate, but not the entire width, there being a narrow uncalcified edge along the upper border and a short blunt point (the descending process) projecting downward into the foramen magnum. The paired centers for the exoccipitals are situated in and behind the jugular tubercles. These tubercles are distinct ridges which lie just lateral to the canals for the hypoglossal nerves and run back to the posterior condyloid notches on the border of the foramen magnum. At these notches the cartilaginous change involves the entire thickness of the plate.

In the basioccipital cartilage is a small area of modified cartilage which represents the single center of the basioccipital bone. In the temporal wings the cartilage is still less modified, but paired centers can be made out. The sphenotic centers are just beginning, and the cartilage here, at the outer ends of the alar processes, shows only a very small degree of change. There are paired centers near the lower ends of Meckel's cartilages, and here the perichondrium is ossified and represents part of the mandible.

The *central stem* is bent at the body of the sphenoid, the angle between the chordal and prechordal parts being 115°. It is thus narrower than in no. 460, where my measurement from Lewis's figures shows it to be 125°. The bodies of the cervical vertebrae make with the chordal part of the central stem an angle of 125°. This is probably a more variable angle. The corresponding angle in 460 was 110°.

The *foramen occipitale magnum* is relatively larger than that of Ia, and the tips of the occipital vertebral arches are farther apart, making the superior incisure much wider. These arch tips are the same distance apart as those of the atlas, but as we proceed down the spinal column the arch tips come closer and closer together. Those of the seventh cervical vertebra, however, are still some distance apart. Closure of the cervical spinal canal is evidently following the familiar course, in being completed earlier below than above.

It seems possible that the occipital vertebra may always present a spina bifida, the arch tips not coming into actual contact and fusing to complete the foramen magnum behind, as I formerly held. This is undoubtedly the case in certain dogs, notably of the short-nosed type. Dr. Adolph H. Schultz has shown me mature skulls of bulldogs and pugs, nos. 71, 381 and 382 of his collection, where the extremities of the occipital neural arches are separated by a distinct interval and where, accordingly, the superior occipital incisure has persisted. It is a conspicuous notch which projects dorsally as an extension of the main part of the foramen occipitale magnum.

The *occipital vertebral arch* is not quite so heavy and well marked in no. 886 as in Ia. The entire cartilage of the occipital region is somewhat lighter in structure. The lateral occipital eminence is not so prominent, nor is the cartilage here so thick.

The *condylar fossa* is represented upon the occipital cartilage by a depressed area, but as yet the superior articular process of the atlas does not lie far enough out to occupy it. It is relatively larger than that of the mature bone.

The *jugular process* is represented by a conspicuous transverse cartilaginous projection, which far overreaches the transverse process of the atlas below, in contrast to the condition in the adult.

There is a well-marked, though small, *processus ascendens*. It is a spheroidal mass of cartilage of rather young type which projects upward in the midline from the upper border of the tectum posterius—the central part of the supra-occipital cartilage. It is attached by a very short cartilaginous pedicle to the upper margin of the tectum. To either side, and closely associated with it, are the paired osseous spicules which represent the young interparietal bone, in their thin investment of condensed mesenchyme. The ascending process is thus attached to the unchondrified upper edge of the supra-occipital cartilage, already referred to, and which has been called by Bolk ('04) the 'Knorpelspange,' and other names.

Fawcett, in 1910, described this process in a human embryo of 30 mm., and homologized it with the processus ascendens of the reptiles. This homology seems to me to be quite in order, but I would point out that the process in mammals does not bear the same relationship to the saccus endolymphaticus that it does in reptiles. Gaupp ('00) and Rice ('20) have described the saccus in lizards as lying just lateral to the ascending process, and Rice regards the process in the skink as affording protection to the saccus. In mammals, it need hardly be said, the saccus is far distant from this region, having accompanied the otic capsule in its evolutional downward and outward rotation, and it follows that such a function on the part of the ascending process, if it ever existed, has become obsolete.

