X. *On the Structure and Development of the Skull and Laryngeal Cartilages of Perameles, with Notes on the Cranial Nerves.*

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[Plates 29–34.]

Contents.

Introduction.

The research described in this paper was begun by Mr. R. W. Palmer in 1912, at the suggestion of Prof. G. Elliot Smith. During the following year he published a short paper "On the Lower Jaw and Ear Ossicles of a Fœtal Perameles," the specimen to which he referred being the 23·0 mm. greatest length fœtus mentioned below. Palmer also modelled the skulls of the 15·5 mm. and 16·0 mm. stages and the internal labyrinth of the 23·0 mm. fœtus, making notes on the work as far as he had taken it. On Mr. Palmer's appointment to the Indian Geological Survey the work was handed over to me for completion.

I am glad to have this opportunity of thanking Mr. Palmer for giving me the use of his models and notes; some of the latter are embodied in the present paper.

I wish to record my grateful thanks to Prof. F. J. Cole, D.Sc., of University College, Reading, under whose guidance the work has been carried out. He has been untiring in giving me help and advice.

The specimens described were drawn from the collection of Prof. J. P. Hill, D.Sc., F.R.S., of University College, London, and my thanks are due to him for allowing me the use of his excellent material, and also for his ready help in obtaining for me

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much of the literature. I have also to acknowledge the kind help of Dr. ROBERT BROOM; the advantages of discussing the work with one who is pre-eminently an authority on the skull have been great.

HISTORICAL.

The literature concerned with the development of the Mammalian skull is very extensive. However, but little refers specially to the Marsupialia, and most of this consists of observations in embryological papers dealing with comparative anatomy. OWEN (34) in his 'Anatomy of Vertebrates,' published in 1866, gives an account of the skeleton of the adult Marsupials, in which he describes the points of special interest in the skulls of *Perameles nasuta* and *P. lagotis*. In 1885 W. K. PARKER (36) discusses at some length the characters of the Marsupial skull, and this paper may still be looked upon as a good ground-work for the study of the skulls of the group. The table of characteristic features which he gives is still used, with certain additions and alterations, as illustrating the diagnostic features of the Marsupialia. The following list is a summary taken from his Hunterian Lectures on "Mammalian Descent":—1. Vomerine bones present. 2. Bony palate gradually formed and adult fenestration a secondary character. 3. Squamosal hollow. 4. Alisphenoid takes part in forming the bulla. 5. Internal carotid artery passes through the basis cranii. 6. The malleus has a long processus gracilis and two auxiliary processes. 7. Stapes not always stirrup-shaped. 8. Angle of lower jaw inflected, with a large hollow fossa in the upper and inner surface. 9. Hyoid dilated to form a wedge-shaped plate. 10. The optic nerve passes through the foramen lacerum anterius. However, PARKER was unable to carry out his original plan of work, his death, in 1890, preventing the continuation of the series of monographs on the development of skulls.

BROOM (2) in 1896 considers the question of the "Comparative Anatomy of Jacobson's Organs in the Marsupialia," figuring and describing many forms, including that of *P. nasuta*. SYMINGTON (43), in 1899, gives a description of the Marsupial larynx. OPPEL (32), in 1905, quotes and adds to this description, mentioning in particular that of Perameles, but giving no figures. BROOM (3), in 1902, discusses the homologies of the Mammalian and Reptilian vomerine bones, and also describes the palatine process of the premaxilla (1) as being a true process of this bone, but replacing in position and function the prevomer of Reptiles. Also in 1902, the same author (4) describes the fœtal skulls of *Trichosurus vulpecula* and *Dasyurus viverrinus*, figuring those of the 10·0 mm. and 14·0 mm. specimens of *Trichosurus*, and an 8·0 mm. specimen of *Dasyurus*. Through the kindness of Prof. HILL it is possible to include in the present paper further notes on both younger and older stages of these forms. In 1910 GREGORY published his paper on the "Orders of Mammals" (24). This deals, in the first part, with the stages in the history of the ordinal classification of the Mammals, while in the second part the evolution and genetic interrelations of the Mammalian orders are discussed. In this part a chapter is devoted to the question of the

Marsupialia, their affinities with the Monotremata, and in many cases their Reptilian characteristics. The problem of the auditory ossicles is also discussed at some length. In 1913 GREGORY criticises the recent work on the morphology of the Vertebrate skull (25), and again reviews the theories concerning the origin and homologies of the auditory ossicles.

In 1913 PALMER (35) published an account of the posterior end of the lower jaw of the 23·0 mm. specimen of *Perameles*, and in the same year GAUPP (23) in his paper "Die Reichertsche Theorie" describes and figures the corresponding region of a 42·0 mm. specimen of *Perameles*, giving a full and detailed discussion of the homologies of the different bones.

MATERIAL, METHODS, AND NOMENCLATURE.

The Perameles material used for this research consisted of six specimens, full particulars being given in the following list:—

Stage.	Species.	Greatest length.	Head length.	Thickness of sections.
		mm.	mm.	μ
I	*P. obesula*	12·25	6·5	12
II	—	15·5	6·0	16
III	—	16·0	7·0	16
IV	*P. nasuta*	23·0	11·0	16
V	—	35·0	18·5	22
VI	—	45·0	26·0	25

Stage I is the only uterine specimen, the others are pouch-young.

The skulls of the different stages have been studied by means of serial sections and by models made of cardboard on the reconstruction method. It was found convenient to remodel the skull of Stage II, and the figures given are of the new model and not of that made by Mr. PARKER. For further use a list of the models of the various stages is appended.

Stage I. Specimen too young to model satisfactorily, no true cartilage being present.

Stage II. Model of whole skull with lower jaw and hyoid apparatus × 50.
Model of ear ossicles × 130.

Stage III. Insufficient data available.

Stage IV. Model of whole skull with lower jaw and hyoid × 40.
Model of ear ossicles × 80.
Model of internal labyrinth of ear × 50.

Stage V. Model of whole skull with lower jaw and hyoid × 30.
Model of ear ossicles × 60.

The models are coloured so that cartilage (blue), membrane-bone (yellow), and ossified cartilage (red) are readily distinguishable and the formation of the centres of ossification of the cartilage bones is clearly seen.

In a subject which has attracted so many students working independently in so many countries it is not surprising to find that a large number of synonyms are used. When possible the old accepted term has been adopted in this paper; but in the case of a structure recently described by many writers the difficulty of choice has arisen. A certain consistency has been achieved by the use, wherever possible, of Latin terms. My thanks are due to Prof. G. D. THANE for his kindness in revising the list of nomenclature.

STAGE II. (Plates 29–32.)

The model (figs. 1–5) reveals a skull which, while on the whole distinctly primitive, is yet strangely advanced in some features. Of the advanced part, the palate is the most striking. It is quite well developed, and its elements are, with the possible exception of the dentary, the earliest membrane bones to be formed. It is, however, very unlike the adult palate. The other bony tissues formed at this stage are the primitive dentary and a small lachrymal and frontal. The extremely primitive jaw, as well as the palate, will be described in detail later. The rest of the skull, or cranium proper, and the sense capsules are formed entirely of pro-cartilage, cartilage and membrane. No ossification of the cartilage is visible. Of the series available for examination this model shows the chondrocranium at the most complete stage of differentiation. In Stage IV both ossification and absorption of the cartilage have taken place.

Chondrocranium.

The *chondrocranium* forms an extremely deep or boat-shaped chamber for the brain (fig. 1). Membrane alone closes this above, and at the lower parts of the sides are great gaps (figs. 4 and 5), at present out of all proportion in size to the nerves and vessels which pass through them. These gaps in later stages will be greatly reduced in size, partly by the development of membrane-bone and partly by a great growth of cartilage during its subsequent ossification. The sides of the brain case are for the most part formed by the auditory capsules, so that the true cranium is but a very frail structure. Indeed the basis cranii is the only substantial part of it.

At this stage the base of the skull is very much curved, the basi-facial axis being placed at the angle of 45° with the basi-cranial axis (figs. 4 and 5). This gives the skull a curious appearance, which is accentuated by the large size and massiveness of the lower jaw. Further, in correlation with the fact that the young is now firmly fixed to the nipple, the lower jaw is directed downwards and the mouth is open for the insertion of the teat. The occipital plane is at an angle of about 60° to the basi-cranial axis. A comparison of this model with the models of older specimens and with the skull of the adult shows that this steep slope of the basi-cranial axis is an embryological characteristic which is gradually reduced, till in the adult the basi-cranial and basi-facial axes are in the same straight line.

Below the brain the *basis cranii* (*b.c.*) forms a thick layer of cartilage, the basilar portion of the occipital; this is wide posteriorly and sends up alæ, or the *partes laterales* (*pars.l*) of the occipital at the back of the auditory capsules (fig. 1).

At the junction of the pars lateralis and the basis cranii is the *processus par-occipitalis* (*pro.p.o.*) which is a short prong of cartilage projecting forwards, laterally to the *foramen nervi hypoglossi* (*for.n.h.*) (condylar foramen) (fig. 2). At this stage there is no *tectum posterius* (*t.p.*), the *foramen magnum* (*for.mag.*) being bridged by membrane only.

The planum basale, as GAUPP (19) terms the basal portion of the pars chordalis, is pierced by two pairs of foramina, which serve for the exit of the hypoglossal nerve (*for.n.h.*, figs. 1 and 2). The anterior branch of this nerve has two roots, anterior and posterior, while the posterior has a single root. No dorsal roots have been observed. BROOM describes two pairs of foramina in his reconstruction of the skulls of *Trichosurus* and *Dasyurus* (4). The two pairs are persistent in the adult but variations occur. In some specimens the foramina on each side unite as they pass through the skull, thus forming two pairs of foramina on the internal surface of the basis cranii and one pair on the external surface.

Between the auditory capsules and towards the sphenoidal region of the skull the floor narrows somewhat and the *foramen lacerum posterius* (*for.l.p.*) is left as a gap between the basal plate and the capsules (figs. 1 and 2).

Immediately in front of the capsules at the *pituitary region* the basis cranii again narrows. Here its compound nature, formed as it is from a pair of parachordals, can be detected in the sections. In the middle of the pituitary region the floor is pierced by a tiny foramen, the *foramen hypophyseos* (VOIT, 45) (*for.hy.*). To the outside of this a pair of much larger canals pierce the basisphenoid and allow the entrance of the *internal carotid arteries* (*for.c.*) in the usual Marsupial manner, *i.e.*, the carotids do not pierce the petrosal and enter the skull cavity by means of the foramen lacerum anterius as is the case with most Mammals. In this respect the Marsupialia are similar to the Monotremata.

Anterior to the pituitary region the base of the skull narrows, and this time rapidly until it becomes an almost cylindrical, but not very stout, rod which merges in front into the *lamina infracribrosa* (fig. 1, *l.i.*), as GAUPP names the transverse cartilage forming part of the posterior wall of the nasal capsules (19).

It has been stated above that the greatest part of the cranial wall, apart from the posterior portion formed by the occipital ring, is formed by the auditory capsules. This statement, however, does not apply to the upper part of the wall, for running back from the *paries nasi* (*p.n.*), and indistinguishably fusing with the flap of cartilage above the canalicular portion of the auditory capsule (*pars v.*), is a thin wall of cartilage forming, for the whole length of the cranium, the supports of its membranous roof.

Hitherto this has been called the *orbitosphenoidal cartilage*, but bearing in mind its great extent, and the fact that only a small portion of it will eventually be ossified to form the orbitosphenoid bone, GAUPP'S system (19) of assigning different names to the different portions of it seems preferable. Hence, following GAUPP, four regions will be distinguished, namely, in front the portion which unites with the paries nasi will be called the *commissura spheno-ethmoidalis* (figs. 4 and 5, *c.s.e*), behind this the portion giving off the downwardly projecting *processus orbitonasalis* (*pro.n.o.*) is named the *ala orbitalis* (*a.o.*); posterior to this is the *commissura orbito-parietalis* (*c.o.p.*), connecting the ala orbitalis with the *lamina supracapsularis* (*l.s.*), the posterior portion of the bar which unites with the dorsal edge of the auditory capsules. It should be emphasised that the lamina supracapsularis does not fuse with the pars lateralis, but is still separated therefrom by a suture. This is readily seen in the sections but does not show very obviously in the model, as the suture is inconspicuous. However, in the latter stages the lamina merges imperceptibly into the cartilage of the pars lateralis, lending support to the contention that the orbito-sphenoidal cartilage assists in the formation of the superior portion of the occipital ring. Special attention might be drawn to the fact that in *Perameles* the coalescence of these cartilages synchronises with the roofing over of the foramen magnum.

In the presphenoidal region the ala orbitalis sends down towards the mid-ventral line a thin cartilaginous flap, the *processus orbitonasalis* (*proc.o.n.*, figs. 4 and 5). In this fœtus, head length 6 mm., the flap is very fragile and does not reach the base of the skull. In Stage IV, head length 11·0 mm., however, it is much stronger and joins the cranial keel (figs. 12 and 13); in this way it completes a foramen in the wall of the skull. No structures pass through this foramen, but it is found also in early stages of *Ornithorhynchus* and *Echidna*, and is seen in BROOM'S reconstructions of the chondrocrania of *Trichosurus* and *Dasyurus*. GAUPP calls it the *fissura orbitonasalis* (*f.o.n.*), and it is noteworthy that its posterior limiting bar is here less developed than in the Prototheria or in *Trichosurus*.

Posteriorly to the processus orbitonasalis the orbitosphenoidal cartilage runs as a narrow vertical band forming a freely hanging wall to the brain base until it is continued above the auditory capsule as the lamina supracapsularis.

At about Section 334 there is a foramen, through which nothing appears to pass, between the lamina supracapsularis and the pars canicularis of the auditory capsule, probably corresponding to the *foramen jugulare spurium* (*for.j.s.*) described in *Sus* (31), *Talpa* (13), and *Lepus* (45).

It must be noticed that no bar descends from the orbitosphenoidal cartilage to meet the pituitary region. That is to say, there is no trace whatever of GAUPP'S "*taenia-clino-orbitalis*," which is so conspicuous in his reconstructions of the early skull of *Echidna* (19). Also there is no *processus clinoideus posterior*, as described by MEAD in Sus (31). There is thus no foramen abducens, the sixth nerve leaving the skull by the foramen lacerum anterius (sphenoidal fissure) (*for.l.a.*).

Partly occupying the gap in the cranial wall but lying to the outside of the skull in the same vertical plane as the ala orbitalis is the *ala temporalis* (figs. 4 and 5, *a.t.*). This is nearly free from the basal bar, while in the 12.2 mm. foetus it is quite a separate element corresponding to the same structure in the 10 mm. *Trichosurus* described by BROOM (4). The ala temporalis can be described as consisting of two portions, the *lamina ascendens alæ temporalis* (*l.a.a.t.*), and a proximal portion the *processus basipterygoideus* (*proc.b.pt.*). The lateral portion chondrifies later than the medial processus, but, as is clearly seen in the later stages, it ossifies much sooner.

The lamina ascendens is hollowed out to the inside to receive the *Gasserian ganglion* (*g.g.*), chondrification having taken place so as to enclose the second branch of the trigeminal, and thus forming what will later be the *foramen rotundum* (figs. 4 and 5, *for.r.*).

It is interesting to note that in Sus, as observed by MEAD (31), the ala temporalis is similarly hollowed out to receive the Gasserian ganglion, but it is not perforated by the maxillary nerve, which passes out of the cranium, together with the second, third, fourth cranial nerves and first division of the fifth, by the foramen lacerum anterius.

The first branch of the fifth nerve passes out together with the second, third, fourth, and sixth cranial nerves through the foramen lacerum anterius, that is to say, the gap between the ala temporalis and the processus orbitonasalis. That the optic nerve passes through the foramen lacerum anterius indicates a primitive character of the Marsupialia and a similarity to the Reptilia; in higher mammals the optic nerve pierces the orbitosphenoid.

The third branch of the fifth nerve passes out behind the ala temporalis, and between it and the auditory capsule, *i.e.*, through what will later on be the *foramen lacerum medium* (*for.l.m.*).

As has already been stated, the occipital ring is incomplete, the foramen magnum not being bridged over by cartilage. There is no apparent differentiation between cartilage which will later ossify to form the basioccipital and the exoccipitals, but there is a deep undercut notch which marks the anlage of the exoccipitals from that of the supraoccipital. The *condyles* (*c.o.*) are not prominent, and articulation is continuous across the basioccipital cartilage. The atlas forms a complete cartilaginous ring; the centrum is continuous with those of the other cervical vertebræ.

Auditory Capsules.

The *auditory capsules*, as is usual, are very large in the early stage, but the most striking feature about them is the extent to which they form the side wall of the cranium (figs. 4 and 5). In Reptiles the auditory capsules are placed well to the side of the brain; in adult Mammals, owing probably to the great development of the brain, they lie distinctly underneath it. In this foetal *Perameles* they are well to the side of the brain, *i.e.*, their position is Reptilian, and this is emphasised by the foramina.

