

XII. *On the Structure and Development of the Skull in the Common Snake*

(Tropidonotus natrix).

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[PLATES 27–33.]

THE most important work on the development of this type appeared as long ago as 1839. It was by the late Professor H. RATHKE, ‘Entwicklungsgeschichte der Natter (*Coluber natrix*).’ Königsb., 4to.

From time to time during the last twelve years I have worked at the Snake’s skull, my guide being Professor HUXLEY’S translation of so much of RATHKE’S work as bears especially upon my line of research; this I have had at hand, both in the ‘Croonian Lecture’ and in the ‘Elements of Comparative Anatomy.’ My earliest studies of the embryonic conditions of the Snake’s skull were made on half-grown embryos of the Python (*Python Sebæ*), and of the Anaconda (*Eunectes murinus*); these were the gift of my friends Dr. EDWARDS CRISP, F.Z.S., and Dr. P. L. SCLATER, F.R.S. Meantime I have been acquiring younger and still younger specimens of the Common Snake, but only lately have I succeeded in obtaining any embryos sufficiently immature for my *first* and *second* stages. During the last winter (February, 1877) these earlier stages happily came to hand. At the instance of Mr. P. H. CARPENTER, M. BRAUN, of Wurzburg, sent me a considerable number of reptilian embryos in very early stages, from Professor SEMPER’S laboratory. These included, besides the longed-for specimens of the Common Snake, others of the Blind Worm (*Anguis fragilis*), the Nimble Lizard (*Lacerta agilis*), and the Gecko (*Platydictylus*). These other three types I intend to work out in due time. The Snake has the simplest skull of all; and yet, simple as it is, it is a key to that of any member of that great bundle of Vertebrate life which, including the reptiles and birds, is termed “Sauropsida.” (See HUXLEY, “On the Classification of Birds,” Proc. Zool. Soc., April 11th, 1867, pp. 415–472.)

Having wrought very much at the morphology of the Birds’ skull, the simple condition of the skull in such a type as the Snake—which lies down at the very base of the huge group of which the Bird forms the very top and crest—has been to me the most instructive; many things in the utterly specialized avian skull would, but for this key, have been quite beyond my power of interpretation.

In this stage of my work I am able to compare the early conditions of the Ophidian

embryo with what may be seen in several other important Vertebrate types; in none is this comparison more instructive than in that of the Selachians with the Snakes. (See Trans. Zool. Soc., Vol. 10, plates 34–42, pp. 189–234.) Moreover, Mr. F. M. BALFOUR'S researches on the embryology of the Sharks and Skates\* begin to shed a most welcome light upon the development of those most instructive fishes from the blastoderm; his work dovetails with mine in the most convenient manner. But for the development of the "Sauropsidan" embryo the reader is referred to a joint work by Professor FOSTER and Mr. F. M. BALFOUR—their 'Elements of Embryology,' Part I., 1874. So completely at one are the processes by which a Snake and a Bird—the root and the branch of the great group of the Sauropsida—are developed, that these accomplished authors might have taken the *Snake* and not the *Bird* as their subject; scarcely a single figure would need to be altered, if a counterpart work, taking the Snake as the subject, were to be prepared and published. My earliest snake-embryo (Plate 27, figs. 1, 2) corresponds very accurately with that of the Fowl at the end of the fourth day of incubation (FOSTER and BALFOUR, p. 142, fig. 46); the *allantois* in my specimens had exactly the relative size shown in their figure of the chick at that date.

I shall, once for all, refer the reader to RATHKE'S descriptions of the early stages of the skull (both in the original and in Professor HUXLEY'S translation), and use my own terms and modes of speech in endeavouring to make the matter plain.

*First Stage. Embryo Snakes,  $\frac{3}{4}$  of an inch in absolute length.*

Notwithstanding the length of these embryos, the *testa* of a mustard seed would have sufficed to enclose one of them; the figure (Plate 27, fig. 1) shows only the root of the tail, which is tucked in amongst the folds of the body; the neck is partly unwound, to display the huge head better.

The embryonic membranes are now perfect, and the embryo, on the whole, is a finished form; yet the huge loop-shaped heart is only covered by the pericardium, as it lies in the re-entering angle of the throat (fig. 1, *h.*, *pcd.*).

The head is bent upon itself at an angle which is less than a right angle (Plate 27, fig. 1; Plate 29, fig. 1); this great degree of flexion is retained even in the next stage (Plate 27, fig. 3, and Plate 29, fig. 2).

Of the three brain-vesicles, the hindmost ( $C^3$ ) is the longest, and is least elevated; the fore brain ( $C^1$ ) is becoming lobulate by reason of the budding out of the rudiments of the hemispheres; and the mid brain ( $C^2$ ) is most regular in shape.

There are large spaces in each division, filled with a glairy fluid (Plate 29, fig. 1), and the more solid tract is of great length in the hind brain.

The hollow space within the loop of the brain ("middle trabecula" of RATHKE) is

\* Journ. of Anat. and Phys. (a series of most important papers), and Phil. Trans., 1876, Part I., Plates 16–18, pp. 175–195; and his work on the 'Elasmobranchs,' 8vo., MACMILLAN and Co., 1878.

very large and projects forward, horizontal in position, in front of the parachordal region (Plate 29, fig. 1, *m.tr.*, *py.*, *nc.*).

The infundibular (ascending=posterior) part of the fore brain (*inf.*) has not yet united with the small pituitary involution (*py.*), which is *closed* above and *open* below.

The cranial notochord is slightly curved downwards at its apex; it has (relatively) retreated somewhat from the pituitary space (Plate 29, fig. 1, *nc.*, *py.*).

The hypoblastic lining of the alimentary canal has met and united with the epiblast of the face and outer part of the rudimentary throat (Plate 27, figs. 1 and 2; and Plate 29, fig. 1); the oral cavity is, therefore, open.

Behind the mouth those two layers of the blastoderm meet in the *clefts* between the descending visceral folds (see also FOSTER and BALFOUR, p. 118, fig. 37); these folds are the rudiments of the visceral (hæmal) arches and their investments.

These visceral folds are very rudimentary at present; behind the mouth there are only *four* marked off from the rest of the tissue at present; a fifth appears in the next stage.

All but the first two of the post-oral folds are evanescent, and develop no cartilage; in front of the mouth two pairs more of these visceral fringe-like reduplications are developed (figs. 1, 2, *mx.p.*, *n.f.p.*).

The structure, the transformations, and the relations, of these descending or hæmal growths of the head are of the utmost importance to morphology; they form the palate, the jaws, the hyoid arch, and, in branchiate types, the gill arches.

They are related to the cranium, the sense-capsules, and the cranial nerves; their interspaces are the mouth, the naso-lachrymal passages, and the post-oral clefts, (tympano-eustachian passages, and gill openings).

So that, above all things, it is necessary to find out how these parts arise at first; from what layers of the blastoderm they are formed; and with what region, right and left, of the body, they may be compared.

The developing core of these folds, the solidifying floor and walls of the brain-case, and the capsules of the principal organs of the special senses—these three groups of skeletal structures together make the Vertebrate skull.