Mead, in 1909, made the same homologization for a small free nodule which he found in the pig's skull, just above the tectum posterius. In 1914 I described a free nodule of cartilage (with a very small grain of cartilage beside it) in the skull of Ia, and looked upon it as possibly representing the most superior cartilaginous mass described by Bolk ('04) in human skulls of about this stage and a little older. On account of the fact that the sections immediately posterior were missing from the specimen, I was unable to determine its relationship to the upper edge of the tectum posterius. It seems possible that these free cartilaginous masses may be vestiges of the tectum cranii anterius, a band which connects the parietal plates dorsally. Although this tectum is generally looked upon as rudimentary in man, Kernan ('16) has reported it as complete in his 20-mm. human embryo. Kernan has discussed the subject of the two tecta, lending support to the view of Levi ('00) that the anterior tectum disappears as the posterior appears. An interesting finding is reported by Fawcett ('18 b) in the embryonic skull of Weddell's seal. Two cartilaginous masses, lying side by side and showing slight signs of fusion with one another, appeared well forward in the membranous cranial vault, and are thought by Fawcett to belong to the anterior tectum.

I have found the ascending process in a number of embryos of the Carnegie collection, and am now engaged in a survey of this collection with the purpose of making a study of it. The process is represented in mesenchyme as early as the 21-mm. stage.

The work of Bolk ('04) upon the occipital region of human embryos has been much quoted in the literature, and has led a number of recent investigators into error because of a misinterpretation which it contains. Bolk used the van Wihje method to study the cartilage of this region, but the dyestuff (methylene blue) did not stain the calcified area of the supra-occiptal cartilage representing the ossification center of the supra-occipital bone. Since this area did not give the tinctorial reaction for cartilage, and since he did not check his work with sections, Bolk concluded erroneously that it was membrane. His later stages show distinctly that this region does become ossified. He attempts to explain the occurrence of this 'membrane' by saying that rapid growth of the brain in this region has interfered with the development of cartilage; he fails, however, to account for the development of the 'Knorpelspange,' a band of cartilage which, as I have shown, represents the upper edge of the supra-occipital cartilage which has remained uncalcified, and which consequently stains blue in Bolk's preparations. It seems obvious that if the growth of the brain interferes with the development of cartilage in the region of Bolk's 'membrane,' it should certainly do so in the case of the 'Knorpelspange.' As a matter of fact, cartilage develops in the supra-occipital region quite early. I have found it at the 21-mm. stage in a human embryo. Calcification in the center for the supra-occipital comes on quickly. It should be said for one recent investigator (Fawcett, '10 b) that he was skeptical of this work of Bolk, saying (p. 306): "I must confess the appearances in his figures scarcely explain what is seen in this cranium."

It would seem that the upper edge of the supra-occipital cartilage, judging from Bolk's work, as well as my own, remains cartilaginous for a considerable time, and it may be that thus growth of the band in width is promoted through proliferation of the cartilage and subsequent invasion of it by the process of calcification, just as expansion of any endochondral center of ossification is brought about.

Bolk found, too, the region of the apex of the superior occipital incisure remaining cartilaginous, as shown by the staining with methylene blue. The same reason may underlie the persistence of this cartilaginous mass. In one case, at least, Bolk finds that this paired mass of cartilage agrees in position with the later developing bones of Kerckring. These masses of cartilage, which Bolk thinks are in membrane, are doubtless really connected above with the calcified cartilage of the supra-occipital, and correspond probably to the processus descendens, as described in no. 886.

The *otic capsule* is well developed, the cochlear part showing the youngest type of cartilage, in accordance with the familiar order of chondrification. The walls are thin. A large massa angularis is present. The spiral septum is forming, but is far from complete. The cavity of the capsule was modeled as a solid, and the membranous labyrinth was also modeled. The latter is almost fully differentiated, and occupies but a small fraction of the available space within the capsule. The foramina are all large, and the edges are for the most part thin and of young cartilage.