The *foramen acusticum internum* (fig. 1, *for.a.i.*) (internal auditory meatus) is vertical and faces directly inwards. It is large and is not yet divided by a bar, *i.e.*, the cochlear and vestibular branches of the auditory nerve have a common entrance. The *fenestra ovalis* (*fen.o.*) faces directly outwards, and not outwards and downwards as is the rule in adults. The *semicircular canals* in this stage are well developed and normal. The *aquæductus vestibuli* (*aq.v.*) opens immediately behind the internal meatus (fig. 1), and lies in the same position as in *Sphenodon* (27). The internal meatus and the aquæductus vestibuli are confluent in the model, owing to the fact that the extremely young procartilaginous division has not been modelled.

The *fenestra rotunda* (*fen.r.*) faces outwards and backwards. It is hidden in the lateral view by the overlapping *tegmen tympani* (*t.ty.*). This is very large, and hides a considerable portion of the capsule, as well as most of the course of the facial nerve. The *aquæductus Fallopii* (fig. 1, *aq.f.*), or foramen faciale, which transmits the seventh nerve from the cranium, is formed by the hooked-shaped upper part of the pars cochlearis, termed by MEAD (31) "the roof of the foramen faciale," and by VOIT (45) the *commissura suprafacialis*. In this stage the commissura is very slight, but with development it increases in strength.

The *nervus facialis*, on passing through the aquæductus Fallopii, curves downwards and outwards, and, traversing the sulcus facialis, it leaves the skull; the sulcus facialis being hidden in the lateral view by the tegmen tympani.

The cochlea (*coch.*) is only slightly bent, and not coiled at all. The coiling takes place gradually, and can be traced in the different stages. This ontogenetic change undoubtedly corresponds with the phylogenetic development of the coil. In Cynodonts —for example, in *Diademodon* (48)—the cochlea is slightly bent, as in young Marsupials and in the Prototheria. In Eutheria, on the other hand, the cochlea is strongly coiled from the first even in a procartilaginous condition (45).

Olfactory Capsules.

Olfactory Capsules.—The basis of these is the septum nasi, or median nasal cartilage (*s.n.*), which is directly continuous with the presphenoidal region of the basis cranii (fig. 1). At the junction of the ethmoidal and presphenoidal regions this basal cartilage gives off a pair of stout lateral wings, or, it may be more correct to say, expands outwards, so forming an incomplete posterior wall to the nasal chambers. Laterally this *lamina infracribrosa* unites with the commissura sphenoethmoidalis, which on each side runs forward continuously into the paries nasi (*p.n.*).

In front of the ethmoidal transverse bar the median nasal cartilage rises rather steeply till, attaining its maximum elevation, it is joined by or gives off the paries nasi which above forms the *tectum nasi* (*t.n.*). This is hollowed out in the middle line to form the *sulcus supraseptalis* (*s.s.s.*), which lodges the *ligamentum suspensorium*. This is found to be specially well developed in long-snouted Mammals. There is a moderately prominent *crista galli* (*c.g.*).

Thus at the back of the olfactory capsules there are two large gaps—the *fenestræ cribrosæ* (*fen.c.*). These are bounded below by the lamina infracribrosa, laterally by the paries nasi, and separated from one another in the middle line by the vertical nasal septum, which is unfenestrated. In the fœtus these gaps are closed by membrane, which is pierced in a sieve-like manner for the passage of the strands of the olfactory nerves. The membrane will later chondrify before forming the lamina cribrosa.

In front the olfactory capsules run forwards as a pair of cartilaginous tubes. They open anteriorly by the external nares (*a.n.e.*), which are large apertures facing outwards and slightly forwards, and below they open by large foramina, the *fenestræ basales* (*fen.b.*). The *lamina transversalis anterior* (*l.t.a.*), bounding the anterior end of the fenestra basalis, and connecting the paries nasi with the septum nasi, is narrow, and forms but an incomplete floor to the nasal capsule, presenting a condition similar to that of the 10·0 mm. *Trichosurus*, and differing from that of the 8·0 mm. *Dasyrus*, where the fenestra basalis is comparatively small (4). However, in this stage the palatal plates of the maxillæ are much developed, and to a great extent close the fenestra basalis.

From the posterior border of the lamina transversalis anterior the *cartilago paraseptalis* (fig. 2, *cart.p.*) projects backwards, forming the capsule for Jacobson's organs, which are short, as in *Trichosurus*.

As in *Trichosurus* and *Dasyurus*, there is no palatine process of the solum nasi.

Differing from the specimen of *Trichosurus* described by Broom, there are no indications of an ascending *internasal process* in the cleft at the anterior extremity of the nasal capsule. The *processus paranasalis* (*proc.p.n.*), enfolding a portion of the ductus nasolacrimalis, is seen on the external lateral wall of the paries nasi (figs. 4 and 5).

At the anterior dorsal end of the processus paranasalis is a thickening in the cartilage, the *processus alaris superior* (*pro.a.s.*), which roughly divides the anterior nares into two parts, the ventral portion giving entrance to the nasal capsule for the ductus nasolacrimalis, the other being the exit of the nares to the exterior (figs. 2 and 5).

The *ethmoturbinal bones* of the adult are represented in this stage by small internal ridges on the paries nasi. These arise quite distinct from the membrane bones with which in later stages they will be connected.

As might be expected, there is as yet no indication of the ridge representing the *maxillo-turbinal*. This is seen in the later stages.

The tectum nasi is pierced by a pair of small foramina which lie to the sides of the middle line, and just anterior to the great gaps in which the cribriform plate is to be developed. These are the *foramina epiphanialia* (fig. 1, *for.ep.*), and serve for the passage of the ramus lateralis of the ethmoidal branch of the trigeminal.

Meckel's Cartilage, Auditory Ossicles, and Dentary.

Though somewhat hidden in the side view by the dentary, *Meckel's cartilages* (*cart.m.*) form a stout and complete primitive jaw. Anteriorly they unite to form the short but thick symphysis. Meckel's cartilage is a curved rod which passes without distinction into the *malleus* (*mal.*). This, as will be seen in fig. 4, is a thickening forming the head of the malleus and the manubrium, which at this stage is mainly procartilage.

A comparison of the ventral views of the models of the three stages (Plate 29, fig. 3; Plate 30, fig. 11; Plate 32, fig. 22) reveals the fact that the Meckel's cartilages of the youngest are very much bowed. In the older stages they are very much straighter and even become curved inwards, forming a long symphysis. An explanation of this developmental change might be that the widely separated condition of the younger stages allows of a firmer hold on the teat.

The hollowed external surface of the head of the malleus articulates with the rounded body of the incus, forming a close-fitting joint (fig. 8). The incus is provided with two projections—the crus breve, which passes backwards and upwards in close relationship with the overhanging portion of the auditory capsule; the other, the crus longum, passing downwards and inwards, and eventually articulating with the stapes.

The condition of the crus breve is very similar to that described by KINGSLEY (29) in the pig, which he interprets as being a trace of an old articulation between the incus and the auditory capsule.

The stapes, at present in a procartilaginous condition, is imperforate, and does not articulate with the incus. It lies in the fenestra ovalis.

The form of the *dentary* (*d.*) is interesting. At this stage it is the only bone in the lower jaw. It develops as a thin sheath of bone to the outside of Meckel's cartilages; it is formed in front of the basimandibular cartilage, the two bones—*i.e.*, right and left—not meeting in the middle line (fig. 3). For nearly half the length of the jaw the dentary is seen in section as a narrow triangle of bone placed above Meckel's cartilage, and not extending below it. As it travels back it loses this triangular section, until it finally becomes a curved lamina of bone to the outside of, and free from, Meckel's cartilage. Posteriorly it ends abruptly, and there is practically no trace of a condyle and no corono-condylar notch (fig. 2). The inflection of the angle of the dentary is practically absent, being represented only by a slight curve on the bone as it tends to enwrap Meckel's cartilage.

Palate and Upper Jaw.

Even in Stage I, greatest length 12·25 mm., the membrane bones of the upper jaws are well developed. It is rather surprising to find this early differentiation; and since it does not occur in Eutherians it seems probable that it may be correlated with the early attachment of the young to the teat.

The palate as a whole is strongly arched. The maxillæ form a veritable penthouse, but the premaxillæ and palatines are flatter.

While the median sutures are represented by rather wide gaps in the model, the palate is otherwise complete, so that the characteristic Marsupial fenestration is, as PARKER maintained, a secondary feature in the adult. The *premaxillæ* (*p.mx.*) are on the same horizontal plane as the maxillæ, making the surface of the palate level at the anterior end, though, as stated above, the maxillæ are strongly arched from side to side.

The *palatal processes of the premaxillæ* (fig. 2, *proc.p.p.mx.*) lie immediately under the paraseptal cartilages which they partly hide in the ventral view. The processes are short, not extending further than about one-third the length of the paraseptals. In fact, the premaxillæ are mere flat plates of bone developed below the floor of the olfactory capsules; but further back they become triangular in section, and rise rapidly on the plates of the capsules. The relative positions of the premaxillæ and the anterior nares are interesting, being intermediate between that observed by BROOM in *Trichosurus* and *Dasyurus*. The premaxilla in *Dasyurus* is entirely posterior to the anterior nares; in *Trichosurus* it occupies a more anterior position, overlapping the ventral floor of the anterior nares.

The *maxilla* (*mx.*) rises higher on the sides of the capsules than does the premaxilla (fig. 5). Its triangular form in section is broken by the large tooth groove, which is a conspicuous feature of the bone in a palatal view (fig. 2). The tooth germs are present, and are of a considerable size. In the lateral view of the skull the deep groove, in which the infraorbital nerve lies, is seen. This will later be surrounded by bone forming the large infraorbital foramen which is so characteristic of the adult maxilla.

The *palatal processes of the maxillæ* (fig. 2, *proc.p.mx.*) are far from meeting anteriorly in the middle line, but further back they come close together; thus these processes are not fully formed, and are in an intermediate condition.

The *palatines* (*pal.*) are fairly large and massive bones; the ascending plate is not yet developed, the bone merely being a curved plate forming a bed for the nasopharyngeal duct. The inner plates are not long, and the ducts are as yet not separated from one another by bone. The palatal surface of the palatines is much lower than that of the maxillæ.

The *vomer* (*v.*) is a thin, delicate, trough-like median bone found ventral to the nasal septum; its anterior limit is some ten or fifteen sections behind the posterior end of the paraseptals, and it extends behind the lamina infracribrosa.

A thin membrane bone develops on the under side of the ala temporalis; this is the *pterygoid* (*pt.*).

The other membrane bones present at this stage are the *lachrymals* (*lac.*) and frontals (*f.*). The former are very small and thin, and can only be described as forming a ring bone round the nasal duct of the lachrymal gland immediately it has left the orbit.

The *frontals* are present as small sheath-like bones in a dorso-lateral position above the commissura spheno-ethmoidalis after it becomes free from the paries nasi.

Nasals, parietals, and squamosals are not yet formed, though in each case there is a grouping of the osteoblasts preparatory to the formation of the bones.

The *corpus hyoideum* (figs. 6 and 7, *c.hy.*) is a horizontal mass of cartilage almost as thick as it is long, giving off the short, thick anterior cornu, projecting upwards and outwards, and the long, slender posterior cornu, which curves downwards and backwards, and unites with the anterior cornu of the thyroid.

The *thyroid* (*cart.th.*) is a concavo-convex plate of cartilage placed vertically immediately behind the hyoid, with the convex surface in front. The posterior cornu is large, and unites with the dorso-lateral portion of the cricoid in the characteristic manner. The ventro-anterior border of the cricoid articulates with the ventral edge of the plate-like thyroid—that is, in the 15·0 mm. fœtus the thyroid and cricoid cartilages are not united, but are separate in the usual Mammalian manner. Resting upon the upper side of the cricoid are the *arytenoid cartilages* (*cart.a.*); these are tetrahedal in form, and serve as a dorsal protection to the larynx. As SYMINGTON (43) describes, the posterior or external processes of the arytenoids articulate with one another. Indeed, in this fœtus the cartilages of the two sides appear to be confluent. However, I have failed to find what SYMINGTON describes as the interarytenoid cartilage, or, as DUBOIS has termed it, the "*procricoid*" (9).

The hyoid apparatus is not connected with the skull; but that such a connection has at some time occurred is indicated by a slender rod of cartilage given off by the tegmen tympani passing forwards, downwards, and slightly inwards (figs. 4 and 5). In the 12·25 mm. fœtus the remnant of this *stylohayle* (*st.hy.*) approaches approximately near to the hyoid apparatus.

Description of Sections of Stage II.

Fig. 29 shows a section taken near the anterior end of the maxilla. It indicates the method in which the organ of Jacobson (*o.j.*) is formed as an invagination of the membrane lining the nasal passage. The processus paraseptalis (*proc.p.*) and the processus palatinus of the premaxillæ (*proc.p.p.mx.*) are seen in section immediately to the inside of this. The massive imperforate septum nasi gives off, or rather joins, the paries nasi.

Fig. 30.—This section is taken from near the posterior end of the organ of Jacobson. Here it is seen to be separated from the nasal passage, and appears as a thick-walled tube, supported by the processus paraseptalis. The maxilla is cut in two places, the infraorbital nerve lying between them.

Fig. 31.—The plane of section here is through the Gasserian ganglion (*g.g.*). This lies in the hollow of the ala temporalis (*a.t.*) To the inner side of the base of the ala temporalis is the thin lamina of the pterygoid (*pt.*) Again passing towards the middle line is the ductus nasopharyngeus, and below this is the pharynx itself. The

dentary (*d.*) lies to the outside of Meckel's cartilage and the mandibular nerve, which appear oval in section, the nerve lying dorsal to the cartilage. The commissura orbito-parietalis forms an inadequate lateral wall to the brain.

Fig. 32.—The hypophysis is seen dorsal to the basis cranii, which is fused with the ala temporalis. The dentary is considerably shorter than was observed in the more anterior sections, and Meckel's cartilage is therefore seen to extend below it.

Fig. 33 shows the portion of the seventh nerve after it has traversed the aquæductus Fallopii. The auditory capsule is seen in section, and the septum spirale is indicated. The incus and the malleus lie externally to the capsule, while the cavum tympani is seen between the base of the manubrium and the auditory capsule.

Fig. 34.—The section figured here is cut directly through the fenestra ovalis (*fen.o.*), in which lies the still precartilaginous stapes. The fenestra ovalis to the outside and the foramen acusticum on the inside appear to show that the ventral portion of the auditory capsule is severed from the dorsal portion. This is, however, only the case where these two foramina are in apposition. The dorsal portion of the incus or the crus breve is seen, as described above, to be in close relationship with the capsule. There is as yet no articulation of the incus and the stapes. The lamina supracapsularis is seen to be fused with the dorsal portion of the capsule.

Fig. 35.—The aquæductus vestibuli is figured here, and to the outside of this lies the ductus endolymphaticus. The group of nerves and jugular vein are seen ventral to the capsule, having passed through the foramen lacerum posterius (*for.l.p.*). The twelfth nerve is ventral to the basis cranii, and the section is anterior to the foramen nervi hypoglossi, by means of which the nerve has made its way through the skull.

Fig. 36 depicts a condition very much more posterior. The lamina supracapsularis is seen dorsal to the pars vestibularis of the auditory capsule. It should be emphasised that the cartilages of these two structures do not fuse posterior to the foramen jugulare spurium. The exoccipital is the large mass of cartilage ventral to the pars vestibularis.

Stage IV. (Plates 30 and 33.)

The model of this fœtus shows the skull at a much later stage of development. The roofing membrane bones are all present, and the bones observed in Stage II have greatly enlarged, so that the gaps noticed there are smaller, and the model has a more skull-like appearance.

Chondrocranium.

The condition of the chondrocranium is interesting, as the centres of ossification are present in many places. Absorption of the primordial chondrocranium has begun, notably in Meckel's cartilage.

The *occipital region* is more complete, the cartilages of the two sides having united, closing the dorsal side by the *tectum posterius* (figs. 9 and 10, *t.p.*). Ossification has also taken place, and the exoccipitals consist almost entirely of bone, there only remaining a thin covering of cartilage on the ventral side. The ossification extends forwards to the posterior border of the foramen lacerum posterius (*for.l.p.*) The foramen nervi hypoglossi posterius (*for.n.h.p.*) is completely surrounded by bone, ossification of the exoccipital extending as far as the posterior side of the foramen nervi hypoglossi anterius (*for.n.h.a.*). On the ventral side of the tectum posterius is the centre of ossification for the supra-occipital (*s.oc.*). The ossification for the basi-occipital covers a great area (figs. 9 and 10), extending from the plane of the anterior condylar foramen to a position slightly anterior to the aquæductus Fallopii. At only one point, however, does the ossification extend right across the planum basale. Thus in the occipital region there are four centres of ossification noted—one each for the two exoccipitals, the supra- and basi-occipital.

In the *sphenoidal region* ossification has also taken place. The centre for the basi-sphenoid (*b.s.*) is present immediately posterior to the pituitary foramen, and it passes caudally from this point through some twenty sections, its lateral boundary on each side being the foramen caroticum.

The *orbitonasal process* at this stage has developed considerably, and it now fuses with the basis cranii, thus closing the fissura orbitonasalis (figs. 13 and 14, *f.o.n.*).