So that it is easy to see that this part of a Vertebrated creature differs as much from the rest of the skeleton as the brain and cranial nerves differ from the spinal marrow and spinal nerves. Moreover, the capsules and labyrinths of the special sense-organs add largely to the sum of differences.

Both the problem itself, and the methods to be used in attempting to solve it, are quite similar to the growth of a flower from axial and foliar rudiments, and the patient work necessary for tracing out its steps and stages.\*

*The Primordial or Membranous Cranium.*—At present, the investment of the brain

\* The vegetative processes that have mysteriously brought the cell-layers of the blastoderm into the fundamental "Sauropsidan" portrayed in fig. 1, are surely well worthy to be sought out; that, however, is the work of the general embryologist, and is, in order, antecedent to my special inquiry.

is merely a layer of cells belonging to the "mesoblast," and clothed with the epiblastic cells of the epidermis; dura-mater, skull-wall, skin—all these are, as yet, one stratum.

This stratum, however, is thickening, and becoming differentiated into secondary laminæ in the floor of the head. One remarkable fact is that this floor is imperfect at one part. Where the fore and hind brain meet below and behind the mid brain, there we see a large circular fontanelle, with a clear margin. Through this gap the brain can be clearly seen.

In the gap, however, there is a remarkable structure, the rudiment of the pituitary body, which is either formed by an involution of the buccal cavity (epiblast), or cut off from the fore-gut (hypoblast). The latter is the view taken by WILHELM MÜLLER; the former by GOETTE. (See FOSTER and BALFOUR, pp. 91-93.)

Where this remarkable structure passes into the cranial cavity, there the epiblast and hypoblast unite; there the axial notochord ends, and, as on a pivot, the skull first bends itself into a hook and then gradually straightens itself again.

On each side of the cranial notochord (Plate 27, fig. 2, and Plate 29, fig. 1, *nc.*, *iv.*) the floor of the hind brain is thickening to form the investing mass or parachordal tracts. The innermost cells of the stratum ultimately become cartilage.

These bands, however, which correspond to a vertebral tract, although not segmented, pass forwards on each side of the basal opening or pituitary space; these *prochordal* bands are the trabeculæ cranii (*tr.*).

These are the first, and at present the only, rudiments of skeletal structure in this membrano-cranium; the fore part of the floor, the roof and side walls, are at present merely a single cellular lamina (Plate 29, fig. 1).

But each division of the brain has on each side of it the rudiment of what will soon become a highly complex sense-capsule.

The lowermost swelling of the brain, the rudiment of the hemispheres, has on each side, a large, shallow, inverted cup, whose lower margin is sinuous and lobate (Plate 27, figs. 1, 2, *ol.*); these rudiments of the *nasal sacs* grow by their base to the skull wall, and look like cup-shaped Fungi (*Stereum*).

Down on each side, in the hollow between the fore and mid brain, the young eyeball is seen (fig. 1, *e.*); it is an imperfect oval, the reduplication which makes it being unclosed below; the notch widens into a triangle above, and shows the crystalline lens as a small seed-like body.

The forepart of the eyeball comes very near the olfactory cup, and is far from the third sense-capsule (or ear); its hind part rests against a visceral fold in front of the commencing mouth (*m.*).

The rudiment of the ear is like a depressed gourd, whose short neck is somewhat constricted from the bulb; this sac lies on each side of the hind brain, behind its middle, and is more than its own longest diameter from the eye.

This oval sac is encrusted with crowded mesoblastic cells below and at the sides, but a large oval space above is only covered with a thin gelatinous layer. (For a



description of the development of this capsule in the Chick, see FOSTER and BALFOUR, pp. 111–117.)

The visceral folds and clefts can now be considered ; they are equally related to the sense-capsules and to the brain pouches or membrano-cranium.

These descending visceral or hæmal parts are represented in the body by a pair of laminæ on each side, the somatopleure and the splanchnopleure (FOSTER and BALFOUR, pp. 62–67) ; but this division only exists *above* and *in front* when the visceral folds are first formed ; there is a cavity in each fold, but it soon closes.

The pericardium (Plate 27, fig. 1, and Plate 29, fig. 1, *h.*, *pcd.*) is the foremost permanent part of the cavity formed by division of the ventral lamina into two folds.

Thus the hæmal parts of the mouth and throat are formed in a *generalized tract* ; and, moreover, this does not grow into a *wall*, but (at first, at any rate) into a mere *balustrade*—columns and interspaces.

Then as there are no structures in the body answering to the sense-capsules, and as the visceral folds are most intimately related to those special cephalic structures, we get *three* things in which the *pleural* elements of the head and throat differ from the costal elements of the body.

A *fourth* difference might be mentioned, namely, that each rib arises from a distinct axial segment ; whereas the visceral growths of the head, even when they can be most clearly followed up to the axial parts, are downgrowths from a continuous structure.

These folds with their interspaces (Plate 27, figs. 1 and 2 ; and see also in the Chick, ‘FOSTER and BALFOUR,’ p. 118, fig. 37 ; p. 142, fig. 46 ; p. 180, fig. 56 ; and p. 181, fig. 57) form a regular series, some of which are in front of the mouth and some of them behind it.

Of course those in front of the mouth are the most aberrant in form, the parts from which they grow being so much more specialized than the rootstock of the post-oral rods.

At present there are only two post-auditory folds ; these answer to the gill-arches of the Ichthyopsida ; a third appears afterwards (Plate 27, fig. 3). These are the smallest of the series in the Snake.

These folds are somewhat bulbous, so that the clefts are larger and more open above than further down ; their present development very partially walls-in the face and throat, and the pericardium lies between and below the three hinder pairs.

The second post-oral or *hyoid* processes are larger than the branchial, and each has a large root above ; this broad, fan-shaped “origin” embraces the whole lower face of the ear-sac.

In front of this “root” we see the largest of the clefts, and, moreover, that the flexure of the head brings the bulbous distal ends of this fold, and the one in front of it, together.

Thus this cleft becomes high in position as well as wide ; it is called the “spiracle” in Sharks and Ganoids, and is well seen in the Selachians ; in adult Batrachians, and in the higher Vertebrata, it forms the tympano-eustachian passage.

Between the eye and the ear we see the fore part of the hyoid "root;" the root or origin of two more folds; and *three* visceral clefts. This state of things asks some consideration. The two large visceral folds in front of the hyoid rudiment arise from a thick mass of mesoblast lying in the valley between the mid and hind brain, below.

The cleft between these two is the *oral* cleft (*m.*), the thick bulbous fold behind is the mandibular rudiment (*mn.*), and the fold in front, which is high above and rounded below, is the maxillary rudiment or maxillopalatine fold (*mx.p.*).

The oral cleft is, like those behind the ear, larger above than lower down, and then gently widening below.

These clefts all open freely into the buccal and pharyngeal cavities, and these cavities, which meet inside the mandibular rudiments, are lined, the former with epiblast and the latter with hypoblast.

In my last paper (Phil. Trans., 1877, Part II., Plate 21, fig. 4) I showed in the unhatched Axolotl's embryo the *future oral cavity* filled with mesoblastic cells, which cells separated the buccal from the pharyngeal cavity.

Here, however (Plate 29, fig. 1), we are past that stage, and these two spaces pass the one into the other.