The *malleus* and *incus* are separated by membrane, but do not show a distinct joint cavity. The crus breve of the incus is connected with the otic capsule by a small area of young cartilage. There is a small fragment of bone developing in the perichondrium of Meckel's cartilage, which represents the processus Folianus of the malleus, or goniale. It is as yet connected with the malleus only by membrane. The *stapes* has the well-known ring form, and the arciform base bends in the membrane filling the vestibular window. This membrane resembles precartilage, and is not everywhere sharply marked off from the stapes. Anteriorly the latter is joined to the otic capsule by a narrow junction of young cartilage.

There was no *supracochlear cartilage*, as in Ia.

The *perilymphatic foramen* is large and shows evidence of the development of a partition which will separate it into its future parts; there is a small anterior and a somewhat larger posterior intraperilymphatic process.

The *styloid process* is directly attached to the crista parotica of the otic capsule by cartilage, whereas in Ia it was free from cartilaginous union with the capsule.

The *mastoid process* is a small free nodule in 886, whereas in Ia it was connected by cartilage with the otic capsule.

The *parietal plates* are relatively larger than in Ia. They have not, as yet, begun to be overlapped by the parietal bones. They are marked off from the occipital cartilage upon the cranial surface by the occipitoparietal groove. The cartilage along this groove is thinner than that of the plates above and below. Dorsomedially the parietal plate and occipital cartilage are separated by a distinct occipitoparietal notch, which, however, is not quite so deep as in Ia. There were no isolated nodules of cartilage in the vicinity of the upper margins of the parietal plates, as in Ia.

The *body of the sphenoid* is large, stout, and unperforated. From its side the *alar process* projects, and from the outer end of this process the temporal wing depends. From the caudolateral end of the alar process, which here is knobbed, projects backward the conical *alicochlear commissure*, whose pointed caudal end is confluent with the cochlear part of the otic capsule just below the pole of the latter. This commissure was not present in Ia, being represented by a short process, projecting backward from the processus alaris. The commissure subsequently develops into the lingula. The alar process, as Lewis ('20) points out, is largely taken into the body of the mature sphenoid, the carotid sulcus appearing upon its upper surface. The *carotid foramen* is closed by the alicochlear commissure in 886, and is much larger than the internal carotid artery which traverses its outer corner. Its posterior boundary is in part formed by a projection from the basisphenoidal cartilage which forms a union with the cochlear portion of the otic capsule, and represents the posterior petrosal process of the adult bone.

The *temporal wing* shows a distinct lamina ascendens and a pterygoid process. The foramen rotundum is complete, but the medial border is as yet thin and composed of young cartilage.

The *medial pterygoid plate* is a thin strip of bone, to the lower end of which is attached the cartilaginous hamular process. The line of junction between the two is not well marked.

The *orbital wing*, larger than the temporal, is thin. Its posterior root is stout and rounded, but the anterior root is of precartilage, is very slender and is evidently just forming. From the caudal edge of the anterior root there passes back a slender strand of precartilage, the fundament of the *prechiasmatic commissure*, which was represented in Ia in cartilage, and was much stouter. This commissure cuts off the small prechiasmatic foramen from the larger optic foramen. The prechiasmatic foramen is relatively larger in 886 than in Ia. Contrary to my former statement (Macklin, '14), it may persist in adult skulls—at least in those of younger age. I have recently noted these foramina in the sphenoid of a young adult in the osteological collection of Johns Hopkins Medical School. In several older skulls it was not present.

From the edge of the presphenoid, just in front of the posterior root of the orbital wing, there projects outward the *ala hypochiasmatica*. According to Kernan ('16), this structure represents a separate center of chondrification for the ala orbitalis. In 886 it is of a young type of cartilage, edged with precartilage, and is noticeably less developed than in Ia.

Each orbital wing has a well-marked dorsolateral process, which turns upward a little, as well as outward and backward. With the limbus sphenoidalis these two points make an angle of 131°, contrasting with the average of the corresponding angles taken from four mature skulls, which was 150°. Thus there is a flattening out of the orbital wing with subsequent development, associated, no doubt, with the growth of the brain in this region.