The orbitosphenoidal cartilage takes an important part in the formation of the lateral walls of the cranium, especially the commissura orbitoparietalis and the lamina supracapsularis (fig. 12). There is as yet no ossification, but these two portions are now broad plates of cartilage, the commissura orbitoparietalis articulating with the alisphenoid. In a lateral view the membrane bones hide a good deal of the orbito-sphenoidal cartilage. There is no sign of the nucleus of the presphenoid.

The ala temporalis shows at this stage a considerable amount of ossification, thus forming the alisphenoid. As the bone replaces the cartilage the structure becomes much slighter and thinner, or, as W. K. PARKER expresses it (40), "the parts which persist as cartilage bones being reduced in relative size, and being more elegantly shaped."

The entire dorsal part of the cartilage is now ossified, and it is only the extreme ventral part, the processus basipterygoideus (*proc.b.pt.*) which shows the cartilage. The alisphenoid extends upwards and articulates with the commissura orbitoparietalis (figs. 13 and 14). At this stage the alisphenoid extends backwards as a thin sheath of bone formed in membrane. There is no distinction between the bone of the portion ossified in membrane and that ossified from cartilage, but that at the anterior end is thicker.

Auditory Capsule.

The *auditory capsule* again takes a large part in the formation of the side walls of the cranium (figs. 12 and 13), and the foramina are therefore in very much the same positions as in Stage II. These will be described and seen more clearly in the special model of the cast of the cartilaginous labyrinth which was prepared by PALMER (figs. 18 and 19). The cochlea (*coch.*) shows distinct advance on the Cynodont condition of Stages II and III. The slight bend has become a coil, and the adult spire is about half-formed. The vestibular and sacculo-utricular regions show no special features, but in the external view (fig. 19) the fenestra ovalis (*fen.o.*) is seen above, and the fenestra rotunda (*fen.r.*) below. Since the model represents the cast of the inside of the labyrinth the fenestræ are represented by projections, and these have been coloured black in the models to show up against the rest of the model, which is painted white. In the internal view (fig. 18) the *internal meatus* differs from that of Stage II in that it is divided by a bar of cartilage which forms a separate entrance for the branches of the auditory nerve, the vestibular branch entering by the upper foramen (*n.vest.* VIII), and the cochlear branch by the lower (*n.coch.* VIII.). Posteriorly to the foramen for the cochlear nerve is the cast of the ductus endolymphaticus (*d.e.*), passing through the opening of the *aquæductus vestibuli*. Coming off from the utricular region are the three semi-circular canals (figs. 18 and 19, *c.v.a.*, *c.v.p.*, *c.h.e.*). Their form is exactly as in the adult. The external canal is particularly well shown, and the ampullæ of all three are well reproduced. The aquæductus vestibuli opens at the base of the commissural canal or sinus utriculi superior (*s.u.s.*); its opening is relatively smaller in the model than in that of Stage II. The bar of cartilage roofing the aquæductus Fallopii is of considerable thickness (fig. 9).

The *tegmen tympani* (figs. 12 and 13, *t.ty.*) again sends forward a rod of cartilage the stylohyale (*st.hy.*), which is shorter and even more slender than in Stage II.

The *fossa subarcuata* (*f.s.*), or fossa floccularis, is of some depth, to accommodate the increase in size of the floccular lobe of the cerebellum. The fossa is oval in shape, but still small when compared with that of Stage V.

Olfactory Capsules.

The olfactory capsule in this specimen is relatively larger in proportion to the total length of the skull. Comparisons as regards size cannot be made between these two models, as Stage II is of a specimen of *P. obesula*, and Stage IV of *P. nasuta*. However, such comparisons can be made between Stages IV and V and the adult, and it is interesting to notice the head assuming the adult characteristics. Stage IV might be described as short or even snub-nosed; Stage V has a decidedly long nose, which is only outdone by the adult, whose olfactory organs are still longer in proportion. As yet no ossification has taken place.

The *lamina infracribrosa* is stouter, and with the development of the cribriform plate the nasal capsules have the appearance of being closed in; the cribriform plate, however, still consists to a greater extent of fenestræ and membrane than it does of cartilage.

The projections on the paries nasi, representing the turbinals, are of considerable size, and the *ethmoturbinals* (*eth.*) are already complicated in structure, and are connected with the lamina infracribrosa and with the cribriform plate. The *maxillo-*

turbinals are clearly to be seen, though as yet they are only small outgrowths on the paries nasi, and show no great complication.

The *nasal capsule*, with the exception of the anterior palatine foramen, is completely floored by the secondary palatal plates of the maxillæ, which articulate in the middle line.

The *paraseptals* (fig. 10, *proc.p.*) are short and extend no further back than some six or eight sections behind the anterior palatine foramen (fig. 10). The palatine processes of the premaxillæ are larger than in the last model, they reach almost to the back of the anterior palatine foramen, also they are beginning to enwrap the paraseptals, thus forming a double-walled capsule for Jacobson's organs. There is an increase in size of the processus alaris superior (*proc.a.s.*) to be noted and a strengthening of the processus lateralis anterior (*proc.l.a.*).

Meckel's Cartilage, Auditory Ossicles and Dentary.

The changes in the *lower jaw* consequent upon development are interesting and worthy of a detailed description in spite of the fact that they have been previously described by PALMER (35). At this stage *Meckel's cartilages* appear to occupy quite a secondary place in the formation of the lower jaw; they no longer meet at the anterior end but have shrunk back and are not seen in the sections until No. 70 (fig. 12). Each is also much slighter, and in section is quite small and almost circular. Between the anterior ends and separating the dentaries is a median mass of cartilage (fig. 11) which, from the sections, would appear to have no connection with Meckel's cartilage but to be merely the early representation of the symphysial cartilage. As in Stage II, Meckel's cartilage passes imperceptibly into the *malleus*. In comparison with the size of the skull this is much smaller than in the young stage, and it is more elaborate in form. The articulating surface for the incus is deeply concave (fig. 17), the manubrium, now ossified, has what PARKER has termed the auxiliary process formed in cartilage. The *incus* (*i.*) also is much more differentiated and more highly developed; the crus longum (*c.l.*) is appreciably longer than the crus breve (*c.b.*). The *stapes* (*st.*) is chondrified and has assumed an almost typical, though short, columella form. It consists of a disc of cartilage fitting the fenestra ovalis so closely that it is easy to appreciate the old simple but erroneous theory that the stapes is a severed portion of the auditory capsule. From the disc there passes outwards a short thick bar of cartilage which articulates with the crus longum of the incus.

The *dentary* is the most important part of the lower jaw from this stage onwards. It is now almost massive in parts. There is no symphysis. At some little distance behind the anterior end of the dentary a groove is formed on the lower internal side, it is in this groove that Meckel's cartilage lies. Here the dentary is below the latter. From this point the upper side of the groove becomes thick, and grows upwards, thus making with the main lamella of the dentary the mental canal, as yet open, but which will be seen to be closed in certain places in the model of Stage V On the same vertical plane as the posterior ends of the palatines the dentary is again produced below Meckel's cartilage; the dorsal side of the part of the dentary forming this groove in which Meckel's cartilage has lain terminates a short distance behind this, so that in section the dentary is a curved lamina of bone enfolding Meckel's cartilage. The posterior portion of the dentary shows a great advance on the previous stage; the *coronoid* is well developed, there is a deep *sigmoid notch* bounded below by a conspicuous *articulare.* The angle is small and only slightly inflected.

Two other bones are present in the lower jaw, both having been described by PALMER (35) and GAUPP (23). Lying ventral to Meckel's cartilage and forming a trough in which the cartilage rests is the *goniale* of GAUPP, or as it is named by other writers the *prearticular.* There is no doubt that GAUPP's interpretation of this bone is correct, and that PALMER is wrong in terming it the supra-angular. The bone, as mentioned above, enfolds the base of Meckel's cartilage and is pierced by the foramen for the chorda tympani as shown in GAUPP's figures. The second bone to be described in this connection is the *tympanic.* In this stage, 11·0 mm. head length, it is triradiate, the two dorsal radii running parallel and ventral to the prearticular, while the third arm, which persists in the adult together with the posterior dorsal portion, forms a semicircular rod of bone with the concavity towards the back of the skull.

Palate and Upper Jaw.

The *palate,* beyond the fact that the palatal plates of the maxilla now meet in the mid-ventral line, is little changed. The anterior palatine foramen is seen bounded posteriorly, and for the most part laterally, by the palatal plates of the maxillæ. The posterior palatine foramina are seen bounded by the maxillæ and the palatines; they are very different in appearance to those of the adult, as they are small and some distance from the middle line. Also, the palate being much arched laterally, they open inwards and not downwards as in the adult.

The *premaxillæ* are now important bones, the tooth groove is deep and the septa between the loculi are high. The premaxilla passes up the side of the nasal capsule, almost meeting the nasals.

As stated before the palatal plates of the *maxillæ* articulate in the middle line. The tooth groove is deep and the ridges on either side well marked. The palatal surfaces of the maxilla are strongly arched. The infraorbital nerve is now enclosed by the maxilla and passes to the lateral side of the nose by means of the infraorbital foramen.

The *palatines* are much more highly developed in this stage, they have greatly extended in length, and have also sent up a considerable ascending plate which, however, does not yet enclose the sphenopalatine foramen; this is bounded on the dorsal side by the paries nasi. The secondary palatal plate or pars horizontalis of the palatine is strongly developed. The dorsal shafts of the palatines curve to the centre, meeting the basis cranii, and with it and the secondary palatal plate form the two tubes for the naso-pharyngeal ducts.

The *vomer* at this stage extends from the posterior end of the paraseptals to the anterior end of the lamina infracribrosa. It has thickened in a dorso-ventral direction, and enwraps the base of the nasal septum. No foramina or fenestræ are present similar to those observed in two specimens of Macropus (sp. ? ; head length ?). The vomers in these specimens of Macropus, kindly lent by Prof. ELLIOT SMITH, have two large median fenestræ, anterior and posterior. There is no indication whatever that the vomer is paired. The fenestræ are clearly openings in a single median bone, and not foramina formed by the imperfect fusion of a paired structure.

The *pterygoids* articulate with the basis cranii, and send down quite a stout process about midway of their length.

The *lachrymals* show an increase in area. They are produced dorsally on the anterior border of the orbit. The hamular process is short, and does not meet the maxilla (fig. 13). The facies orbitalis is not developed. The foramen for the nasal duct is small (*for.l.*), and, as is frequently the case in Marsupials, it is external to the orbit.

The *nasals* are small, delicate bones, lying closely applied to the dorsal surface of the tectum nasi, extending through about fifty sections. They do not articulate with one another along the mid-dorsal plane, and the tectum nasi is seen between them. Neither do they articulate with premaxilla or maxilla, although they extend a considerable distance laterally, and come very close to them. There is no absorption of the tectum nasi to be noted.

The *frontals* (*f.*) are large, and, in certain places, massive bones, which, however, are far from articulating with each other in the middle line. A large fontanelle still remains between the posterior margin of the frontals and the anterior margins of the parietals; this is the *anterior fontanelle* or *fonticulus frontalis* (*fon. f.*). Anteriorly, the frontals do not extend farther forward than the foramina epiphanialia, the posterior border of the nasals being about twenty sections anterior to this. Laterally, the orbital surfaces of the frontals cover the external surface of the commissura orbitoparietalis, and in one place, immediately anterior to the orbitonasal process, they extend beneath it, forming part of the lateral wall of the skull.

The *parietals* are very thin, delicate bones, roofing the posterior part of the skull, but are widely separated at their anterior ends, forming the anterior fontanelle. The parietals as yet do not articulate with the frontals.

The *squamosal* is present in this stage as a thin bone covering the junction of the lamina supracapsularis with the auditory capsule. It conceals part of the incus. The zygomatic process passes forwards, overlapping both the coronoid process of the dentary and the jugal, but not yet articulating with the latter. A large foramen is present, piercing the squamosal immediately above the incus.

The *jugal* is a small, flake-like bone, which extends between the zygomatic processes of the maxilla and the squamosal, but as yet it does not articulate with either. It should be pointed out that, so far, the posterior portion, which will form a long articulation with the zygomatic process of the squamosal, even taking part in the formation of the glenoid cavity, is quite short.

The "hyoid apparatus" shows relatively little change to that described above, the chief difference being that the ventral anterior edge of the cricoid has fused with the base of the body of the thyroid. It should be noted that the internal processes of the arytenoids are no longer united (fig. 16).

Description of Sections.

Fig. 37 shows the organ of Jacobson protected by the processus paraseptalis. The increase in size and importance of the processus palatinus of the premaxilla is also demonstrated. The ductus naso-lacrimalis (*d.n.l.*) lies between the maxilla and the paries nasi. The lamina-like nasal (*n.*) is dorsal to the tectum nasi.

Fig. 38.—The great increase in area of palatine process of maxilla and the depth of the alveolus is clearly shown in this figure. The vomer (*v.*) is seen ventral to the septum nasi. The swollen appearance of the paries nasi indicates that the section is from near the region of the processus maxillaris posterior.

Fig. 39.—The ala temporalis is partly ossified; it lies between the fifth nerve and the Gasserian ganglion (*g.g.*). The dentary is now of considerable thickness; its ventral portion curves inwards, and, as it were, supports Meckel's cartilage. The mental nerve (*n.m.*v.) lies dorsal to this. The jugal appears as an oblique flake of bone external to the dentary.

Fig. 40.—This diagram illustrates the extent of the ossification of the ala temporalis to form the alisphenoid; the basal portion only consists of cartilage. The dorsal border of the alisphenoid approaches the commissura orbito-parietalis, but does not actually articulate with it.

Fig. 41.—The alisphenoid in this more posterior section articulates with the commissura orbito-parietalis. The arteria carotica interna (*a.c.i.*) lies in the foramen caroticum, which is situated between the basis cranii and the basal portion of the ala temporalis. The hypophysis is a large body dorsal to the basis cranii. The dentary is more delicate near the posterior border and the jugal also shows a decrease in thickness.

Fig. 42.—This section is through the region of the aquæductus Fallopii, which is dorsal to the pars cochlearis of the auditory capsule. The pars cochlearis is separate from the basis cranii. The septum spirale is now completely chondrified (*s.s.*). Different portions of the ossicles can be seen, the oval-shaped malleus with the trough-shaped pre-articular lying immediately below it. The manubrium of the malleus is a small circular mass exterior to the long cavum tympanic. Ventral to the pre-articular is the anterior bar of the tympanic. To the outside of the

malleus is the articular of the dentary, and dorsal to this is the zygomatic process of the squamosal.

Fig. 43.—The now perfectly chondrified stapes is seen lying in the fenestra ovalis; it does not, however, articulate with the crus longum of the incus. The crus breve is situated in close connection with the squamosal, and lies in a hollow of the pars vestibularis of the auditory capsule. The increase in area of the lamina supracapsularis is to be noted, and also the downward growth of the parietal which overlaps the lamina. The squamosal is a thin sheath of bone covering the lateral portion of the pars vestibularis.

Fig. 44.—The plane of this section is through the foramen lacerum posterius (*for.l.p.*) and ventral to this lie the ninth nerve and the jugular vein. The twelfth nerve is seen passing through the foramen nervi hypoglossi (*for.n.h.*). The seventh nerve is to be observed lying in the sulcus facialis, which is protected laterally by the tegmen tympani.

Stage V. (Plates 31 and 34.)

This skull is in many ways similar to that of the adult. It is much longer in proportion to that of Stage IV, and this is in a great part due to the growth of the nasal capsules and also to the flattening of the base of the skull.

Chondrocranium.

The cranium is almost completely roofed over by the membrane bones; the foramina and fontanelles of the skull are becoming reduced, and the former are more in proportion to the size of the nerves and vessels passing through them.

The basioccipital ossification has not spread appreciably. The pituitary fossa is smaller than in Stage IV, and is now surrounded by bone, the basisphenoid having extended forwards. No ossification of the presphenoid is present, but the presphenoidal region of the basis cranii is much elongated.

The *orbitosphenoidal* cartilage still shows no sign of ossification. The ala orbitalis remains comparatively narrow while the commissura orbitoparietalis and the lamina supracapsularis are even greater in area than was observed in Stage IV (fig. 23). The *processus orbitonasalis* has increased slightly from before backwards, and with the downward growth of the orbital plate of the frontal the fissura orbitonasalis is much reduced in size (fig. 24).

The *alisphenoid* is, in this stage, one of the most important bones forming the lateral walls of the cranium. The posterior portion, ossified in membrane, articulates dorsally with the commissura orbitoparietalis along the whole extent of the bone, which now considerably overlaps the pars cochlearis of the auditory capsules. The processus basipterygoideus is still unossified.

Auditory Capsule.

The *auditory capsule* is little changed; its position with regard to the base of the skull is relatively the same. The fossa subarcuata has increased in depth. The cochlea is more coiled and closely approaches the adult condition. The stylohyale is still further reduced.

Olfactory Capsule.