The oral cavity is now almost uniform with the whole space between the head and throat, for the maxillary, hyoid, and branchial folds, are all imperfect below, only the mandibular have united (fig. 2). What, then, is the relation of the *oral* to the other clefts in further stages? If we compare this with the next stage, we shall get some light upon the subject (Plate 27, figs. 1 and 3; Plate 29, figs. 1 and 2).

In front of the pericardium the mandibular rudiments have united, and thus have formed the *lower lip* (fig. 2, *mn.*); whilst the maxillary rudiments, which seem to be narrow as seen from the side, are, indeed, thick masses, directed inwards. (See lower view, fig. 2, *mx.p.*)

In the next stage (fig. 3) the folds in front of and behind the mouth have become widely divergent, so that the apex of the front fold is set on the apex of the hind fold at more than a right angle; hence the gaping oral cavity (figs. 3 and 4, *m.*).

The angles of the mouth are the top part of the right and left *oral clefts*; the opening of the mouth is caused by the suppression of the ventral floor of the head; the opening into the cavity of the mouth (buccal cavity) is caused by absorption of the mesoblastic mass before spoken of. Hence the mouth of the Vertebrata, like that of the higher Invertebrata (all but the lowest), is "deuterostomatous."

In front of the maxillary rudiment we have the *foremost cleft*; it is the naso-lachrymal (*l.cl.*), and runs between the postero-inferior margin of the eye (*at present*; afterwards more completely below the eye) and the maxillary rudiment.

On account of the immense development of the head in front, and the forward position of the nasal sacs, this cleft is a good way behind the foremost visceral fold.

In the Batrachia ("Frog's Skull," Plate 3, figs. 2 and 10) this cleft cannot be seen; this arises from the fact that the maxillo-palatine fold is suppressed until the time of transformation.

But in the Salmon ("Salmon's Skull," Plates 1-3) and in the Pig ("Pig's Skull," Plate 28, figs. 1-3) this part is clearly seen; in the Fowl ("Fowl's Skull," Plate 81, fig. 1) it is represented by the line between the eye (*e.*) and the sub-ocular bar (*pa.*).

I am not certain whether this cleft is quite open within; if not, its morphological importance is the same.

The ventral region is finished in front by an elegant double fold of skin, separated by a rounded emargination at the mid line, which grows from the head across the valley between the fore brain and the rudiment of the hemispheres.

These, together, form the "naso-frontal process (*n.f.p.*);" they are attached each to the corresponding olfactory dome, at its postero-internal part. These two folds grow more together, and receive, afterwards, a double growth of cartilage from the trabeculæ—the conjoined trabecular cornua, rudiments of the foremost visceral arch. (See Plate 28, figs. 6 and 9, *c.tr.*)

The relation of the cranial nerves to these ventral (visceral) folds, and their intervening clefts, is of the utmost importance in the morphological interpretation of the parts of the face and throat.

Leaving out of question for the present those cranial nerves which cannot yet be classified, such as the olfactory, optic, and motores oculorum, the rest have very definite relations to the folds and clefts of the head.\* The trigeminal, facial, glosso-pharyngeal, and vagus nerves (5th, 7th, 9th, and 10th) break up into two or three principal branches that run on each side of the clefts.

Both the facial and trigeminal have three main branches; the glosso-pharyngeal two; and the vagus as many as there are branchial arches to be supplied by it behind the glosso-pharyngeal, this latter nerve supplying the back of the hyoid arch and the front of the first branchial.

The facial nerve (7th), besides sending its main part to the front of the hyoid arch, and giving off the *chorda tympani* branch to the back of the mandible, sends forward a third branch, the vidian, which is distributed to the maxillopalatine regions.

This nerve runs outside and below the first branch of the great trigeminal or 5th, whose second and third branches supply the parts round the oral cleft.

But the first branch of the 5th, the ophthalmic or orbito-nasal, runs over the optic nerve into the nasal region, and, whilst the second and third branches in a normal manner fork over the oral cleft, the first branch runs in front of the lachrymo-nasal cleft to supply the rudimentary terminal arch, whose skeleton is formed by the cornua trabeculæ.†

\* The "portio mollis," 8th or auditory nerve, may be a dorsal branch of the facial or seventh nerve; I leave it out of special consideration here.

† The later researches of Mr. BALFOUR (Phil. Trans., 1876, Part II., Plates 16-18, pp. 175-195), showing that these nerves are formed in the "Elasmobranchs" from epiblast, give us some hope of a true classification of the cranial nerves; for it now looks as though the olfactory and optic nerves were not so widely diverse from the others as was supposed. Dr. A. MILNES MARSHALL has set this at rest with regard to the 1st nerve; it does arise like the rest (see Quart. Journ. Micr. Soc., vol. 18, new ser., plates 1, 2, pp. 1-31).

Thus the highly-specialized parts round the oral clefts get an additional nerve-supply from the 7th; and the 5th gives off its first branch to the front of the face, which has no other chance of a supply of this kind, the neural outgrowths of the fore brain being specialized to the utmost for the 1st and 2nd sense-capsules, and three of the motor nerves going to the orbital muscles.

*Second Stage. Embryo Snakes, about 1 inch in length.*

This stage (see Plate 27, figs. 3-6, and Plate 29, fig. 2) gives us some important characters in the fast modifying head, which is now one-third larger than in the last stage.

The bend of the head is fully as great as it was (figs. 1 and 3); the mid brain ( $C^2$ ) projects still more; and the hemispheres are now fairly divided (fig. 4,  $C^{1a}$ ).

The brain is much more solid and complex (Plate 29, fig. 2); the space between the mid and hind brain (middle trabeculæ, *m.tr.*) is much less; the pituitary body is much larger, but is quite distinct from the infundibulum (*py., inf.*).

The notochord (Plate 29, fig. 2, *nc.*) is straight and has receded from the open, oval, large pituitary space (Plate 27, fig. 6, *py.*); the roof of the head, over the long hind brain (figs. 3 and 5,  $C^3$ ) is very thin, and the cerebral cavity is still large (Plate 29, fig. 2,  $C^3$ ).

The large splanchnic pouch (pericardium) has retreated; its end was opposite the first post-oral cleft (fig. 2); it is now opposite the middle of the third post-oral fold (fig. 4). It is evident that the visceral folds are above and in front of the permanent division of the body wall into "somatopleure" and "splanchnopleure."

The oral cavity (*m.*) is now a large square space, with extended angles that open out between the maxillary and mandibular rudiments (fig. 4, *m.xp., mn.*).

A comparison of the side views shows how this has taken place; those rudiments, the second pre-oral and first post-oral folds, instead of being nearly parallel, are placed at right angles to each other, the dorsal end of the maxillary fold abutting against the front of the dorsal end of the mandibular fold.

The distal ends of these folds are much enlarged; this is best seen in a lower view (fig. 4). They both project inwards, but the foremost pair are far apart; the mandibular folds have an extensive *symphysis*, and form a very solid chin.

The pre-oral cleft (*l.cl.*) is shallow and imperfect; the first post-oral cleft is a large, long, sinuous, and perfect slit; it passes downwards and backwards, a definite part of the root of the next fold lying between it and the ear-capsule.