The anterior part of the orbital wing is bordered medially by the orbitonasal fissure, but laterally it is continued forward into the spheno-ethmoidal cartilage, which is connected with the anterior part of the ectethmoid by the spheno-ethmoidal commissure.

The *nasal septum* is not so stout as that of Ia, particularly along the lower border. It presents no superior paraseptal cartilages, as in Ia. The *cartilages of Jacobson* are not so far developed as those of Ia, but the different parts can be made out in them. They are of young cartilage and precartilage, and the medial plate is connected anteriorly with the ventrolateral process and with the nasal septum. They are situated considerably below the level of the *vomeronasal organ*.

The *vomeronasal organ* was modeled, and is fusiform in shape. It is connected with the nasal cavity through a developing duct in which a definite lumen has not yet formed. The main portion of the organ suggests a coiled duct, but the lumen is not definite. The septum, medial to the organ, is not hollowed out, as in Ia.

The *mucous membrane* covering the septum is fairly flat, and shows an indistinct wide and low elevation which runs almost parallel with the upper border.

The *ectethmoid* is a thin, irregularly shaped plate of cartilage, upon the inner surface of which are to be seen the representatives of the future conchae. The superior concha is as yet of precartilage, almost entirely, and is wide, low, and rather indefinite. The middle concha is well marked, though not so well as in Ia, and it does not show such a definite continuity caudally with the maxilloturbinate as in Ia.

In the middle meatus there is a long slender process which may represent the *uncinate process* of the adult. It is altogether of precartilage and corresponds to the cartilage of the middle meatus of Ia, where it was a small nodule of young cartilage attached by a pedicle of precartilage to the ectethmoidal wall. The region of its attachment corresponds outwardly to the location of the posterior maxillary process.

The *inferior concha* is the largest of the three, and is the lower portion of the ectethmoid which has been bent upward and inward. Anteriorly it slopes downward, but posteriorly it projects almost directly inward, and the inner edge, covered with young cartilage, turns downward. Anteriorly it is bounded by the posttransverse incisure. The medial extremity of the maxilla, underlying the paraseptal process, makes of the incisure a foramen, leading into the inferior nasal meatus. There is a small cavity representing the spheno-ethmoidal recess, and one representing the superior nasal meatus. Anteriorly the agger nasi is represented very indefinitely by a low eminence.

The roof of the nasal capsule is very incomplete, the cribriform plates having only begun to form, and their loci being represented by gaping foramina; posterior to these there is a fenestrated covering of young cartilage.

The outer wall presents posteriorly the familiar flattened planum antorbitale which bears, near the upper surface, a very small paraethmoidal process, directly attached to the wall. In Ia this was a free nodule. The anterior portion of the plate shows several eminences. The superior nasal prominence is low and makes no corresponding concavity upon the inner surface. The middle prominence, or Sakterwulst of Voit ('09), is very conspicuous. The inferior prominence is represented in the interior by a hollow, and is continued backward into the long and slender paraseptal process. Upon the lower edge of the prominence there is a small tubercle, the superior alar process which appears to be taken into the lateral crus of the greater alar cartilage in later stages, according to the researches of Remke ('13), as stated in the atlas of Peter ('13). The paraseptal process, too, is shown by the same investigator to become separated later on into fragments to form the lesser alar cartilages. This process represents part of the anterior transverse lamina of the lower forms, and it is of interest that the lesser alar cartilages of the nose are derived from it.

There is a distinct posterior nasal prominence which leads backward, outward and downward as a ridge to join with the sharp lower edge of the planum antorbitale. The process is partially cut off by a distinct cleft from the posterior maxillary process, which is edged with a young type of cartilage, and which shows projecting forward from it the very slender spicule of osseous tissues representing the lacrimal bone. Lateral to these structures is the nasolacrimal duct. There is a distinct club-shaped paranasal process, the narrow end being attached to the capsular wall, while the blunt anterior end, which also points downward, lies just lateral to the nasolacrimal duct. In Ia it was free. In subsequent ossification this region is apparently included in the lacrimal bone.