The *olfactory capsules* have again increased in length, as seen in the diagrams. Further complications have taken place in the internal structure which cannot be seen from the outside owing to the growth of the lamina cribrosa. This, with the tectum nasi, roofs the capsules, and the secondary palatal plate completes the flooring. The capsules, therefore, consist of two tubes separated by the imperforate nasal septum, each wider about the middle of their length at the *processus maxillaris posterior* (fig. 20, *proc.m.p.*), tapering in front and opening by the anterior nares and narrowing behind towards the lamina infracribrosa. The capsules can be divided for descriptive purposes into two parts, the pars anterior lying ventral to the tectum nasi, and the pars posterior ventral to the lamina cribrosa. In the pars anterior the ventral enlargement of the paries nasi indicates the positions of the rudiments of the maxilloturbinal. This is, however, but slightly developed and extends for only a short distance. Its inner surface is flattened but not bifurcated. The anlage of the nasoturbinal projects forwards and inwards from the lateral wall of the paries nasi behind the processus maxillaris posterior (*n.t.*) dividing the nasal cavity into the recessus lateralis and the recessus posterior or ethmoidalis. In its turn, the recessus lateralis is divided into two portions by a vertical fold of the paries nasi. This encloses the recessus lateralis inferior, which is extended backwards into a narrow cavity, the sinus maxillaris. Considering now the recessus posterior or ethmoidalis, this contains the anlage of the ethmoturbinals, which are seen as projections of varying size on the walls of the posterior portion of the nasal capsule.

Still further reduction has taken place in the size of the *paraseptals* (fig. 21), the palatine processes of the premaxillæ completely enfold them and are continued for some little distance behind them. In the ventral view, therefore, they are completely hidden and the anterior palatine foramen is bounded on all sides by bone and has more of the slit-like appearance of that of the adult.

Lying ventral to the palatine process of the premaxillæ and giving support to the papilla is the *papillary cartilage*. This has been fully described and figured by Broom (2) in a 21·0 mm. head length fœtus of *Perameles nasuta*.

Meckel's Cartilage, Auditory Ossicles, and Dentary.

Meckel's cartilage does not extend farther forwards than Section 228. When first observed it is a small group of cells at the base of the V-shaped dentary. A short distance behind this Meckel's cartilage pierces the inner lamella of the dentary and runs back as a thin bar of cartilage lying on the inside of the dentary. The *manubrium of the malleus* (fig. 28) has increased in size and complication; it is now almost completely ossified. The *incus* is little changed, but the *stapes* has further developed and now articulates with the incus.

The chief points to be noted in the *lower jaw* are the development of the dentary and the great decrease in size and extent of Meckel's cartilage. With regard to the *dentary*, the internal lamella is now formed, so that in section the dentary shows itself as a deep trough of bone with the mental canal running through it at the bottom. The mental canal is at one point roofed over, but in most places it is as yet open, indications of the roof being seen in the ridges on the bone which will grow out and eventually meet. The septa between the alveoli are not yet formed. Anteriorly the dentaries project forwards as three prongs, a deep notch at the base of each dividing one half from the other. The posterior end of the dentary is very similar in form to that of the adult. The *coronoid process* (fig. 24, *cor.*) is high and the notch consequently deep. The angle is larger and more inflected. The articular condyle has greatly increased in size and, as GAUPP (21) has figured it, it mainly consists of cartilage. This is of no morphological significance, as cartilage is frequently found in the extremities of many membrane bones, not only of the skull but of the visceral skeleton.

Near the anterior end, between the right and left dentaries, is the median mass of cartilage (fig. 22) observed in Stage IV, while posterior to this is a small pair of cartilages which may possibly be the remains of the anterior end of Meckel's cartilage

The tympanic is no longer triradiate, the anterior ramus having disappeared. The bone, therefore, consists of two rami, or rather somewhat approaches the semicircular form of the adult tympanic. The dorsal bar extends posteriorly as far as the back of the condyle and the ventral portion has greatly increased in length and is also stouter than that observed in Stage IV. The posterior limit of this ventral portion of the tympanic is on the same plane as the articulation of the malleus and incus. The pre-articular has remained unchanged.

Palate and Upper Jaw.

The condition of the *palate* has little advanced from that observed in Stage IV. Great elongation to accommodate the lengthening olfactory capsule has, of course, taken place. The surface is flattened antero-posteriorly, but the maxillæ and palatines are still strongly arched laterally.

There is still no indication of the characteristic fenestration of the posterior portion of the palate of the adult; the posterior palatine foramina are small (fig. 21, *for.p.p.*).

The *premaxillæ* and *maxillæ* have increased in extent and importance; the tooth grooves are deeper, but there is no point of particular interest to be noted.

The *palatines* have extended greatly in length, and the spheno-palatine foramen is now entirely surrounded by the palatines, the ascending plate having still further developed.

The *vomer* is a comparatively massive bone; thickening has taken place in a dorso-ventral direction. Its length is proportionately the same as in Stage IV.

The *pterygoids* have become more massive and have lengthened, assuming the proportions found in the adult. The process is prominent, though curved towards the middle line rather than outwards, as in the adult.

The *lachrymal* at this stage shows great development, the crista and the hamulus are large, the latter articulating with the zygomatic process of the maxilla, and also with the jugal. The facies orbitalis is large, and articulates with the vertical plate of the palatine.

The *nasals* show much greater development, and they now roof over a considerable portion of the capsule extending from Section 92 to 215, and articulating laterally with the premaxilla and the maxilla, and posteriorly with the frontals (figs. 20 and 24). On the dorsal surface they all but meet in the middle line. The nasals above and the premaxillæ below and laterally form a kind of tube, out of which the cartilaginous rostrum projects as in the adult *Perameles nasuta*.

The *frontals* have extended vertically, and almost entirely close the space between the orbitonasal and the paries nasi, leaving only a slit-like foramen between the orbito-nasal process and the basis cranii (fig. 24).

The *parietals* at this stage cover a very large area, extending from Section 470 to 710; from Section 500 to about Section 700 they completely roof over the skull (fig. 20). Laterally they cover the lamina supracapsularis (fig. 24), and extend as far as the dorsal boundary of the auditory capsule. Anteriorly the parietals are very thin and delicate; posteriorly it becomes thicker, and is in some places almost massive.

Between the posterior borders of the parietals and the tectum posterius is the *posterior fontanelle*, much reduced in size.

The *squamosal* has developed mainly in a dorsal direction, so that it approaches very near to the downwardly-growing parietal. The anterior end of the zygomatic process now articulates with the jugal (fig. 24).

The *jugal* shows considerable elongation anteriorly, but the portion articulating with the zygomatic process of the squamosal is still very short compared with that of the adult.

Hyoid Apparatus.

With the gradual flattening of the base of the skull the *hyoid apparatus* has also become more horizontal. This gives it a different appearance from that of the previous stages, but on examination the cartilages are seen to be little changed. The thyroid has become more concave (fig. 26), corresponding closely to SYMINGTON's description of the same structure in Marsupialia (43).

Descriptions of Sections.

Fig. 45.—Further growth has taken place in the size and importance of the processus palatinus of the premaxilla, and it offers the main support of the organ of Jacobson. The articulation of the nasal and maxilla is to be observed. The tectum nasi and the paries nasi have decreased in relative thickness.

Fig. 46.—This section is taken near the posterior end of the organ of Jacobson. The processus palatinus of the premaxilla alone forms the support for the organ of Jacobson. The *vomer* (*v.*) has increased in thickness, and lies ventral to the base of the septum nasi. The deep tooth groove of the maxilla is very striking.

Fig. 47.—The alisphenoid has extended, and articulation takes place between it and the commissura orbitoparietalis. The pterygoid, with its incurved process, is seen in section. The zygomatic process of the squamosal approaches the posterior portion of the jugal, but so far there is no actual articulation visible.

Fig. 48.—This section is in the plane immediately posterior to the foramen rotundum. The alisphenoid is a thin lamina of bone, forming a considerable portion of the lateral wall of the skull. The ossification of the basis cranii forming the basisphenoid is internal to the base of the alisphenoid. The squamosal and the jugal are in relatively the same position as in the last figure.

Fig. 49.—The section here represented, like the corresponding figure of Stage IV (fig. 42), passes through the aquæductus Fallopii. The malleus is more elongated, and its ventral side lies in the trough formed by the prearticular. The basal portion of the tympanic is situated at the ventral side of the cavum tympani. The manubrium of the malleus (*m.mal.*) is dorsal to this tympanic and to the outside of the cavum tympani. The squamosal is pierced by a large foramen through which passes a branch of the occipital portion of the external carotid. This foramen appears to be of unusual size in the Marsupialia.

Fig. 50.—The plane of this section is through the fenestra ovalis, which is almost closed by the columelliform stapes. This articulates with the incus (*c.i.*). The crus breve (*c.b.*) is to the inside of the squamosal. The foramen acusticum internum on the inside of the auditory capsule serves as the exit from the cranium for the eighth nerve. This is seen lying inside the auditory capsule.

Fig. 51.—The foramen jugulare spurium separates the lamina supracapsularis from the pars vestibularis of the auditory capsule (*for.j.s.*). The extent of the ossification of the exoccipital is to be observed.

Stage VI.

Great increase of development is to be noted in all structures. The ossification of the basisphenoid extends further caudally. The presphenoid is partly ossified, but does not occur as an independent cartilage, as described by Gregory (24). The ossification of the exoccipitals has continued. The pituitary foramen persists, but is much reduced in size. The alisphenoid articulates with the frontals on both dorsal and anterior boundaries; also with the squamosal posteriorly, thus forming an almost complete side wall to the skull, closing the fissura orbitonasalis and leaving only the foramen lacerum anterius and medium, the foramen rotundum, and the foramen sphenopalatinum for the passage of nerves, etc. The processus basipterygoideus of the ala temporalis still remains unossified.

Anteriorly the commissura orbitoparietalis is much reduced in size in every direction, but farther back it is a massive bar of cartilage, and at its ventral side there is some indication of the ossification of the orbitosphenoid. Ossification of the auditory capsules has begun from two centres—one at the base of the pars canalicularis, and the other in the region of the aquæductus Fallopii. The aquæductus vestibuli is still further reduced.

With regard to the nasal capsules, ossification has begun in the naso-turbinals. In the region of the recessus lateralis superior there is an absorption of the paries nasi. The maxilloturbinals are bifurcated. The median mass of cartilage is again seen between the two rami of the lower jaw. Meckel's cartilage shows still further reduction. The hyoid is partly ossified.

Conclusions.

Paraseptal Cartilages.—Some doubt has prevailed as to the exact origin of these cartilages, and it is therefore important to consider them in greater detail. Parker supposed that they were the recurved ends of the trabeculæ, hence the meaning of the term he uses, "recurrent cartilages." That is, Parker considered that the recurrent cartilages belonged to the nasal septum. Broom (4) has challenged this statement, and in *Perameles* it seems clear that they are processes of the lamina transversalis anterior, and have no connection with the nasal septum.

As already mentioned in the descriptions of the models of *Perameles*, the paraseptals are cartilaginous rods given off from the lamina transversalis anterior, passing backwards parallel to the base of the nasal septum and ending in free points, the length of the cartilage decreasing in proportion with the increasing size of the specimen. In all stages of the *Perameles* examined the paraseptals end in free points and do not unite with the back of the nasal capsule.

With regard to the length of the paraseptals there appears to be considerable variation amongst the genera of the Marsupialia. Broom, in his description of the 10·0 mm. *Trichosurus*, describes the paraseptals as extending to the posterior wall of the nasal capsule in a procartilaginous state. In this case, however, as shown by the examination of older stages, this condition is observed to be a characteristic of the young specimens only. The paraseptals in a 13·0 mm. stage consist mainly of cartilage in the posterior extremity, and in a 17·5 mm. fœtus they are in a condition similar to that described in *Perameles*, and do not unite with the back of the nasal capsule but end in free points extending about half way along the total length of the nasal capsule.

Through the kindness of Prof. HILL several stages of *Dasyurus* were available for examination. From these it would appear that the 8·0 mm. specimen described by BROOM was atypical in this respect, and in all the stages examined, 6·5 mm., 8·0 mm., 13·5 mm., 17·0 mm., and 20·0 mm., the paraseptals are in each case continued to the back of the nasal capsule. In the two early specimens the posterior portion is procartilaginous, but in the older stages they gradually become thick massive bars of cartilage passing imperceptibly into the posterior portion of the nasal capsule.

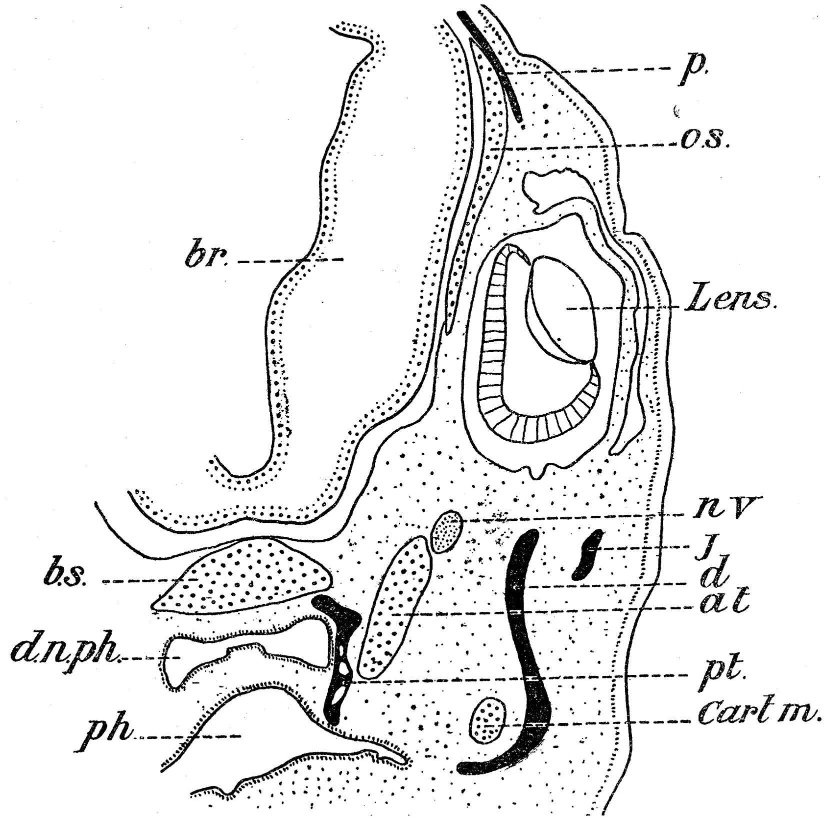
Ala Temporalis.—In his work on the development of the skull in Insectivora, W. K. PARKER brings forward the view that the invariable position of the alipshenoid cartilage in the Eutheria, *i.e.*, a position exactly as in *Perameles*, is due to the great development of the brain. He states that outward pushing has not occurred in Marsupials and makes its position a diagnostic character of the Eutheria. That this is a mistaken view there can be no doubt. In the models under discussion the cartilage is exactly in the Eutherian position, and BROOM has found it similarly placed in Dasyurus and in Trichosurus. The explanation of PARKER'S misconception is that the alisphenoid cartilage is not a "neural" element that has been pushed out from the wall of the skull, but it is in reality a "visceral" element that has been pushed in to form a secondary wall. BROOM has shown this clearly, maintaining that it is homologous with the reptilian epipterygoid. The *Perameles* material certainly supports this contention. The similarity in the position of the cartilage to that of the epipterygoid of Reptiles is indicated in the accompanying drawings of sections, the first from Perameles and the second from Sphenodon.

In the 12·25 mm. specimen of *Perameles* the ala temporalis consists of two small masses of cartilage on either side of, and in the same vertical plane as, the basis cranii in the region of the pituitary foramen. As already described, in the later stages this develops, until the ala temporalis can be described as a large vertically placed band of cartilage united below with the basis cranii and consisting of the basipterygoideus and the lamina ascendens. Later, by ossification the lamina ascendens is converted into bone and unites imperceptibly with a vertically placed plate which is ossified in membrane and which extends posteriorly and later articulates with the squamosal.

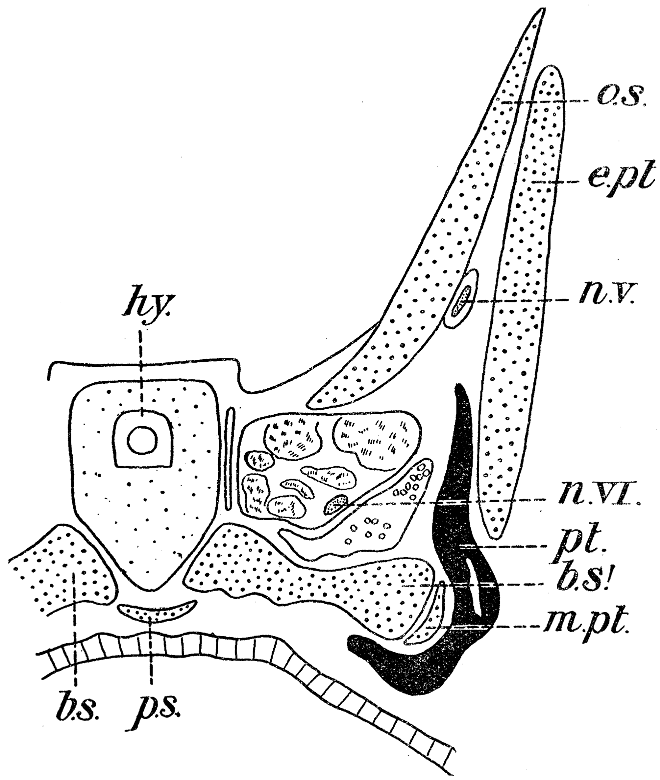
This seemingly compound formation of the alisphenoid is, however, of no morphological significance and the difference in the method of formation of the two portions of the bone cannot be said to indicate that the alisphenoid is a compound bone.