The next or hyoid fold is now, relatively, much smaller, and like the other three—for there are *three* branchial folds now—it is curved forwards; the three other clefts are much smaller than the first post-oral; they are arcuate, and bend forwards.

The small hyoid fold does acquire some cartilage above, but the other three folds remain membranous, and they are now at their fullest development.

In the first stage (fig. 1) the ear-sac was embraced by the foot of the hyoid fold, and

thus the rudiments of the 7th and 9th nerves were emerging at a considerable distance from each other.

Now that distance has greatly increased, for the main branch of the facial nerve (7th) creeps to the front of the hyoid fold, close behind the hyomandibular cleft; thus the space between these serial nerves is greater than the long diameter of the enlarging, egg-shaped ear-capsule.

This capsule (figs. 3 and 5, *au.*) is now well covered above with skin; it is a long distance from the eye.

The eye makes its orbit by nestling in the hollow outside the re-entering angle of the crozier-shaped head; it has no superorbital eave as in the Salmon and the Shark for the chondrocranium, which in those types is very massive, is reduced to its smallest limits in the Snake.

The position of the eyeball in front of the maxillary fold will soon be changed; the straightening of the head will throw it *over* that part.

At first blush, this stage suggests to the observer that the lachrymal cleft and the maxillary fold have their distal ends behind, against the mandibular rudiment. A reference to the first stage (fig. 1) corrects this view; their distal ends are close to the nasal pouches.

These pouches, or inverted cups, are now large and well differentiated, and are growing nearer to each other; between them the leafy folds of the fronto-nasal process (first visceral folds) have approximated and united, so that their interspace is a mere emargination of a single flap (figs. 4 and 6, *n.f.p.*).

If these cyathiform olfactory rudiments (figs. 3, 4, and 6, *ol.*) be compared with their counterparts in the adult Selachian (*Skate* or *Shark*), their likeness will be at once seen. These inverted domes are far apart, the fore brain, growing into hemispheres, swelling down between them.

The crescentic folds that adorn the bottom of these cups, lying concentrically, and enclosing towards the inner side lobate masses of cells, do not become transformed into the elegant, pectinate *membranous turbinals* of the Selachian.

These folds, traced from without inwards, become the septo-maxillary, the two upper labials, the nasal gland, and the vomer; afterwards, these parts crowd towards the septum of the nose, and lie below the olfactory region.

A consistent granular tract, ready to become cartilage, is now formed in the base of the membrano-cranium, which is thus breaking into three main layers (besides the epidermis), viz., the cutis, the layer of young cartilage, and the dura-mater.

When the ventral parts of the post-oral folds are cut away, the hind brain severed behind its middle, and the head examined from below, we get what is shown in fig. 6.

Besides the best view of the nasal cups and first visceral folds, the floor of the skull is better seen.

In the preparation figured the notochord was severed at its apex, and the granular investing mass (parachordal tracts) was cut through the middle.

Behind, these tracts are in contact with the notochord, but in their middle part they are narrow, and form the "posterior basi-cranial fontanelle" of RATHKE.

Then in the part from which the notochord has retired these bands approximate up to the oviform pituitary space (*py.*).

From thence, forwards, they bear the name of "trabeculæ cranii;" they are narrowed between the maxillary rudiments, and become wider as they meet in front of the great opening.

In front of the pituitary space the trabeculæ are close together again, but a dividing line of gelatinous tissue can be seen as they pass to the frontal wall; they *will* be continued as a coalesced process of cartilage into the combined fronto-nasal rudiments; there, of course, they become retral.

The horizontal sections of the maxillary, mandibular, and hyoid, rudiments are very instructive. The first of these (*mx.p.*) is very massive, for in it the maxillary, palatine, and transverse bones will be developed; but it does not acquire any cartilage in its interior.

But the two first post-oral folds have already acquired a pith, which corresponds histologically with the pith of the visceral bars in the first stage of the Salmon ("Salmon's Skull," Plate 1, p. 113), it contains a cavity which soon closes (see p. 389).

The branchial arches do not chondrify; the auditory sacs are not yet cartilaginous; but both these and the other special sense-capsules soon acquire a coat of thin hyaline cartilage.

Between this stage and the next there is a large difference, but the foundations are already laid, and although the building rises almost as rapidly as "an exhalation"—for the development and metamorphosis of the cells is only slower than the formation of dew—yet from what we have just seen we are enabled easily to interpret what we are about to see.

*Third Stage. Embryos of the Snake, from  $1\frac{3}{4}$  to  $2\frac{1}{4}$  inches long.*

The metamorphosis of the head of the Snake's embryo, whilst the body has not doubled its length, is very remarkable.

The flexure of the head upon itself is now almost lost (Plate 28, figs. 1–5); thus the brain segments lie almost in a straight line (fig. 5); the mid brain ( $C^2$ ) forms a very projecting, bulbous "crown."

From that part, over the hind brain ( $C^3$ ), the head sinks rapidly, for the cerebellum is very small. The skin is now well developed. At present the fore brain does not lie flat down upon the floor of the skull, but rises, as in those types that have a septum to the orbital region.

From the primary vesicle ( $C^1$ ) the hemispheres ( $C^{1a}$ ) have budded and developed, and from these have budded the olfactory lobes ( $C^{1b}$ ) which now lie in front, supplying

fibres to the inner walls of the nasal sacs: these sacs have gained their position in front.

The hind brain swells downwards very much, and, like the fore brain of the Amphibia, causes the beams of cartilage on which it rests to bend outwards; we thus get a "posterior basi-cranial fontanelle" in this type equal to the anterior basi-cranial fontanelle (or pituitary space) in the Amphibia (figs. 6 and 8, *p.b.c.f.*).

The space between the hind and mid brain is now a clean fissure, whose convexity is forwards; it is occupied by a membranous "tentorium."

As in the early stages the mid brain is lifted up on high, and thus the fore and hind brains are only separated by the tentorium.

A membranous floor is now placed beneath the hollow pituitary body. I cannot trace any communication between that hollow and the interior of the budding infundibulum, at present (fig. 5, *py., inf.*).

Leaving for awhile the internal structure of the head, we see a very notable outward form. This may be said to be the *Rhynchosaurian stage*.

The earliest condition of my second stage of the Fowl's head is very similar to this, and this is the essential form which is retained in that generalized Lizard, the New Zealand *Hatteria*, and in the Chelonians generally.

The head of typical "Lacertians" and sub-typical "Anguians" (as I shall show in future papers) is precisely like the Snake's head at this stage; it is the common primæval dragon-form, and is also the fundamental form of the head in "every winged fowl after his kind."

The flexure of the head now principally shows itself in the hooking downwards of the *beak*, and the setting of the head on to the arched and hunched neck.

The nasal sacs occupy a considerable space in front of the brain, their outer and inner openings are complete (figs. 3, 4, *e.n., i.n.*); they are roofed by a pair of swelling hollow reniform cartilages that lie back to back, and are confluent below with the confluent fore part of the trabeculæ (figs. 5 and 6, *ol., tr.*).

We thus have, already, a small septum nasi (*s.n.*), which forms an obtuse angle with the distinct interorbital tracts of the trabeculæ (figs. 5 and 6), and which is terminated in front by a hooked flap (figs. 6, 9, *c.tr.*); this flap is formed by the confluence of the "cornua trabeculæ," it grows into the fronto-nasal fold, and is, in reality, the rudiment (combined into one process) of the foremost visceral arch (Plate 27, figs. 2, 4, 6, *n.f.p.*).