An interesting structure in 886 is the *anterior cupular process.* It is a very long and slender hook-like process of precartilage. It is directly attached to the projecting anterior margin of the ectethmoid which forms the front of the anterior naris. It is crescentic in shape, the concavity looking outward, and containing the epithelial plug of the anterior naris. At the summit of the curve the two processes are very close together, and they are also quite close to the nasal septum here. The posterior end of the process is very sharp and turns outward. Rehmke ('13), in a somewhat later stage, has found this process represented in cartilage (Peter, '13), and in the 275-mm. stage (sitting height) he has noted that it joins with the ventrolateral process to form the medial crus of the greater alar cartilage. It is of interest to find the medial crus represented so early in precartilage.

The *nasolacrimal duct* together with the nasolacrimal sac and the lacrimal ducts were all modeled. There is as yet no distinct lumen. The duct is quite slender and has a curved course. The sac is not at all a marked dilation. The lower end of the duct is applied closely to the epithelium of the inferior meatus (which is an uncleft plate in this region), but does not as yet open into the nasal cavity.

The position of the lower end of the nasolacrimal duct is far behind that of the corresponding structure in the lower forms. As an example (taken from many), we may cite the condition in the cat (Terry, '17), where the duct courses forward, laterally to the anterior transverse lamina (represented in homo by the paraseptal process), and opens into the nose in front of this lamina through what is really a extension of the anterior naris. We have noted in Ia that there is no cartilaginous connection between the paraseptal process and the nasal septum, and the same condition obtains in 886, and it would seem that this structure, in man, does not develop. Thus it is not impossible that the retrogression of the lower end of the nasolacrimal duct has been associated with the disappearance of the anterior transverse lamina. When this lamina is removed there is no cartilaginous impediment to the caudal migration of the duct, and its consequent shortening. The shortening of the duct, too, has doubtless been associated also with a shortening in the length of the nose.

The *notochord* was modeled in relief. Its course is very similar to that described by Huber ('12) for his embryo J, no. 47, 32 mm., shown in his figure 10. It presents varicosities in the region between the tip of the dens and the basioccipital cartilage. In traversing the basioccipital it runs through the anterior end of the preossification center, and is here much attenuated—indeed it shows a break in continuity just at its point of exit from the plate. It comes into close relationship with the pharyngeal bursa in the well-known manner, and here presents more varicosities. After traveling close to the pharyngeal epithelium for some distance, it again enters the cartilage of the basal plate to terminate in the basisphenoid just below the root of the dorsum sellae.

Several of the cranial nerves were modeled, including much of the V and VII, and some of the IX, X, XI and XII. The related ganglia, as the semilunar, geniculate, vestibular, cochlear, sphenopalatine, jugular or glossopharyngeal and vagus petrous and nodosum, were modeled. The internal carotid artery, auditory tube and tympanic cavity, and stapedius muscle and tendon are among other structures modeled. The relation of the skull to the brain and to the external form is shown in a profile reconstruction.

Membrane bones. The membrane bones are all present excepting the nasal. Some of them are very small, as the tympanic interparietal, lacrimal, goniale and medial pterygoid plate. The maxilla is of interest in that it presents a groove upon the palatine surface which leads up to the tip of the frontal process. This groove represents the incisive suture, separating the maxillary and the premaxillary elements, as recently described by Felber ('19); (abstract by Schultz, '20). The upper end of this suture is imperfect, representing the region latest to close.

The cartilaginous branchial arch skeleton was modeled. The *hyoid cartilage* has a lesser cornu of young cartilage connected by a membranous strand with the styloid process. There is a perforation in the *thyroid cartilage* which is closed below by precartilage. The *cricoid cartilage* bears the small *arytenoid cartilages*, which are very small nodules of young cartilage enclosed in a thick layer of condensed mesenchyme which shows several of the characters of the adult cartilage, and which is directly continuous with the mesenchyme of the cricoid cartilage. The tracheal rings are rudimentary as yet.

A full description of this skull with illustrations will appear at an early date in the Contributions to Embryology (Vol. 10), published by the Carnegie Institution of Washington.

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