This mode of ossification of the alisphenoid is to be observed in the other examples of the Marsupialia, *Trichosurus*, *Dasyurus*, and *Macropus*. It is to be noted that the portion of the ala temporalis which chondrifies first is the portion which ossifies latest.

Variation is found in the shape of the processus basipterygoideus. BROOM describes this in *Trichosurus* and *Dasyurus* as being a horizontal rod of cartilage. This is not



TEXT-FIG. 1.—Section of *Perameles*, through the ala temporalis, Stage IV, No. 287.



TEXT-FIG. 2.—Section of Sphenodon through the epipterygoid. (After HOWES and SWINNERTON.)

the case in Perameles, where this portion is no larger antero-posteriorly than the lamina ascendens which passes upwards from it. *Macropus* and *Phascolarctos* are in this respect similar in form to that of *Trichosurus*.

The Palatine Process of the Premaxilla.—The specimens of Perameles examined add further proof to the statement that the palatine processes of the premaxillæ are true processes of that bone, and are very definitely continuous with it. But it is also interesting to note that they are in the same position as, and indeed replace in position and function, the prevomers of the Reptiles. It should be noted that with the relative decrease in size and importance of the paraseptals there is in the stages of Perameles examined a corresponding increase in the palatine processes of the premaxillæ. (See BROOM, 1.)

The Cartilages of the Larynx.—The cartilages of the larynx in the Marsupialia are of special interest owing to the secondary changes which take place during development. Though the specimens of *Perameles*, at present under consideration, do not show any further peculiarities, they confirm the facts and theories already known, and, so far as the writer is aware, it is the first series that has been figured.

These secondary changes, as already stated, are the fusing of the cricoid with the body and also with the posterior cornu of the thyroid. This results in the stiffening of the whole apparatus, rendering the larynx very inflexible. SYMINGTON and OPPEL (43 and 32) pointed out that this condition is correlated with the voiceless condition of most of the Marsupialia.

Among the specimens of the Marsupialia examined, there is a striking difference in the attachment or non-attachment of the hyoid to the base of the skull. As described above, the hyoid of *Perameles* does not articulate with the skull, and the representative of the stylohyale becomes shorter in proportion as the creature increases in size. The same thing has been observed by BROOM in *Dasyurus*, another Polyprotodont. In the specimens of *Dasyurus* examined recently there is the same decrease in size of the stylohyale. Three examples of the Diprotodontia, *Trichosurus*, *Macropus*, and *Phascolarctos* show just the reverse condition, and the hyoid articulates with the skull by means of the stylohyale. Whether this is a coincidence or not can only be ascertained by the study of further examples of the two sub-orders of the Marsupialia.

The Auditory Ossicles.

Descriptions of the ossicles of the three models have been given already, but it is instructive to draw comparisons between the different stages. The models illustrate very clearly the kind of evolution which the ear ossicles have undergone, and they indicate very strikingly the change of function which has been accomplished. In figs. 4 and 5 Meckel's cartilage is seen to take a very definite and important part in the formation of the lower jaw. In fact, it might be said that the lower jaw consists mainly of Meckel's cartilages. The portion that has been termed the *malleus* is continuous with the general cartilage, and, from a study of the sections, it can only be considered as the articulare of Meckel's cartilage. By methods of comparison the same conclusion is reached, that is to say, the malleus is the modified articulare of the rod of cartilage known as Meckel's cartilage. This theory rests upon considerable evidence, which is clearly emphasised by many writers, and especially by REICHERT, KINGSLEY, and GAUPP. The proofs put forward in support of this hypothesis are based upon the examination of the morphological relation of the embryonic stages of Mammals compared with the conditions observed in Reptiles. The continuity of the malleus with the Meckelian cartilage is one of the most important facts in the chain of reasoning. The malleus is merely the specialised articular surface of the Meckelian cartilage, just as the articulare is the articulating surface in the lower jaw of an embryonic reptile, as figured by GAUPP in an embryo *Lacerta agilis* (21, fig. 7). The Perameles material examined bears this out to the full. There is no indication whatever that the conditions differ from those of all other mammals examined.

The manubrium of the malleus in the specimens of *Perameles* examined is a definite part of the malleus. Chondrification of the manubrium takes place later than that of the malleus, but the manubrium chondrifies as an extension of the malleus, and not as a separate portion which later fuses with the body of the malleus. This condition is in accordance with that described by MEAD in Sus (31, p. 188), by FISCHER in *Talpa europæa* (13, p. 501), and by BROOM in his figures of Trichosurus and Dasyurus (4, figs. 11A and 26B). The theory that holds that the malleus is derived from the extra columella is questioned by GREGORY (24, p. 133), and, from comparisons of relative positions, it would seem that there is little doubt that the "articulare theory" is the more correct.

The malleus articulates with the *incus*, and, according to the malleo-articulare theory, it would follow that the incus is homologous with the quadrate. The articulation of the malleus and incus would therefore correspond to the joint between the articulare and the quadrate. The position of the incus, lying as it does dorsal to the stapes, external to the cochlea, and internal to and in close connection with the squamosal, seems to give proof to the quadrate homology.

The form of the *stapes* in *Perameles* is primitive. It is columelliform and imperforate, resembling more nearly its homologue, the proximal portion of the columella auris of Reptiles and Amphibians.

COMPARATIVE STUDY OF THE PRIMORDIAL SKULL OF PERAMELES.

(a) *Comparison with the Cynodontia.*

It is generally admitted that the Cynodontia foreshadow the Mammalia, and that it is quite unnecessary to search among the Amphibia for the immediate ancestors of the Mammalia. The large body of evidence brought forward by OSBORN and BROOM in favour of this view is derived from the general consideration of the order, and not from any particular form. In the study of the lower mammals, and, on the present occasion, of Perameles in particular, it is therefore essential to see how far the theory is supported. For though it may be important to observe how far the Cynodontia foreshadow the Mammalia, it is also very necessary to note the way in which the lower Mammalia retain traces of their ancestry.

The lower jaw of the embryo *Perameles* in its structure and in all its relationships is essentially comparable to that of the Cynodontia. The large, thin dentary, curved inwards, enwrapping Meckel's cartilage, has its exact counterpart, as PALMER has shown (35), in the dentary of the Cynodont. The pre-articular and the tympanic of Perameles have their parallel in the pre-articular and angular of the Reptile. The similarity is most striking, and taken in conjunction with the correspondence in the course of the chorda tympani in Perameles and in Reptiles (*e.g.*, Sphenodon and Lacerta), there is little room for doubt that Perameles, during its development, gives evidence of its Reptilian origin.

The formation of the hard palate of *Perameles* has been shown to be gradual. The palatal plates of the premaxillæ and maxillæ are practically absent in Stage I. In Stage II (fig. 2) they have a distinctly Reptilian appearance, and show great similarity to the conditions observed in Cynognathus. In Stage V and VI the characteristics of the Mammalian hard palate are exhibited without the secondarily acquired Marsupial fenestration.

The pterygoids in Perameles are much reduced in size; in fact, in the young stages they are mere flakes of bone on the ventral side of the much-enlarged processus basipterygoideus of the ala temporalis. However, in the later stages (fig. 21), in spite of the reduction in size, the pterygoids exhibit a tendency to form a plate over the ventral surface of the sphenoid. They also retain their old articulation with the palatines. Both of these may be regarded as ancient characteristics, which are retained by the more primitive of Mammals.

The articulation of the exoccipitals and the atlas is also of interest, owing to the fact that articulation is continuous between the condyles. The confluence of the optic foramen with the foramen lacerum anterius is in itself an indication of the Reptilian ancestry of the Marsupialia. It is a condition which is to be observed only in the lower Mammals.

(b) *Comparison with the Prototheria.*

The skull of *Perameles*, as depicted in the sections available for examination, occupies in many ways an intermediary position, in point of view of development, between those of *Trichosurus* and *Dasyurus*. Therefore, in several respects, there are fewer differences to be observed between the skulls of *Echidna* and *Perameles* than between *Echidna* and *Trichosurus*.

The large, massive orbitosphenoidal bar is present in both groups but in Echidna the processus orbitonasalis is very much wider than in the Marsupial. The auditory capsules of the two groups much resemble each other, and the absence of the coil in the cochlea is a common characteristic. In Echidna the foramen nervi hypoglossi is confluent with the foramen lacerum posterius.

The conditions of the laryngeal cartilages of the adult Marsupial are much modified, but it is interesting to observe the great similarity between the hyoid apparatus of the embryo Echidna and a very young specimen of Perameles before the dorsal fusions have begun to take place.

(c) *Comparison with Trichosurus and Dasyurus.*

The interest of the study of *Perameles* is greatly increased when comparisons are made with the descriptions of the embryo skulls of *Trichosurus* and *Dasyurus*, published by Broom. There is a great general similarity and there are evidently no very striking differences between the skulls of Diprotodontia and Polyprotodontia. As might be expected, those of *Dasyurus* and *Perameles* have more in common than those of *Trichosurus* and *Perameles*, and from general considerations it would seem that *Perameles* occupies an intermediate position between the two. This has been indicated in several ways in the following structures: The formation of the solum nasi or floor of the nasal capsules; the position of the premaxilla with regard to the anterior nares; the paraseptal cartilages and the attachment of the hyoid apparatus to the skull.

The orbitosphenoidal bars are strikingly alike, and the processi orbitonasales are proportionately of corresponding size. There is rather a marked difference in the formation of the base of the ala temporalis. In both *Trichosurus* and *Dasyurus* the base is long antero-posteriorly, but in *Perameles* it is no longer in this direction than the rest of the cartilage (fig. 4).

In all three forms, the ala temporalis or the alisphenoid cartilage occupies the Eutherian position with regard to the plane of the orbitosphenoid, and they all agree in the method of ossification of the alisphenoid, *i.e.*, partly from membrane and partly from cartilage.

The condition of the auditory ossicles is much the same and the pre-articular is present in each genus.

The twelfth cranial nerve leaves the cranium by two pairs of foramina.

There is altogether much similarity and the main differences are those of proportion consequent upon the generic characteristics.

(d) *Comparison with Higher Mammals.*

In a comparison of the models of the embryos of *Perameles* with the descriptions and figures of those of the higher Mammals, the primitive characters exhibited by the Marsupial are well brought out.

Already some of these ancient characters which indicate a Cynodont inheritance have been mentioned: The condition of the lower jaw, the early stages of the hard palate, the pterygoids; the articulation of the atlas and the confluence of the optic foramen with the foramen lacerum anterius. Besides these there are other indications that the Marsupial chondrocranium is on a low plane in the Mammalian evolution. Perameles proves to be no exception in this way to the group to which it belongs.

The foramen caroticum pierces the basis cranii laterally to the centre of ossification of the basisphenoid, and the internal carotid artery makes its way into the skull by this means and not by the somewhat circuitous route which is characteristic of the higher Mammals.

The presphenoid, which is observed to occur in the ossified state in Stage VI only, arises as an independent ossification in the basis cranii. It is quite separate from the centres of ossification of the orbitosphenoids, but will eventually articulate with them.

As BROOM pointed out, the Marsupial orbitosphenoid bar is much larger than in most of the higher Mammalia, and in Perameles it is a particularly solid unbroken sheet of cartilage pierced only by a very small foramen jugulare spurium. This shows a very different condition from that observed by MEAD in Sus (31). Here the orbitosphenoid is not only pierced by the optic foramen, but the posterior portion (*i.e.*, the lamina supracapsularis) is almost fragmentary when compared with that of Perameles.

The condition of the cochlea in the embryo Perameles is characteristically very different from that observed in the embryo of the higher Mammals. In the latter case the cochlea is coiled even before chondrification, thus necessitating the large size of the basal portion of the auditory capsule. In Stage II of the Perameles series only the first twist of the cochlea is to be observed. Figs. 18 and 19 demonstrate very clearly the still much undeveloped condition of the cochlea.

The auditory capsules occupy a primitive position in Perameles. They are placed laterally to the brain, and, indeed, form a great portion of the side walls of the cranium. The Eutherian position is almost ventral to the great mass of the brain.

The presence in Perameles of two pairs of foramina for the hypoglossal nerve is also a point of difference from the Eutherian conditions, where the presence of one pair only is the accepted condition.

Also in Perameles there is no clinoid process, and the concavity for the pituitary body is but little developed. The alisphenoid is, however, in the Eutherian position, and is pierced by the foramen rotundum, through which passes the second branch of the fifth cranial nerve.

Taking all into consideration, however, it is rather remarkable to observe the great similarity between the skull of Perameles and those of the higher Mammals. It might have been expected that so lowly a Marsupial would have more closely resembled the Prototheria, or that it would have revealed more evidence of its Reptilian ancestry, showing a more primitive condition as regards the structure of the skull. That this is not the case seems to point very clearly to the view that during the evolution of the Mammalia the Metatheria and the Eutheria must, for a time at any rate, have developed on somewhat the same lines after the separation of the Prototheria.

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EXPLANATION OF PLATES.

(Reference Letters.)

a.c.i. . . . . . . arteria carotica interna.
al. . . . . alveolus.
am. . . . . ampulla.
an. . . . . angulare.
a.n.e. . . . . . . apertura nasalis externa (anterior nares) (fenestra narina, GAUPP), (meatus narinus externus, FISCHER).
a.n.p. . . . . . . apertura nasalis posterior (posterior nares).
a.o. . . . . ala orbitalis.
aq.f. . . . . . . aquæductus Fallopii (foramen nervi facialis, MEAD).
aq.v. . . . . . . aquæductus vestibuli (foramen endolymphaticum, MEAD).
art. . . . . articulare.
a.s. . . . . alisphenoid.
a.t. . . . . ala temporalis.

b.c. . . . . basis cranii.
b.oc. . . . . . . basioccipitale.
br. . . . . brain.
b.s. . . . . basisphenoid.

c.a.hy. . . . . . cornu anterius ossis hyoidis (cornicula, QUAIN).
cap.a. . . . . . . capsula acustica (auditory capsule).
cap.n. . . . . . . capsula nasalis.
cart.a. . . . . . cartilago arytenoidea.
cart.c. . . . . . cartilago cricoidea.
cart.m. . . . . . cartilago meckelii.
cart.th. . . . . . cartilago thyroidea.
c.b. . . . . crus breve.
c.g. . . . . crista galli.
c.h.e. . . . . . . canalis horizontalis externus.
c.hy. . . . . . . corpus ossis hyoidis (corpus ossis hyoidei, B.N.A.).
c.l. . . . . crus longum.
c.o. . . . . condylus occipitalis.
coch. . . . . . . cochlea.
c.o.p. . . . . . . commissura orbitoparietalis.
c.p. . . . . crista parotica.
c.p.th. . . . . . cornu posterius thyroideæ (cornu caudale).
c.s.e. . . . . . . commissura spheno-ethmoidalis.
c.ty. . . . . . . cavum tympani.
c.v.a. . . . . . . canalis verticalis anterior.
c.v.p. . . . . . . canalis verticalis posterior.

d. . . . . dentale (mandibula).
d.e. . . . . ductus endolymphaticus.
d.g.n. . . . . . . ductus glandulæ nasalis.
d.n.l. . . . . . . ductus nasolacrimalis.
d.n.ph. . . . . . ductus nasopharyngeus.

e.oc. . . . . . exoccipitale.
epi. . . . . . . epipterygoid.
eth. . . . . . . ethmoturbinale.

f. . . . . frontale.
fen.b. . . . . . fenestra basalis.
fen.c. . . . . . fenestra cribrosa.
fen.o. . . . . . fenestra ovalis (fenestra vestibuli, B.N.A.).
fen.r. . . . . . fenestra rotunda (fenestra cochlearis, MEAD).
f.o.n. . . . . . fissura orbitonasalis.
fon.o. . . . . . fonticulus occipitalis (posterior fontanelle).
fon.f. . . . . . fonticulus frontalis (anterior fontanelle).
for.a.e. . . . . . foramen acusticum externum (external auditory meatus).
for.a.i. . . . . . foramen acusticum internum (internal auditory meatus).
for.c. . . . . . foramen caroticum (f. entocaroticum, GREGORY).
for.ep. . . . . . foramen epiphanialia.
for.hy. . . . . . foramen hypophyseos (pituitary foramen).
for.i.o. . . . . . foramen infraorbitale.
for.j.s. . . . . . foramen jugulare spurium.
for.l. . . . . . foramen lacrimale.
for.l.a. . . . . . foramen lacerum anterius (sphenoidal fissure) (fissura orbitalis superior, B.N.A.).
for.l.m. . . . . foramen lacerum medium.
for.l.p. . . . . . foramen lacerum posterius (foramen jugulare) (foramen metoticum, MEAD).
for.m. . . . . . foramen mastoideum.
for.mag. . . . . foramen magnum.
for.m.a. . . . . foramen mentale anterius.
for.m.p. . . . . foramen mentale posterius.
for.n.h.a. . . . . foramen nervi hypoglossi anterius.
for.n.h.p. . . . . foramen nervi hypoglossi posterius.
for.o. . . . . . foramen ovale.
for.p.a. . . . . foramen palatinum anterius.
for.p.p. . . . . foramen palatinum posterius.
for.r. . . . . . foramen rotundum.
for.s.m. . . . . foramen stylomastoideum.
for.s.p. . . . . . foramen spheno-palatinum.
f.s. . . . . . . fossa subarcuata (fossa flocculari).