In the obtuse angle between this process and the interorbital, free trabeculæ, on each side of and below the septum nasi, we have the large nasal glands (fig. 5, *n.g.*); each gland is enclosed afterwards in two bony capsules—the septo-maxillary and vomer.

Below the glands and septum there are now well developed pre-palatal folds of skin; the inner nostrils meet behind these and appear as one opening under the fore brain (fig. 4, *i.n.*).

Above the palatal structures, outside, we have the huge, almost perfect, eye-ball (*e.*);

between it and the maxillopalatine bar part of the *first cleft (l.cl.)* is clearly seen towards the "inner canthus."

Above and behind the junction of the maxillopalatine and mandibular regions, therefore above and behind the angle of the mouth *at this stage*, we see the form of the ear-capsule, whose cutaneous investment is very thin, above. Behind the angle of the jaw, and below the ear-ball, the first *post-oral* cleft is still visible, and behind it the other three, the hyo-branchial and branchial clefts, are still evident as chinks fast closing in (figs. 1, 2, *cl.* 1-4).

It will be seen that the angle of the lower jaw (figs. 1, 2, *mn., mk.*) has already gained a position so far backwards as to be directly beneath the involution of the ear-sac; it looks now directly backwards. In the last stage this angle was placed between the eye and ear, and looked forwards and upwards (Plate 27, fig. 3, *mn.*).

So rapidly has the face taken on that peculiar metamorphosis which results in the formation of the adult Snake's mouth—a mouth which opens *behind the head*, at a distance equal to half the length of the head (Plate 32, figs. 1 and 2).

The immense eye-balls are acquiring sockets, the membrano-cranium adapting itself to their form; but they are too independent of the skull to need more than a casual notice here.

The ear-balls, on the contrary, are becoming part of the skull; they are chondrified now, and much elongated (figs. 6-8).

In the younger embryo (fig. 6) we see the auditory capsules marked off from the investing mass (*iv.*) by younger cells; they reach from the glossopharyngeal nerve (9) to opposite the entrance of the internal carotid arteries (*i.c.*).

Between the capsules and the narrow anterior part of the investing mass there is a large rounded notch; over this membranous space the Gasserian and facial ganglia lie.

The space between the notch and the hind margin shows two important structures below; the first of these is a small pouch containing otoconial granules: this is the first appearance of the cochlea (*cl.*)—first, practically, in the Vertebrata, as well as in the individual embryo.

Behind this ingrowing pouch there is an opening, and to the membrane stretched across this opening the small hyoid cartilage is attached: the membranous space is the fenestra ovalis; the hyoidean rudiment will be the columella (figs. 6, 7, *hy.*).

Partly occluding the notch in front of the cochlea is an ear-shaped flap of cartilage, widest behind, and having its crescentic or concave edge looking outwards; this is the small infero-lateral alisphenoid (*al.s.*).

In front of the optic nerve in the older embryo (fig. 8), a patch of thickening tissue shows the rudiment of a similarly independent orbito-sphenoid (*o.s.*); the independence of these tracts is characteristic of the Ophidia; as yet I have seen no other instance.

Looking now at the side view of the ear-capsule in the younger embryo (fig. 7), we see that the two post-oral cartilages lie on its side; the second is attached, the first lies loosely against it: the meaning of this will soon be apparent.



The form and relations of the ear-sacs are clearly shown in an upper view of the skull of the more advanced embryo (fig. 8).

These large capsules nearly meet above the hind brain, and are separated there by a right-angled tract of cartilage, the super-occipital (*so.*).

The great size and the alteration of form is due to the rapid growth of the semi-circular canals. The two anterior canals (*a.sc.*) bound the great fontanelle; each posterior canal (*p.sc.*) runs alongside the super-occipital cartilage, and the horizontal canal (*h.sc.*) bulges outwards over the fenestra ovalis, and forms the outer edge of the cranium.

All the ampullæ are outside, but those of the anterior and horizontal canals are close together, whilst that of the posterior canal is behind; the tube of this and of the foremost meet above the brain at less than a right angle.

The chondro-cranium is well developed behind, but dwindles down to almost nothing in front of the pituitary body; distinct filiform trabeculæ, and small orbito-sphenoids, make up all there is of cartilage in the fore half of the skull.

The parachordal tracts or investing mass (*iv.*) are large and united; they are forming the occipital condyle (*cc.c.*) behind; have the notochord, short and twisted, between and above them in their hinder half, and have a large oval deficiency in front.

This is what was spoken of just now as the "posterior basi-cranial fontanelle;" there is a cartilaginous bridge both in front of and behind this space.

On each side the cartilage grows out into hooked processes, in front of which we have the carotid foramen (*i.c.*), and the commencement of the trabeculæ (*tr.*).

The narrow bridge of cartilage which divides the two fontanelles (*p.b.c.f.*, *py.*) from each other, is bent forwards; the pituitary body dips immediately in front of it.

But, as in Amphibia, the pituitary space is much larger than the pituitary body; it is, here, a long spatula in form, with an emarginate blade and a pointed handle.

This space is bounded by the trabeculæ (*tr.*) and is caused by their form and relation; for from the post-pituitary bridge (which is formed by their apices), and the carotid foramina, they run at first outwards, then gently inwards, then they are parallel, and lastly they converge, unite, and after a short, free, single tract, they become two-crested, and unite also with the descending olfactory laminæ (figs. 5, 6, 8, 9, *tr.*, *s.n.*, *ol.*).

The olfactory roofs have already been described; but before turning to the facial rods, I must notice that a long styloid tract of granular tissue is wedged between the trabeculæ, and reaches the pituitary body by its broad hinder end; this is the tissue which is ready to become the parasphenoid (*pa.s.*).

The rudiments of the curious palatal basket-work are already apparent (fig. 4, post-oral arches removed); the granular tissue is just ready to develop "osteoblasts," but no hyaline cartilage precedes the bony tracts that soon appear.

Two bands on each side unite in front as an arch by means of a key-stone process; this key-stone is the old fronto-nasal process, and continues above the trabecular cornua

(figs. 4, 5, 6, 9, *c.tr.*), and below the tissue which becomes the single pre-maxillary (fig. 5, *px.*).

From this, the bowed outer edge contains a pith which becomes the maxillary, and the inner, in like manner, the rudiment of the palatine bones, whose ascending process is prefigured by the lobes that constrict the inner nasal passage (*i.n.*).

The outer and inner bands are united obliquely behind by a tract which becomes the transpalatine, and the hind part of the inner band develops the pterygoid.

The two folds in front of the inner nostril contain the tissue that becomes the right and left vomers; the circular marking behind the opening, is the pituitary body (*py.*).

The mandible (figs. 2 and 7, *q., mk.*) is now composed of two cartilages: a suspensory piece or quadrate, and the articulo-Meckelian rod.

The former has an anterior blunt process above, the stunted pedicle; and a longer otic process (fig. 7, *pd., ot.p.*).

As in the Salmon, the segmentation of the rod is such as to make a hinge between the two parts with a long angular process to the lower segment.