g.g. . . . . . . gasserian ganglion.

hy. . . . . . . hypophysis.

i. . . . . incus.

j. . . . . os jugale (malar zygomaticum).

l.a.a.t. . . . . . lamina ascendens alæ temporalis.
lac. . . . . . lacrimale.
l.c. . . . . . . lamina cribrosa.
lens . . . . .
l.i. . . . . . . lamina infracribrosa.
l.s. . . . . . . lamina supracapsularis.
l.t.a. . . . . . lamina transversalis anterior.

mal.	malleus.
m.mal.	manubrium mallei.
m.pt.	meniscus pterygoideus.
mx.	maxilla.
mx.t.	maxillo turbinale.
n.	nasale.
n.coch.viii.	cochlear branch of viii.
n.i.o.	nervus infraorbitalis.
*n.m.*v.	nervus mentalis of v.
n.t.	nasoturbinale.
n.vest.viii.	vestibula branch of viii.
o.	orbit.
o.j.	organ of Jacobson.
o.s.	orbitosphenoid.
p.	parietale.
pal.	palatinum.
pars coch.	pars cochlearis capsulæ acusticæ.
pars l.	pars lateralis.
pars p.pal.	pars perpendicularis palatinum.
pars v.	pars vestibularis capsulæ acusticæ (pars canalicularis).
p.b.	planum basale.
ph.	pharynx.
p.mx.	premaxilla.
p.n.	paries nasi.
pr.a.	prearticulare.
proc.a.i.	processus alaris inferior.
proc.a.s.	processus alaris superior.
proc.b.pt.	processus basipterygoideus.
proc.c.	processus coronoideus.
proc.l.a.	processus lateralis anterior.
proc.m.p.	processus maxillaris posterior.
proc.o.n.	processus orbitonasalis.
proc.o.p.	processus orbitalis palatini.
proc.p.	processus paraseptalis.
proc.p.mx.	processus palatinus maxillæ.
proc.p.n.	processus paranasalis.
proc.p.o.	processus paraoccipitalis.
proc.p.pmx.	processus palatinus premaxillæ.
proc.p.s.	processus perioticus superior.
proc.sp.p.	processus sphenoidalis palatini.
proc.z.mx.	processus zygomaticus maxillæ.
proc.z.sq.	processus zygomaticus squamosi.
p.s.	presphenoid.
pt.	pterygoid.
r.l.i.	recessus lateralis inferior.
r.l.s.	recessus lateralis superior.

s.f.	sulcus facialis.
sig.n.	sigmoid notch.
s.m.	sinus maxillaris.
s.n.	septum nasi.
s.oc.	supra-occipitale.
so.n.	solum nasi.
sq.	squamosum.
s.s.	septum spirale.
s.s.s.	sulcus supraseptalis.
st.	stapes.
st.hy.	stylohyale.
s.u.s.	sinus utriculi superior (commissural canal).
t.n.	tectum nasi.
t.p.	tectum posterius.
t.ty.	tegmen tympani.
ty.	tympanicum.
v.	vomer.
v.j.	vena jugularis.

DESCRIPTION OF PLATES.

Plate 29.

Figures of cardboard reconstructions of chondrocranium of *Perameles obesula*, Stage II. Total length, 15·5 mm. Head length, 6·0 mm.

Fig. 1.—Dorsal view of chondrocranium with basi-cranial axis parallel to the paper. (× 25.)

Fig. 2.—Ventral view of chondrocranium. (× 25.)

Fig. 3.—Ventral view of right ramus of lower jaw. (× 25.)

Fig. 4.—View of left side of chondrocranium without membrane bones. (× 25.)

Fig. 5.—View of left side of chondrocranium with membrane bones. (× 25.)

Fig. 6.—View of right side of "hyoid apparatus." (× 25.)

Fig. 7.—Ventral view of "hyoid apparatus." (× 25.)

Fig. 8.—Postero-lateral view of ear-ossicles. (× 43.)

Plate 30.

Figures of cardboard reconstructions of chondrocranium of *Perameles nasuta*, Stage IV. Total length, 23·0 mm. Head length, 11·0 mm.

Fig. 9.—Dorsal view of chondrocranium, membrane bones removed from left side. (× 12.)

Fig. 10.—Ventral view of chondrocranium, membrane bones removed from left side. (× 12.)

Fig. 11.—Ventral view of right ramus of lower jaw. (× 12.)

Fig. 12.—View of left side of chrondrocranium, without membrane bones. (× 12.)

Fig. 13.—View of left side of chondrocranium, with membrane bones. (× 12.)
Fig. 14.—View of right side of hyoid apparatus. (× 20.)
Fig. 15.—Ventral view of hyoid apparatus. (× 20.)
Fig. 16.—Dorsal view of hyoid apparatus. (× 20.)
Fig. 17.—Postero-lateral view of ear-ossicles. (× 26.)
Fig. 18.—Internal view of cast of interior of labyrinth. (× 25.)
Fig. 19.—External view of cast of interior of labyrinth. (× 25.)

Plate 31.

Figures of cardboard reconstructions of chondrocranium of *Perameles nasuta*, Stage V. Total length, 35·0 mm. Head length, 18·5 mm.

Fig. 20.—Dorsal view of chondrocranium, with membrane bones removed from left side. (× 7).
Fig. 21.—Ventral view of chondrocranium, with membrane bones removed from left side. (× 7.)
Fig. 22.—Ventral view of right ramus of lower jaw. (× 7.)
Fig. 23.—View of left side of chondrocranium, without membrane bones. (× 7.)
Fig. 24.—View of left side of chondrocranium, with membrane bones. (× 7.)
Fig. 25.—View of right side of hyoid apparatus. (× 15.)
Fig. 26.—Ventral view of hyoid apparatus. (× 15.)
Fig. 27.—Dorsal view of hyoid apparatus. (× 15.)
Fig. 28.—Postero-lateral view of ear-ossicles. (× 20.)

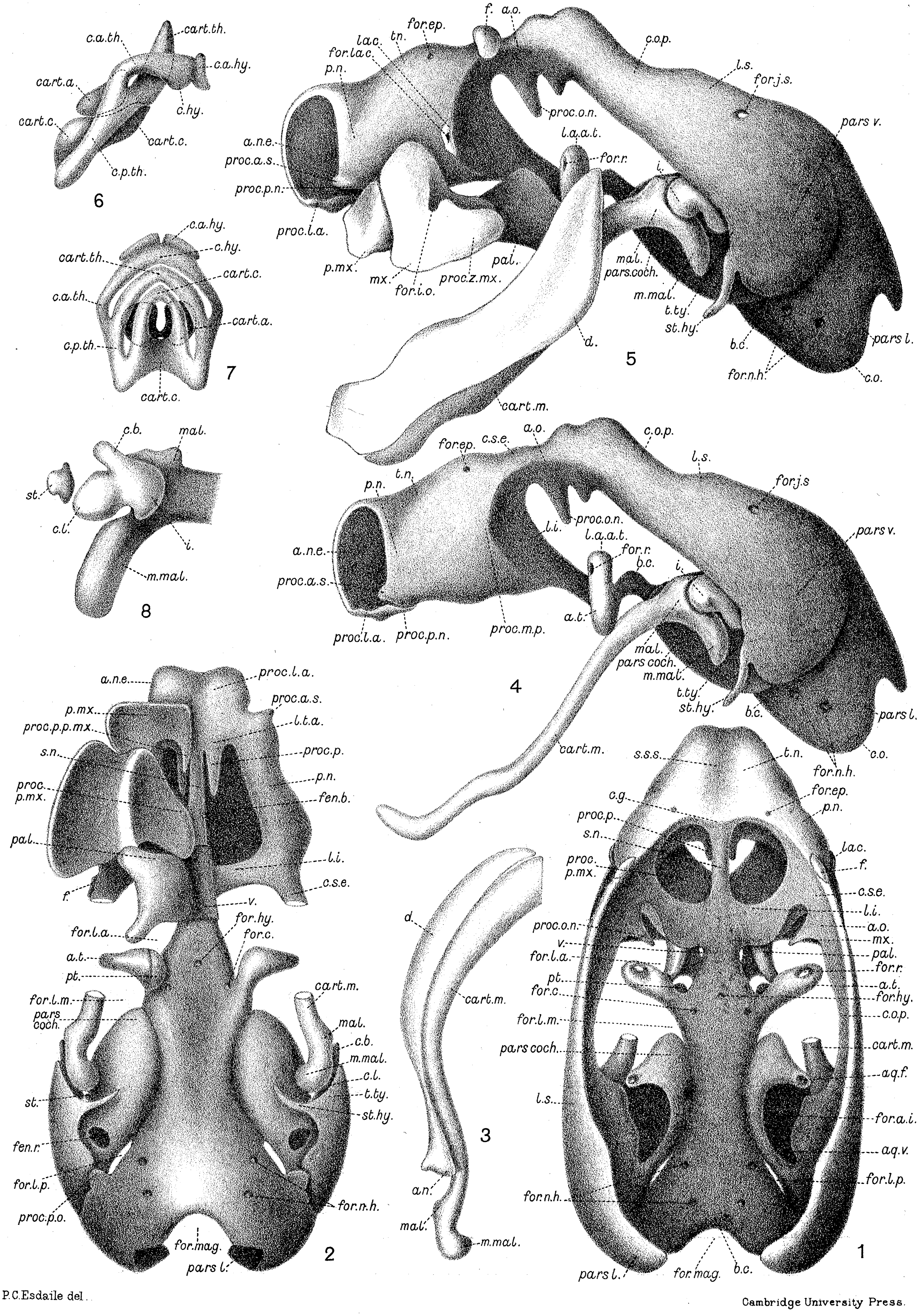
Plate 32.

Figures of sections of *Perameles obesula*, Stage II. Total length, 18·50 mm. Head length, 6·0 mm. (× 43.)

Fig. 29.—Through the anterior end of Jacobson's organ.
Fig. 30.—Through the posterior end of Jacobson's organ.
Fig. 31.—Through the Gasserian ganglion.
Fig. 32.—Through the posterior portion of ala temporalis.
Fig. 33.—Through the geniculate ganglion.
Fig. 34.—Through the fenestra ovalis.
Fig. 35.—Through the aquæductus vestibuli.
Fig. 36.—Through the foramen magnum.

Figure of section of *Perameles nasuta*, Stage IV. Total length, 23·0 mm. Head length, 11·0 mm. (× 28.)

Fig. 37.—Through the anterior end of Jacobson's organ.


c.a.th.
cart.th.
c.a.hy.
cart.a.
c.hy.
cart.c.
cart.c.
c.p.th.
6
c.a.hy.
c.hy.
cart.th.
cart.c.
c.a.th.
cart.a.
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cart.c.
7
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c.o.p.
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l.s.
for.j.s.
proc.o.n.
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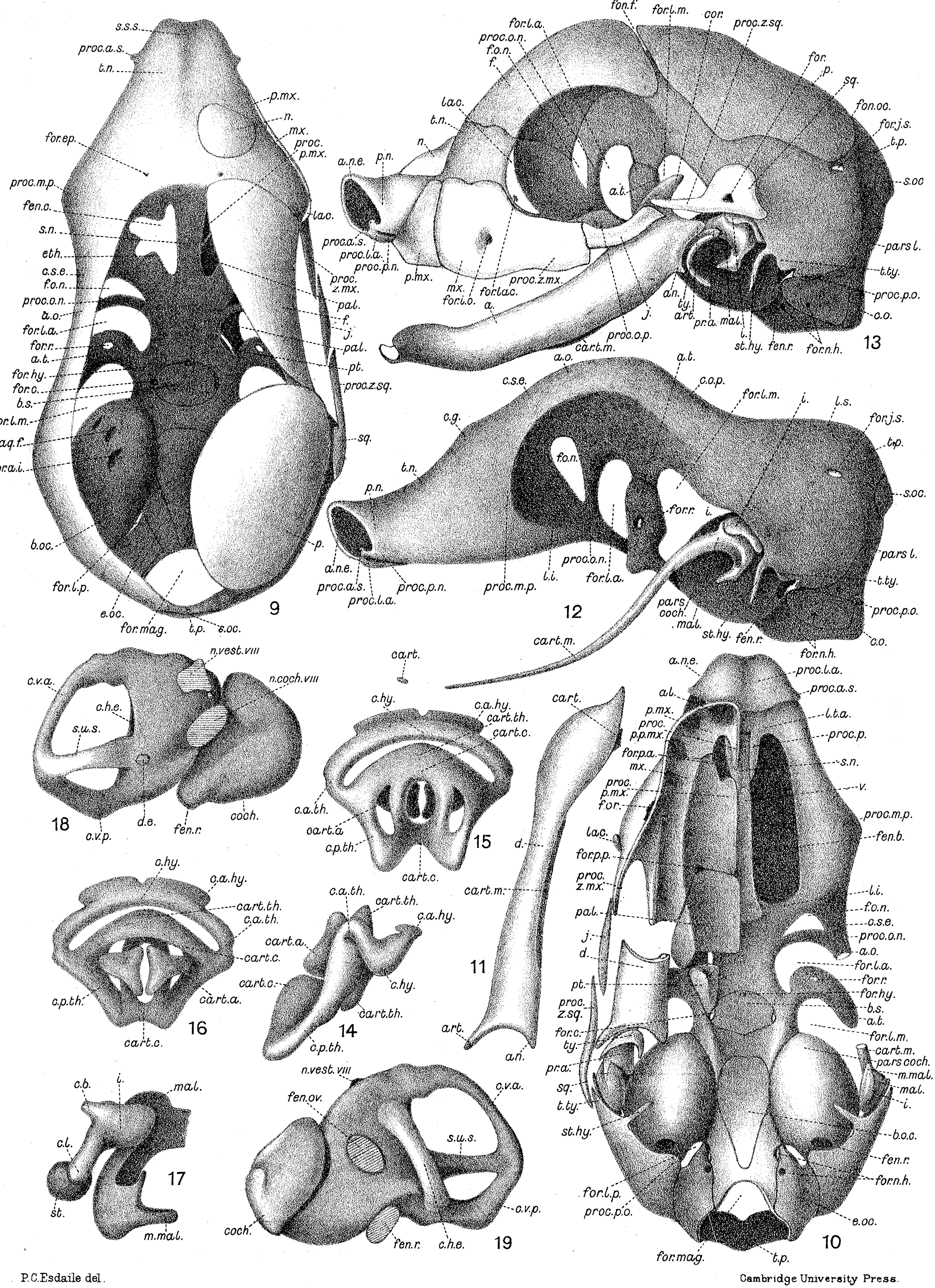

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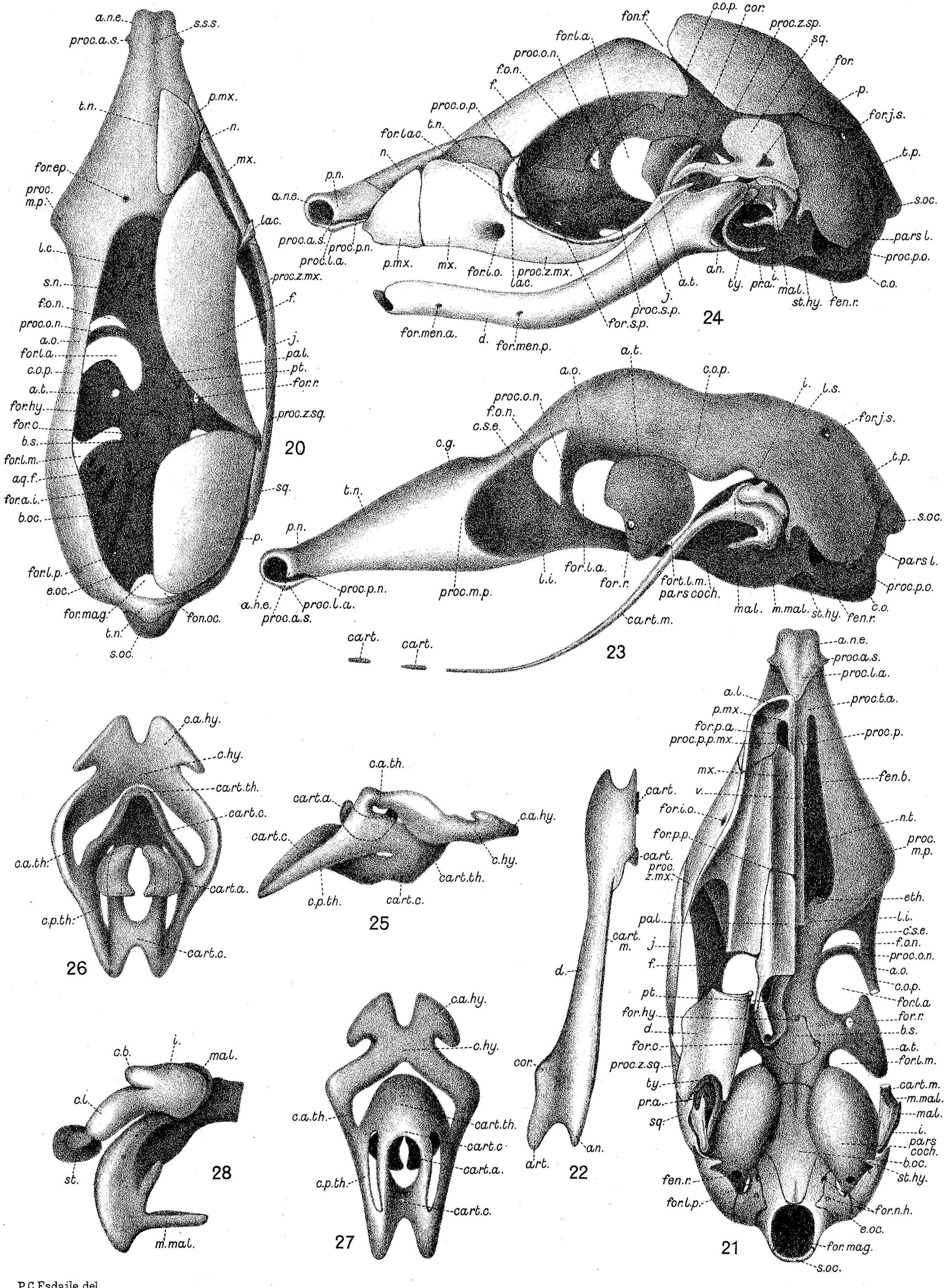
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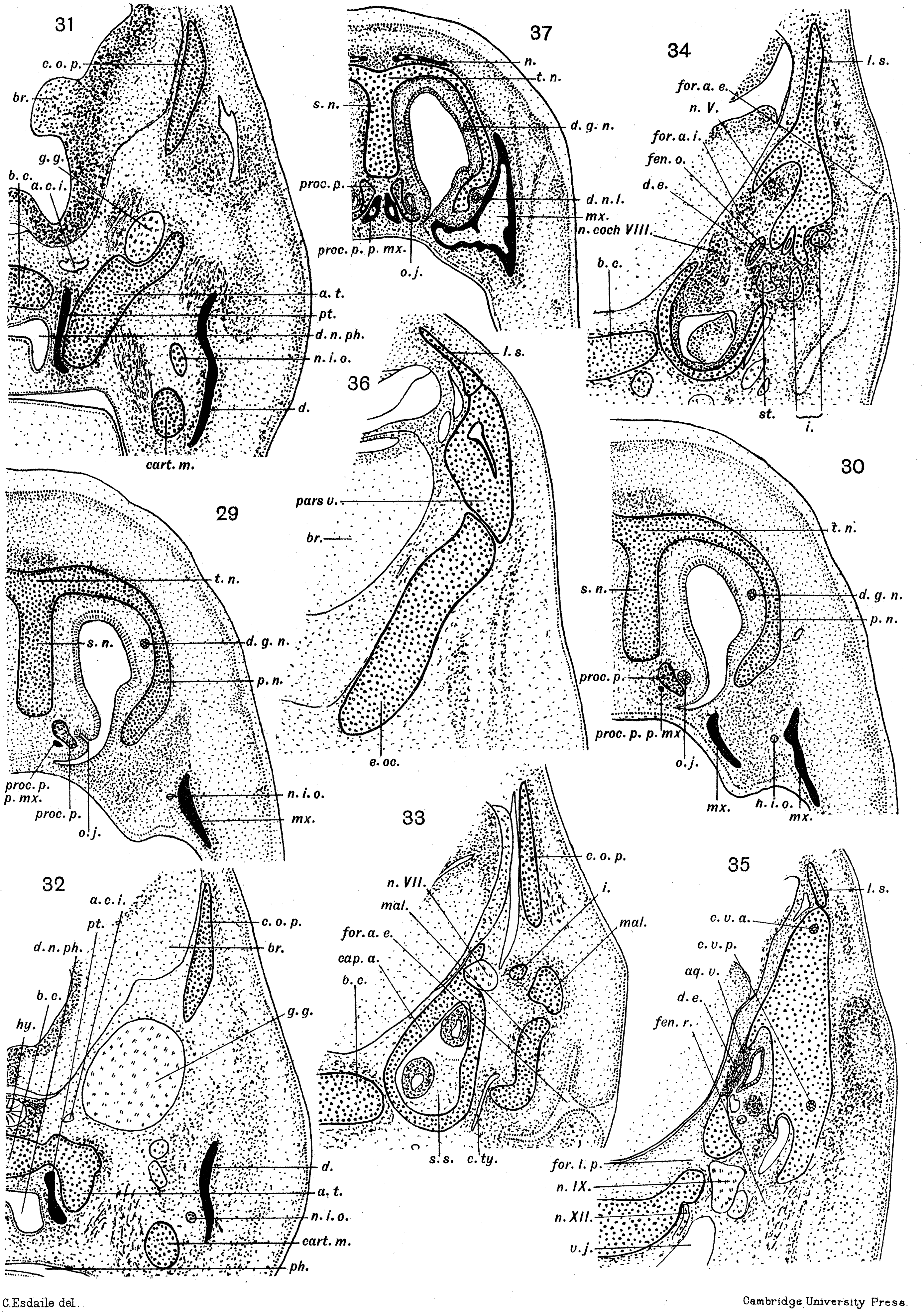
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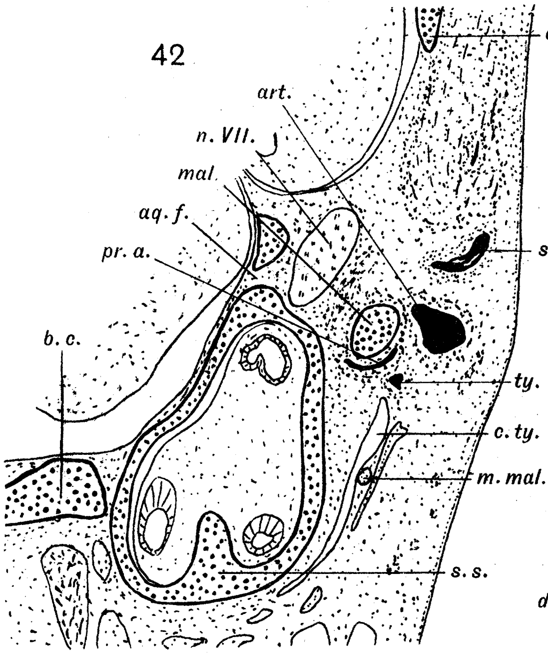

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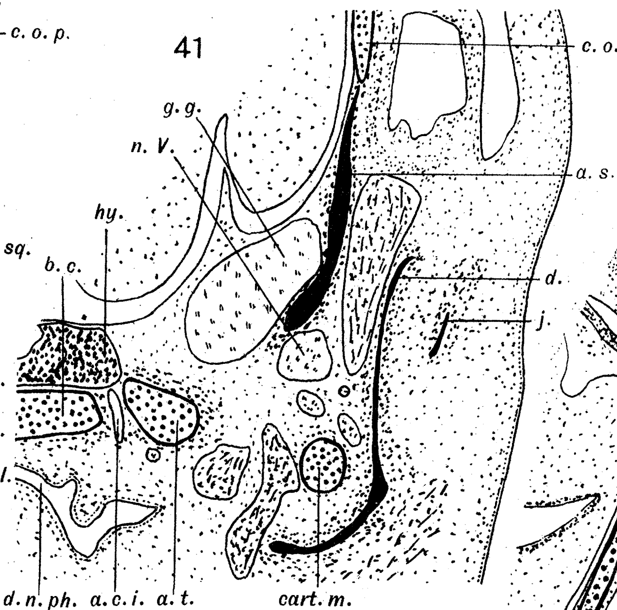

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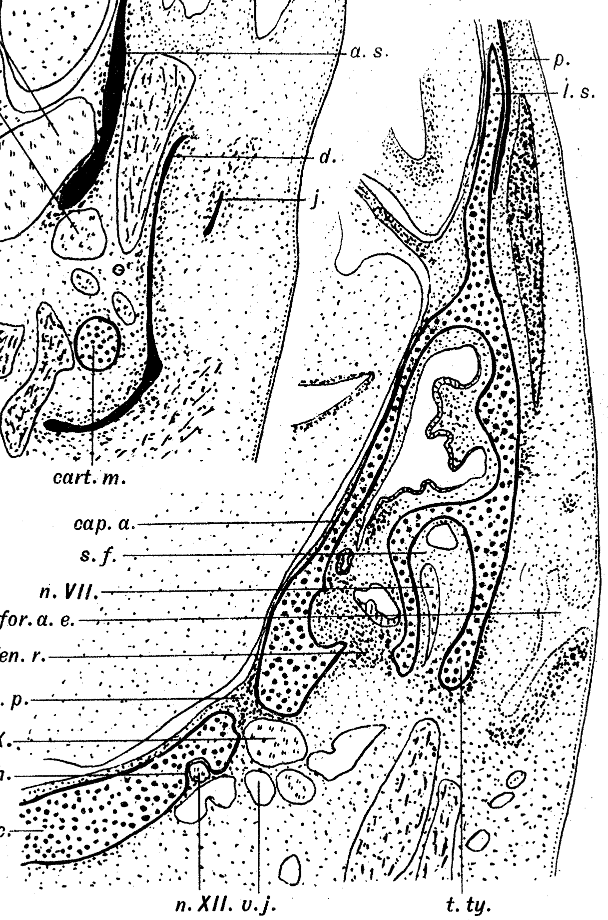

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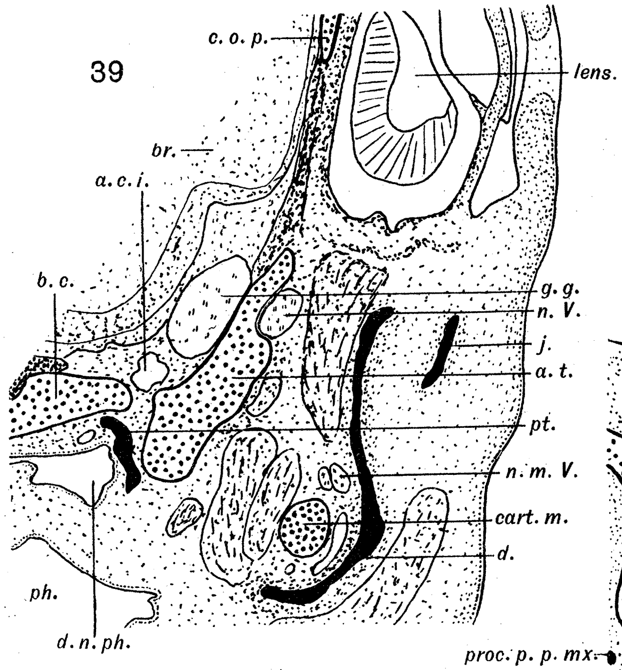

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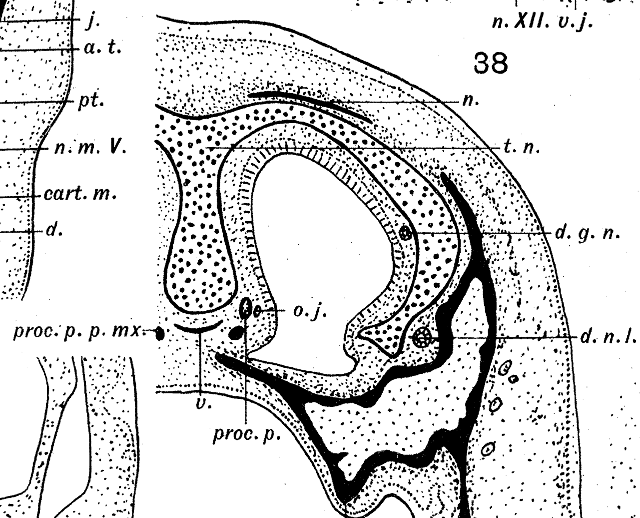

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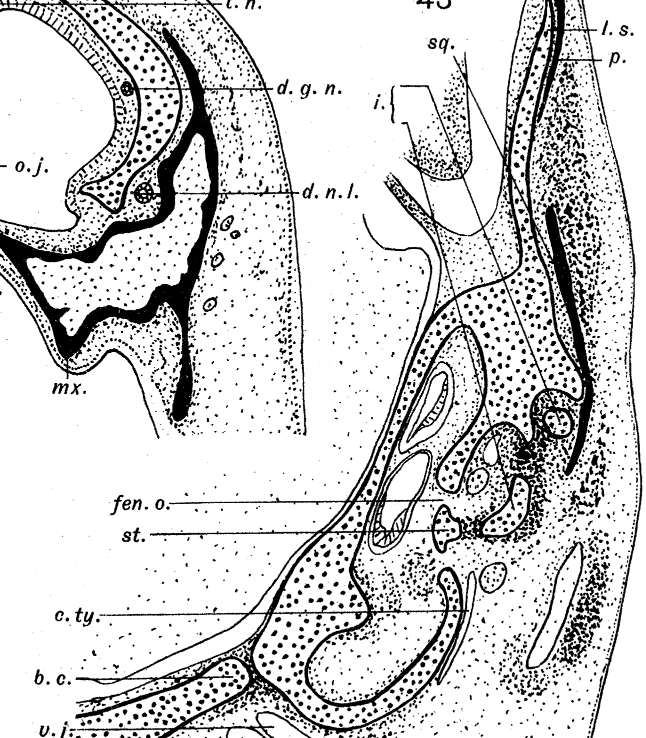

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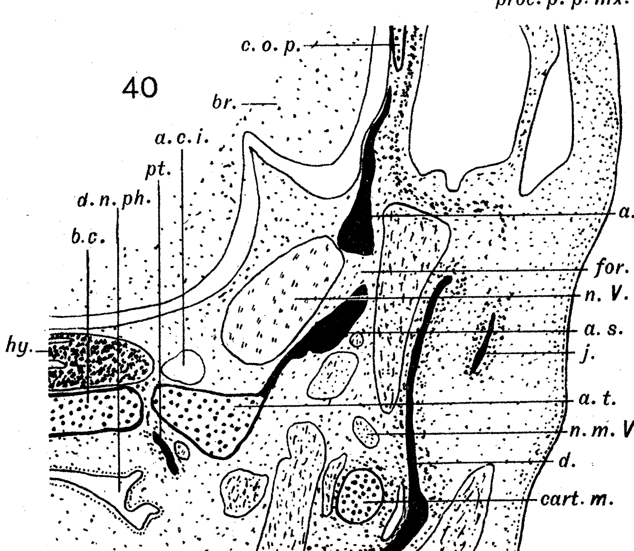

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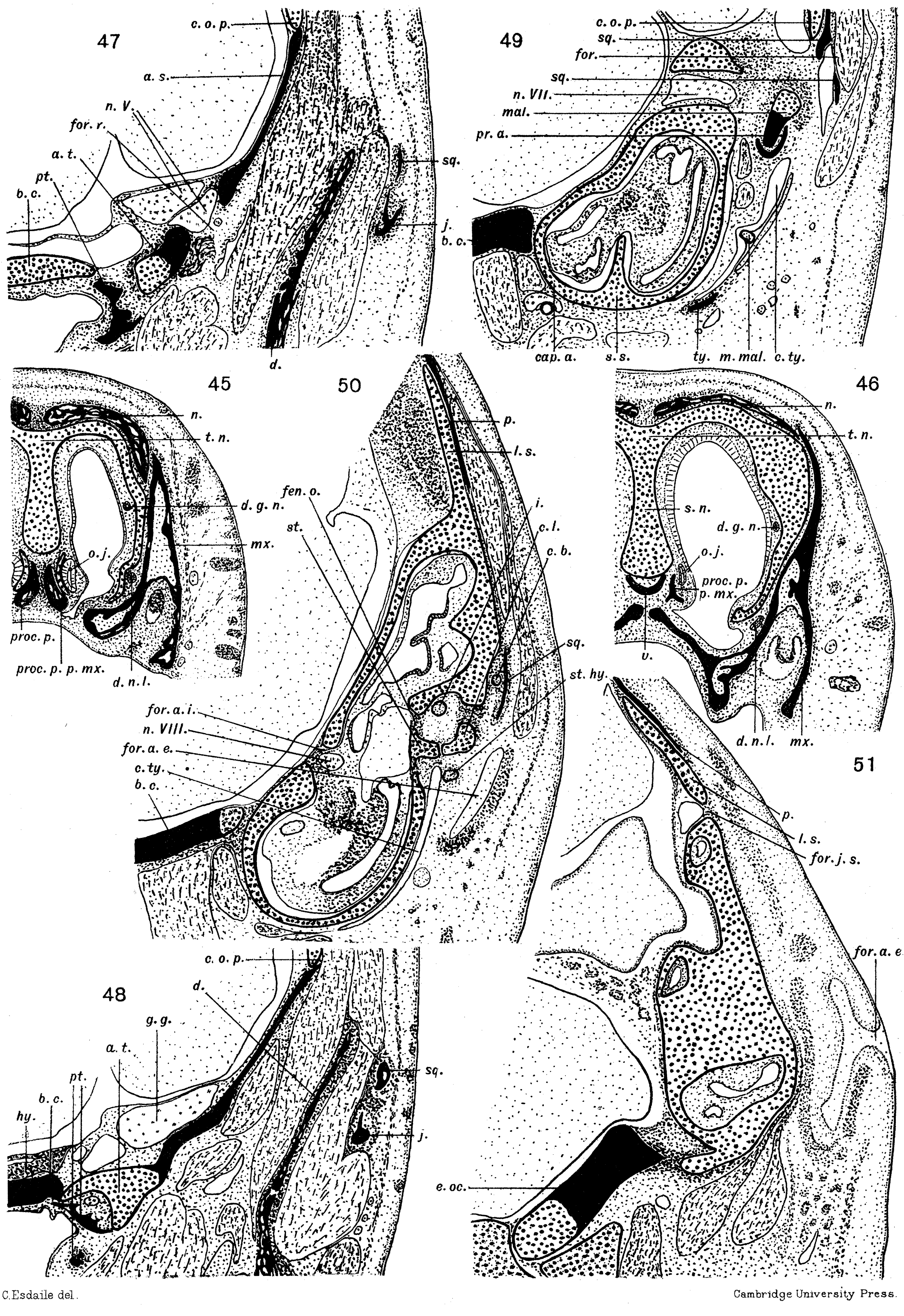

P. C. Esdaile del. Cambridge University Press.

Plate 33.