This lower piece (*ar. mk.*) is a long sigmoid rod, thickest above, and then uniformly terete; the axes of the two segments are coincident, and their direction downwards and forwards forms a very acute angle with the basis-cranii.

The hyoid fold (*hy.*) has cartilage only in its upper third; this is a rib-like piece with a rounded capitulum, a solid tuberculum, and a sickle-shaped shaft, whose convexity is backwards.

The hind edge below has a crest ready to separate from the main part.

The capitulum is attached to the membrane of the fenestra ovalis (*st.*), which is beginning to chondrify continuously with the hyoid rib-like rod; the meaning of these parts will be seen in the next stage.

#### *Fourth Stage. Embryo Snakes, 2½ to 3 inches long.*

In the last stage the chondrocranium was perfect, and granular tracts along the palate and face were beginning to ossify.

Yet only the hind part of the hind brain was covered with cartilage, and the fore part of the cranial floor had merely two rounded threads of cartilage supporting it; all the rest was membrane.

About five-sixths of the Snake's skull is made up of subcutaneous, supplementary bones; is dermo-skeletal, in fact.

This stage shows the origin of most of the endoskeletal centres of the limited chondrocranium, and nearly every centre whose origin is in a mere membranous tract.

The shape of the chondrocranium was perfect in the last stage, so that the main work to be done now is to show its histological transformation.

The first bony part to be noticed is the *cephalostyle* or *bony sheath* of the cranial notochord. It is perfect now, and has begun to infect the cartilage right and left, so as to widen the tract that becomes the broad basi-occipital (Plate 29, fig. 5, *bo.*).

A considerable synchondrosis separates the basal centre from the lateral occipital patches (*eo.*); these are creeping round the foramen magnum, and show themselves on the top (Plate 29, figs. 3-5; Plate 30, fig. 1, *eo.*).

Each is seen to be perforated for the hypoglossal nerve (12), in front of and within the posterior condyloid foramen (*p.c.f.*); and they reach to the foramina for the glosso-pharyngeal and vagus (9, 10), which emerge between the ear-capsule and basal plate.

Where the trabeculæ pass into that plate—the investing mass—there on their outer margin a thin film of bone may be seen (Plate 29, fig. 5, *bs.*): these films are the symmetrical basisphenoids; this deposit takes place exactly where the larger parasphenoid of the Bird grafts itself upon the cartilage.

In some specimens I found a thin ectosteal film over the anterior ampulla (Plate 29, fig. 4, *pro.*): this is the beginning of the prootic.

Besides these ossifications, certain changes in the rest of the chondrocranium have to be noticed.

The small hyoid cartilage now looks downwards and backwards, and the “tuberculum” is behind the “capitulum;” both are attached to the stapedial plate, and the whole structure is cartilaginous: it is the “columella” (*co.*).

The thin hinder edge of the hyoid is now distinct as a heart-shaped stylo-hyal (*st.h.*).

The alisphenoid (Plate 29, figs. 3 and 5, and Plate 30, fig. 1, *al.s.*) is now applied by its dilated ends to the basal plate, and the concave margins of the two conspire to make a large oval foramen for the 5th nerve.

But the first and second branches, only, pass through this double notch; the mandibular (third) branch escapes behind the alisphenoid, between it and the prootic region of the ear-sac: this has to do with the backward route it takes in company with the lower jaw.

The 7th or facial nerve passes through the front of the ear-capsule; close behind the third branch of the 5th and a little behind the 7th the 8th nerve enters the ear (Plate 30, fig. 1; 5, 7, 8).

The triangular tracts that lie in front of the optic nerve (2, *os.*) are now becoming cartilaginous; they are the small, *free* orbito-sphenoids.

The quadrate hinges on to the articular region of the mandible by a condyle like that of the *humerus* for the *ulna*; it forms with it an obtuse and then an acute angle (Plate 29, figs. 3, 4, *q, ar.*).

The re-entering angle of this joint makes the gape, which is getting further and further backwards; a membrane bone, the squamosal (*sq.*), intervening between the quadrate and the skull.

The quadrate (*q.*) is becoming ensheathed with bone; the upper part, like a Mammalian supra-scapula, and the condyle, being soft.

On the left side in fig. 4 a rudiment of the pedicle can be seen, but the main part at top is the otic process.

The articular region of the mandible is ossifying; the rod in the middle is flattened somewhat, and then runs in an arcuate manner to the free end.

The bones formed in non-cartilaginous tracts have now to be described.

In the fore half of the basis-cranii there is a sharp style of bone; it is wedged between the trabeculæ, and broadens out under the pituitary space; this is the parasphenoid (Plate 29, fig. 5, and Plate 30, fig. 1, *pa.s.*): it is seen in longitudinal section in the latter figure.

The infero-lateral regions of the cranium have acquired two bony tracts, the frontals and parietals (*f.*, *p.*); the frontals are rapidly growing round the fore part of the hemispheres (Plate 30, fig. 3, *f.*), whilst the parietals (fig. 5, *p.*) have a lower position.

The nasals (Plate 29, figs. 3, 4, and Plate 30, fig. 2, *n.*) lie on the inner side of the nasal roofs, and dip deep down between them.

The pre-maxillary (*px.*) is seen in front of these capsules, and below the recurrent trabecular cornua.

Over the large nasal gland a thin bone, the septo-maxillary (Plate 30, figs. 1, 2, *s.mx.*), is stretched; it ascends both up the side of the septum nasi and also towards the nasal wall.

Below the gland we see the vomer (*v.*); it is hollow to receive it; and between the two bones on the under surface there is a section of the principal upper labial (*u.l.*).

In the transverse section (fig. 2, *mx.*) the fore part of the maxillary is cut through; it is a thin lath, and is seen also in the next two sections (figs. 3 and 4); it is shown from the side in Plate 29, fig. 3, *mx.*

Three bones have appeared in the inner palatine fold—namely, the palatine, transpalatine, and pterygoid: these are endoskeletal bones. There are also bony tracts outside the nasal roofs: these are the prefronto-lachrymals (*pf.*); another pair is seen in older specimens, namely, the post-orbitals.

The palatines (Plate 29, fig. 3, and Plate 30, figs. 3–5, *pa.*) are also thin laths of fibrous bone; they are rounded in front, pointed behind, and have in front of their middle a thin flat coiled process, the orbital or ethmopalatine process, which arches over the nasal canal (Plate 30, fig. 3).

The transpalatine (Plate 29, fig. 3, *t.pa.*) is a binding bar between the marginal and sub-marginal series; it is a cuneiform bar passing obliquely so as to attach the zygomatic process of the maxillary to the pterygoid.

The pterygoid (*pg.*) is a slender style, and it belongs, morphologically, to the mandible; it binds the quadrate to the palatine.

Another splint binds the quadrate to the auditory capsule (Plate 29, fig. 4, *sq.*): this is the squamosal; it is sickle-shaped, with the point directed forwards.

This bone already is serving as a loose swinging point for the descending and retreating mandibular suspensorium.

The description of this stage may be fitly ended by a short notice of what transverse sections reveal of the form and relation of the elements of the chondrocranium,

besides what has just been noted, namely, the sectional views of the membranous bony tracts.