Figures of sections of *Perameles nasuta*, Stage IV. Total length, 23·0 mm. Head length, 11·0 mm. (×28.)

Fig. 38.—Through posterior end of nasal capsule.

Fig. 39.—Through anterior portion of ala temporalis.

Fig. 40.—Through posterior portion of ala temporalis.

Fig. 41.—Through foramen caroticum.

Fig. 42.—Through aquæductus Fallopii.

Fig. 43.—Through fenestra ovalis.

Fig. 44.—Through foramen lacerum posterius.

Plate 34.

Figures of sections of *Perameles nasuta*, Stage V. Total length, 35·0 mm. Head length, 18·5 mm. (× 21.)

Fig. 45.—Through anterior portion of nasal capsule.

Fig. 46.—Through posterior portion of Jacobson's organ.

Fig. 47.—Through foramen rotundum.

Fig. 48.—Through posterior portion of ala temporalis.

Fig. 49.—Through aquæductus Fallopii.

Fig. 50.—Through foramen acusticum internum.

Fig. 51.—Through posterior portion of pars vestibularis.

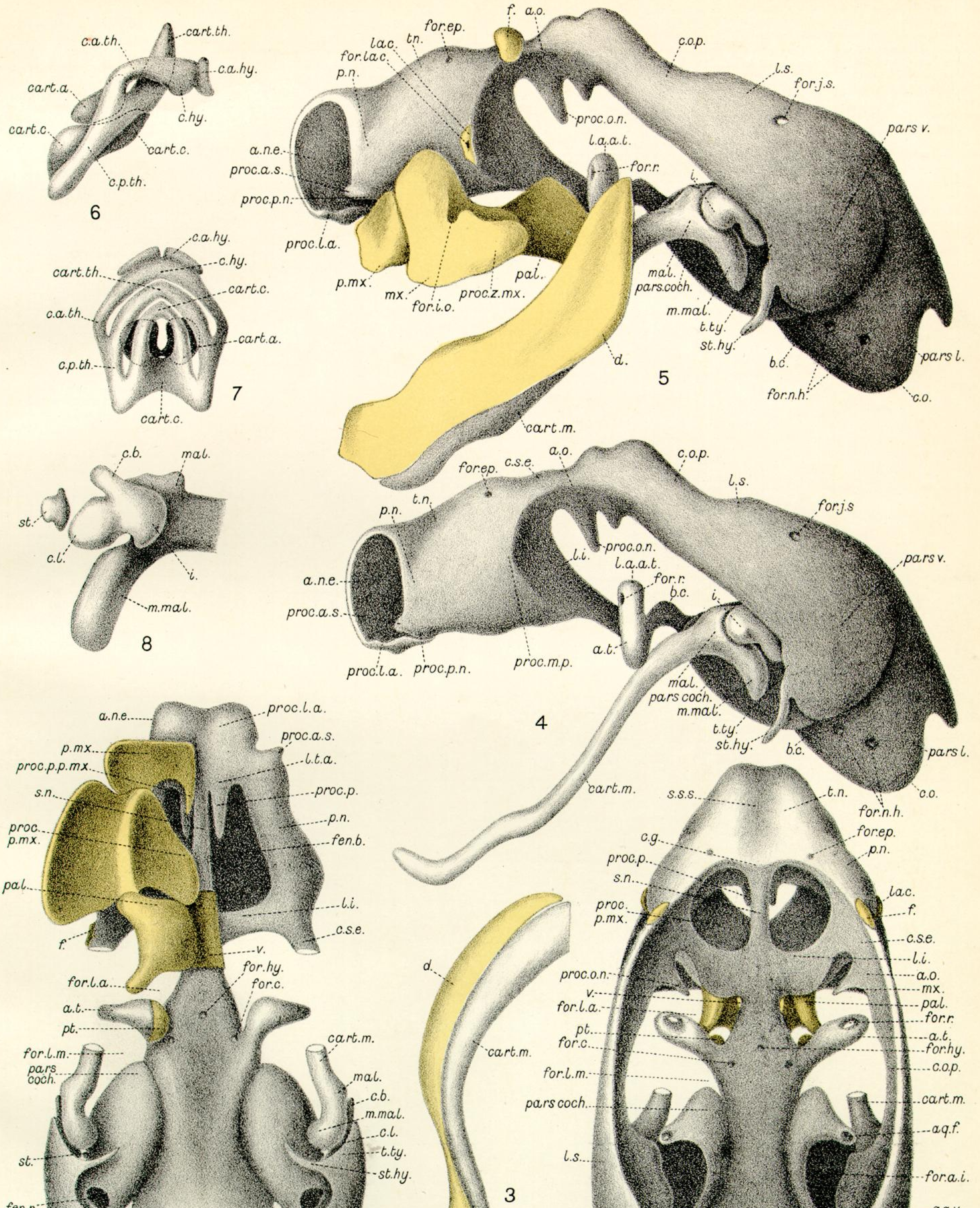

PLATE 29.

Figures of cardboard reconstructions of chondrocranium of *Perameles obesula*, Stage II. Total length, 15·5 mm. Head length, 6·0 mm.

Fig. 1.—Dorsal view of chondrocranium with basi-cranial axis parallel to the paper. (× 25.)

Fig. 2.—Ventral view of chondrocranium. (× 25.)

Fig. 3.—Ventral view of right ramus of lower jaw. (× 25.)

Fig. 4.—View of left side of chondrocranium without membrane bones. (× 25.)

Fig. 5.—View of left side of chondrocranium with membrane bones. (× 25.)

Fig. 6.—View of right side of "hyoid apparatus." (× 25.)

Fig. 7.—Ventral view of "hyoid apparatus." (× 25.)

Fig. 8.—Postero-lateral view of ear-ossicles. (× 43.)

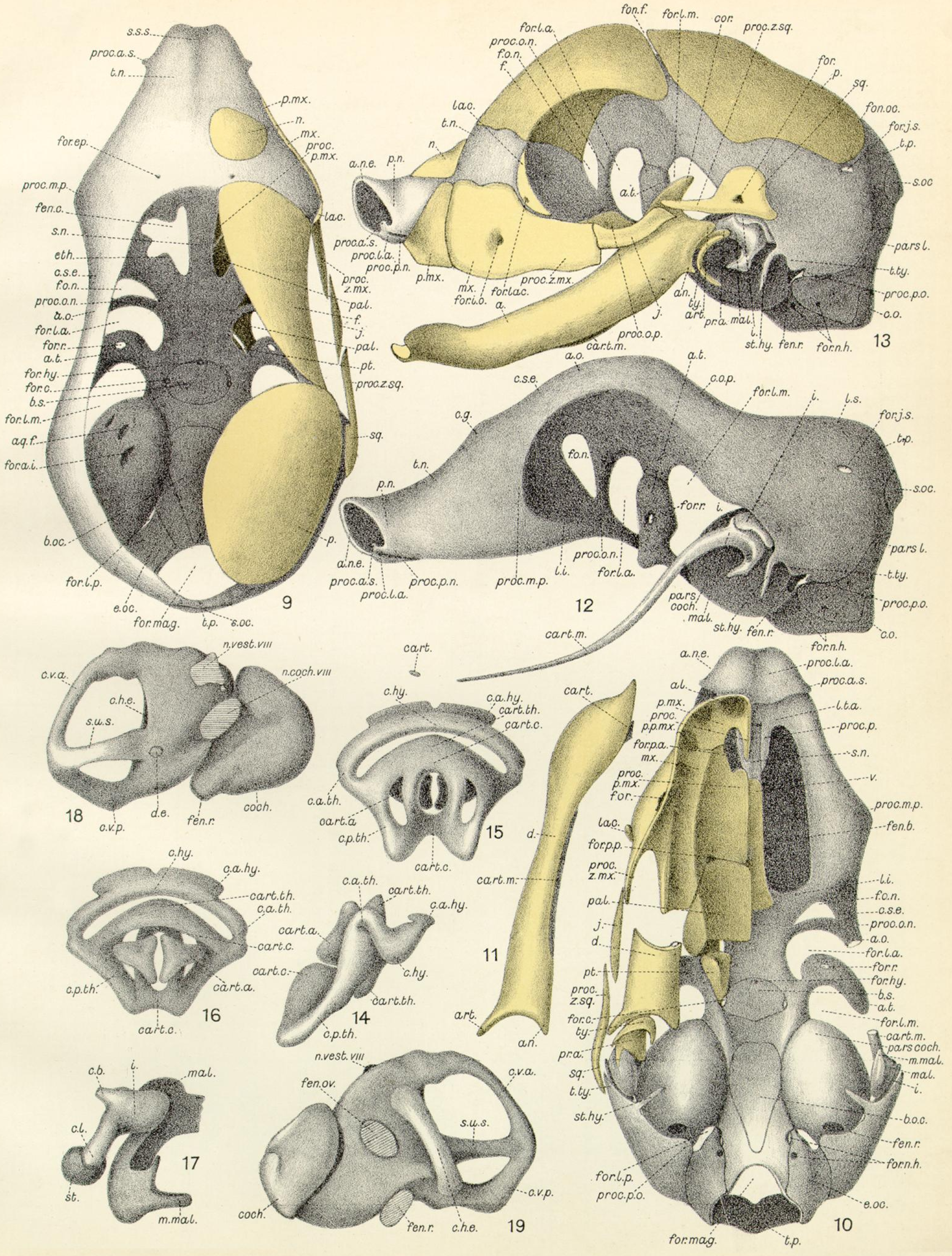

PLATE 30.

Figures of cardboard reconstructions of chondrocranium of *Perameles nasuta*, Stage IV.
Total length, 23·0 mm. Head length, 11 0 mm.

Fig. 9.—Dorsal view of chondrocranium, membrane bones removed from left side. (× 12.)

Fig. 10.—Ventral view of chondrocranium, membrane bones removed from left side. (× 12.)

Fig. 11.—Ventral view of right ramus of lower jaw. (× 12.)

Fig. 12.—View of left side of chrondrocranium, without membrane bones. (× 12.)

Fig. 13.—View of left side of chondrocranium, with membrane bones. (× 12.)

Fig. 14.—View of right side of hyoid apparatus. (× 20.)

Fig. 15.—Ventral view of hyoid apparatus. (× 20.)

Fig. 16.—Dorsal view of hyoid apparatus. (× 20.)

Fig. 17.—Postero-lateral view of ear-ossicles. (× 26.)

Fig. 18.—Internal view of cast of interior of labyrinth. (× 25.)

Fig. 19.—External view of cast of interior of labyrinth. (× 25.)

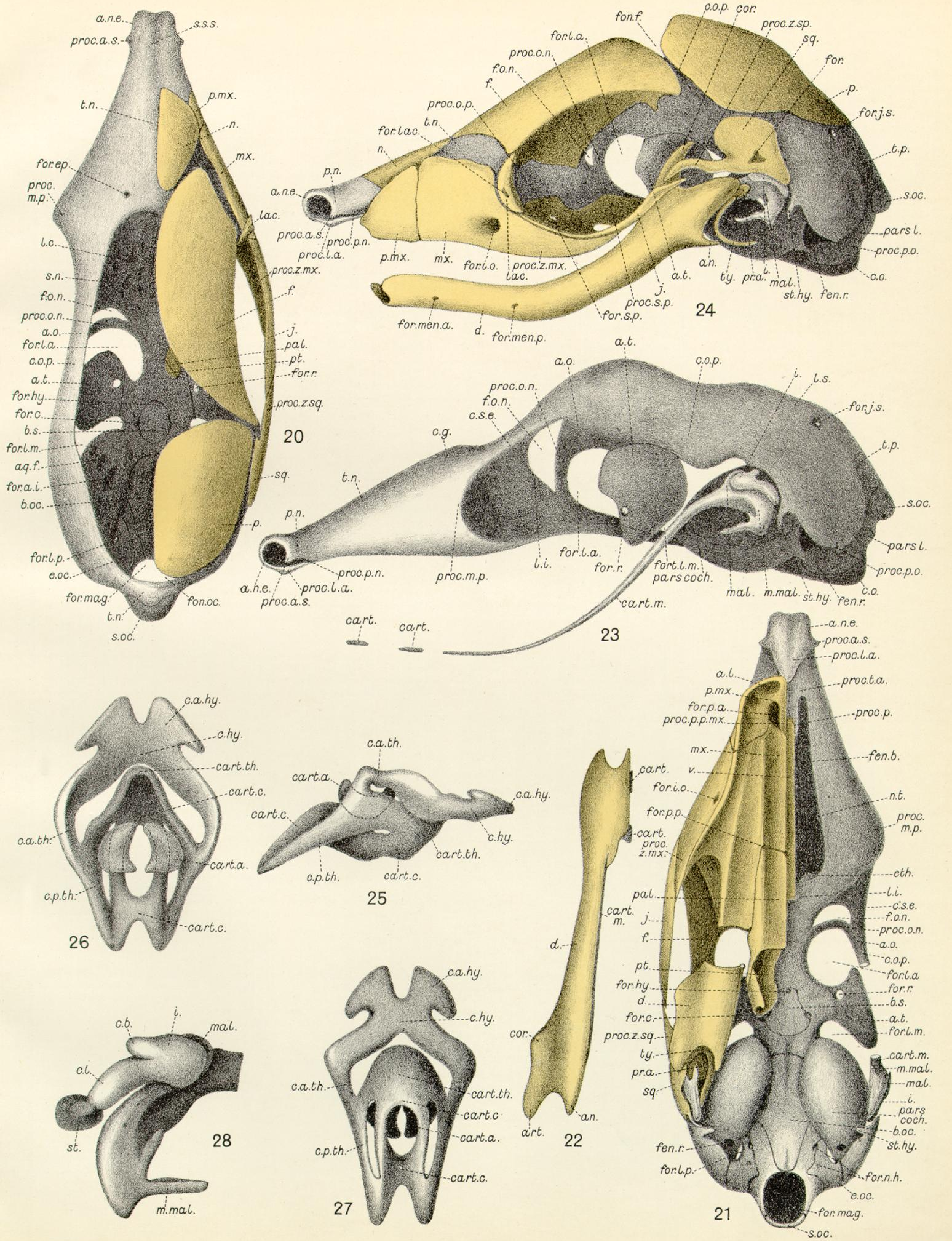

Plate 31.

Figures of cardboard reconstructions of chondrocranium of *Perameles nasuta*, Stage V. Total length, 35·0 mm. Head length, 18·5 mm.

Fig. 20.—Dorsal view of chondrocranium, with membrane bones removed from left side. (× 7).

Fig. 21.—Ventral view of chondrocranium, with membrane bones removed from left side. (× 7.)

Fig. 22.—Ventral view of right ramus of lower jaw. (× 7.)

Fig. 23.—View of left side of chondrocranium, without membrane bones. (× 7.)

Fig. 24.—View of left side of chondrocranium, with membrane bones. (× 7.)

Fig. 25.—View of right side of hyoid apparatus. (× 15.)

Fig. 26.—Ventral view of hyoid apparatus. (× 15.)

Fig. 27.—Dorsal view of hyoid apparatus. (× 15.)

Fig. 28.—Postero-lateral view of ear-ossicles. (× 20.)