The *1st section* (Plate 30, fig. 2) shows the junction of the coalesced trabeculæ with the inner laminae of the nasal roof to form the septum nasi (*s.n.*).

This section shows the utter simplicity of the olfactory cartilages, and how that the huge nasal gland and its bony capsules—dish and cover—fill all the lower part of the nasal canal.

These canals are nearly surrounded by cartilage, for the wall turns inwards, and then there is a floor piece formed by the upper labial (*u.l.*).

In the *2nd section* (fig. 3) the total arrest of the fore skull is shown; there is nothing in the region of the hemispheres and eyeballs save the pair of elegant, rounded, solid trabecular rods (*tr.*).

So, also, in the *3rd section* (fig. 4). Here, however, we see two curious palatal papillæ, such as I long ago showed to exist in the mouth of the Tadpole, and which abound in the mouth of the *Ammocetes-larva* of the Lamprey. In that case they are the rudiments of the armature of the sucking disk.

In the *4th section* (fig. 5) we have the broadest region of the hemispheres ( $C^{1a}$ ) cut through, just where the carotid arteries (*i.c.*) enter, and where the pituitary body (*py.*) is grafting itself upon the floor of the cavity of the infundibulum (*inf.*).

As the trabeculæ are bifurcated by the burrowing of the internal carotids, they appear in section as two cartilages on each side; here the parietals (*p.*) form *floor* and *wall* to the brain cavity.

In the *5th section* (fig. 6) the mid brain is seen lying upon the hind brain ( $C^2, C^3$ ); the anterior ampullæ are cut through (*a.s.c.*), and the wall of the ear-capsule is seen to be imperfect on its inner face. This open part is the internal meatus.

The section was made through the hind part of the “posterior fontanelle,” and the basioccipital bone (*bo.*) had, in this case, just reached that open space; there we see the deep concavity of the basal plate, and the swelling of the hind brain.

Then, also, Meckel’s cartilage (*mk.*) is cut through, and also the angular and surangular (*ag., s.ag.*); the floor of the face has been cut away, but the roof of the throat is shown.

In the *6th section* (fig. 7) we see the huge *optic lobes* resting on the hind brain ( $C^2, C^3, C^{3a}$ ); the section has been made through the middle of the ear-sac and the apex of the notochord.

Here the basal plate is seen to be a large slab of cartilage, hollow above, convex below, and having the notochord lying upon it; it is quite distinct from the ear-capsule on one side.

The razor has cut through the anterior and horizontal canals (*a.sc., h.sc.*), and the vestibule (*vb.*); the columella (*co.*) and Meckel’s cartilage, with the same splints as in the last (*mn.*), are severed.

In the *7th section* (fig. 8) the perfect occipital ring is cut through, close behind the

ear-capsule (*au.*); the space is more than half an oval, the floor sinking downwards; here, thin, ectosteal laminæ are forming the basi- and exoccipital bones (*bo.*, *eo.*).

The most projecting part of the ear-capsule (*au.*) contains the ampulla of the posterior canal.

*Fifth Stage. Embryo Snakes,  $4\frac{1}{2}$  to  $5\frac{1}{2}$  inches long; a few days before hatching.*

Within a short time the development of the bony centres has been so great as to give, in many cases, the form, to each ossification, which is to be permanent.

This is especially the case in those bones which have no cartilaginous groundwork; those that have are still separated from each other by large tracts of cartilage (Plate 31, figs. 1-2; in fig. 1 the upper part of the skull has been cut away).

When a strong osteo-cranium, like that of a Snake, has to be formed, the ossifications soon blot out old morphological landmarks. It is indifferent to bone-tissue what variety of the connective-tissue series it shall get its matrix from: it is as if the *clay* and the *straw* laid out on the original ground-plan should indifferently be made into bricks and tiling.

We see here that the posterior basal fontanelle (*p.b.c.f.*) has grown to its utmost size; but the apex of the egg-like outline is taken off by the extension of the basioccipital (*bo.*) into the membrane. That ossification is very large and heart-shaped, the "cephalostyle" lying on its concave or upper surface; it extends its bony growth into the substance of the bilobate condyle (*oc.c.*).

The exoccipitals (*eo.*) are extending, but the chondrocranium keeps growing also; therefore there is still one large tract unossified between the median and lateral bony centres.

The lateral bones are riddled with holes, and these have added to them others that extend the series to the pituitary space.

Posteriorly, we have the "posterior condyloid foramen" (*p.c.f.*); then within and in front of that the anterior (12), for the hypoglossal nerve, which now, for the first time in our ascent, has become a *cranial* nerve.

For the substance of the parachordal cartilages now gathers to the mid-line, to form the emarginate *single* condyle; this double tract, in many Urodeles, forms an intercalary vertebra—the odontoid ("Skull of Urodeles," p. 575).

Near to the ear-capsule and its fenestræ we see the foramina for the vagus (10) and glossopharyngeal (9); these holes have a bony tract between them, as in most Batrachia.

The super-occipital centre is ossifying; this, however, will be best seen in the next stage (figs. 3, 4, 6, *so.*).

The two films of bone that begin outside the carotid opening are now one large bone: the basisphenoid (*bs.*). This bone now occupies the roots of the trabeculæ, but stops in front, opposite the end of the parasphenoid (*pa.s.*), and at the beginning of the narrow interorbital region.

The bony matter grows off the cartilage, both laterally and behind, into the contiguous membrane; the carotids are en-ringed completely by bone; this is the foremost bone of the cranium, proper, at this stage, for the orbito-sphenoids (*os.*) are still soft, and no presphenoid ever appears.

The alisphenoidal cartilages (*al.s.*) have coalesced with the basal part, and also with the auditory capsules; they are ossifying, and the bone is both notched and perforated by the trigeminal nerve (5).

The main periotic centre, the prootic (*pro.*), is now enclosing the fore part of the capsule; the other two are not visible. These will soon appear.

The frontals and parietals (*f., p.*) are now just gaining the top of the head, and the parasphenoid (*pa.s.*) is well ossified; it is flat below and keeled above, fitting in between the trabecular rods.

The septo-maxillaries, vomers, and labial cartilage (fig. 2, *s.mx., v., u.l.*) are seen on each side and below the septum nasi (*s.n.*); these parts will be fully described in the adult stage.

The single pre-maxillary (*px.*) is edentulous; it has ascending, lateral, and palatine portions.

The maxillaries (*mx.*) are arcuate rods, pointed and bladed behind; the palatines (*pa.*) are hatchets with a coiled blade and an out-turned, pointed handle; the pterygoids (*pg.*) are arcuate and flat, with a spindle-shaped outline; on their outer edge the handle of a small trowel-shaped bone, whose blade is gapped, is attached; the broad end rests on the maxillary. This is the transpalatine (*t.pa.*).

The columella (*co.*) begins to ossify about this time; this part and the mandible will be described in the next or *ripe* stage.

*Sixth Stage. Ripe Embryos of the Snake, 6½ inches long.*

This is a very important stage; the osseous centres are all present, and none of them ankylosed to others; the synchondrosial tracts are mere clearly defined divisional lines.

From this stage to the adult few changes of any importance, except in size, occur. It is a strong skull even now; the changes afterwards go to make it one of the strongest known; this is the case in this and other small Ophidia, but in the gigantic kinds the skull is a marvel of solidity, there being much ankylosis, whilst the bony substance is like ivory.

The roof-bones have reached the top of the skull, but the fontanelle is still large (Plate 31, figs. 4 and 6); a side view of the interior (fig. 3) of the skull, whose septum nasi has been removed, will display most of the cranial characters.

Nearly all the ossified chondrocranium lies behind the eyes; this is almost entirely *occipito-otic*.

The basioccipital (figs. 3-5, *bo.*) is lozenge-shaped and hollow, like the bowl of a spoon. Upon its outer edges there rest three bones—namely, the exoccipitals (*eo.*),

the opisthotics (*op.*), and the prootics (*pro.*); its fore edge is attached by the medium of a band of cartilage to the basisphenoid (*bs.*).

The condyle, which is practically single, although morphologically double, has both this basal and the two lateral bones entering it.

The foramen magnum is finished above by the lateral bones, or exoccipitals (*eo.*); they also send backwards from their upper edge an imbricating process to rest upon the "atlas."

The 9th, 10th, and 12th nerves (9, 10, 12) pierce these bones below; their front margin turns outward in such a manner as to clamp the hind part of the auditory mass, and they thus form a deep salcus on the inner face, the auditory mass swelling out in front of the out-turned exoccipitals (fig. 3, *eo., op.*).

The key-stone of the arch or superoccipital (*so.*) lies on their fore margin; it is a transverse slab, with five sides: the foremost side is emarginate in a concave manner, finishing the rounded outline of the great upper fontanelle (*fo.*).

This roof-slab just touches the opisthotic (fig. 6, *op.*); is imbricated by the epiotics (*ep.*), and is joined to its own side plates (*eo.*) by synchondrosis.

Here we behold a *normal* and *primary* condition, not seen in the hot-blooded "Sauropsidan" Bird—namely, the freedom of the occipital bones from all participation in lodging the labyrinthic canals of the ear; *they* are confined to their own periotic region and bony centres.

The great bones of the otic mass are *three* only, not *five* as in Osseous Fishes. For in the Snake the head is made into a terete wedge; all snags, projections, buttresses, and the like are smoothed down. Thus there is no *endoskeletal* post-frontal ("sphenotic"), nor lateral ear-eave (*tegmen*) over the horizontal canal, to be ossified by the "pterotic."

These three bones are divided by a fine line of cartilage which is bifurcated above, so that it is triradiate (figs. 3, 4).

The huge semicircular canals (*a.sc., h.sc., p.sc.*) have long ago so dominated the whole capsule as to force it into conformity with their arches and swelling ampullæ; the vestibule and cochlea are relatively small.

Also the bony walls being merely the ossified cartilaginous capsule, with but little periosteal deposit, keep the very form, outside, of the elaborately ornate contents.

The foremost of the three, the prootic (*pro.*), is equal in size to the other two; and the opisthotic (*op.*) is the larger of these; the smallest of the three, the epiotic (*ep.*) contains no ampulla; the prootic has two, and the opisthotic one, of the pouches.

The prootic bone encloses the ampullæ of the anterior and of the horizontal canals; it runs along their pipes, and reaches to the middle of the horizontal and to the last third of the anterior canal.

Below, its anterior part rests upon the small alisphenoid, and behind that it runs down and rests equally upon the basisphenoid and basioccipital, wedging in between them. The prootic forms the back to the foramen for the third part of the trigeminal nerve, and encloses the passages of the 7th and 8th (figs. 3, 4; 5<sup>3</sup>, 7, 8); it ensheaths the fore face of the cochlear pouch, and forms the front margin of the fenestra ovalis (*cl., f.o.*).



The opisthotic (*op.*) ensheaths the back face of the cochlea, forms the back margin of the fenestra ovalis, and forks over the fenestra rotunda nearly enclosing it (fig. 5, *op.*, *f.r.*); but this part is left unfinished, and the *fenestra rotunda* does not open into the cochlea.\*

The opisthotic takes in the ampulla and three-fourths of the arch of the posterior canal, which runs up in its hinder edge, close to the exoccipital; its lower margin barely reaches the basioccipital.

The epiotic (*ep.*) is wedge-shaped as seen from without (fig. 4); pyriform as seen on the inner side; and oblong as seen from above.

It takes in the contiguous *fourths* of the anterior and posterior canals, and their common "sinus;" its inner margin, above, slightly overlies the superoccipital; its anterior edge is flanked by a process of the parietal (*p.*) now making the roof.

The sub-reniform stapedial plate is one, both in its cartilaginous, and in this its ossified condition, with the columella (*co.*). I shall describe it with that element.

The alisphenoid (*al.s.*) is planted upon the basisphenoid (*bs.*) and props up the prootic; it is square now, having closed upon the first passage (for the first and second divisions of the 5th nerve, 5<sup>1</sup>, 5<sup>2</sup>), and is notched behind for the third branch (5<sup>3</sup>). These two passages are similar to the *foramen ovale* and *foramen rotundum* of human anatomy; but the *foramen rotundum* here takes two parts of the nerve.

The basisphenoid (*bs.*) does not trespass further forwards along the trabeculæ than to the front of the circumscribed pituitary space; the bone has floored this space, and a cavity for the pituitary body exists above this secondary floor.

Just above the carotid passage (*i.c.*) the parietal (*p.*) is seen mounting up and creeping over the prootic; on the inside (fig. 3) this bone projects strongly inwards in front of the auditory capsule and behind the optic lobes.

The frontal (*f.*) is meeting its fellow above, but there is a considerable space unossified between it and the parietal laterally; at the bottom of this fenestra the small trilobate orbito-sphenoid (*os.*) is seen above, and a little in front of, the optic nerve (2). The highest part of the carinate parasphenoid (*pa.s.*) is seen under and between the optic passages; it is pointed in front and spatulate behind.

The septum nasi (fig. 3) has been removed, and the olfactory cartilage (*ol.*) is seen from the inside; postero-inferiorly we see a crescentic section of the reniform nasal gland (*n.g.*) covered by the septo-maxillary (*s.mx.*), floored by the vomer (*v.*), and having a large labial (*u.l.*) attached to its duct.

Behind the vomer we see the inner nostril, and in the front of the face the pre-maxillary (*px.*) is cut through.

The cartilaginous parts in front of the pituitary space have not altered since the last stage, and only alter in size afterwards.

There is nothing new to mention in the palato-maxillary series of bones, but the mandible is at an instructive stage.

\* In a large Boa, from Demerara, I find no *inter-fenestral* bar of the opisthotic; in *Python sebae* it exists, as in our native Ophidia.

The suspensorium is now, in the closed mouth, placed at less than a right angle to the "ramus;" besides this, it is now firmly attached by its upper edge to the outer face of the hinder half of the long sub-falci-form squamosal (fig. 7, *q.*, *sq.*).

Inside the middle of the squamosal there is a small sub-oval scale of bone, the supra-temporal: here it is only distinct for a time, but in Lizards it is so permanently.

The quadrate (*q.*) is flat and fan-shaped above, and terete below: the upper part is still soft: the lower end only at the condyle.

The articulare (*ar.*) has almost ossified the whole of the long angular process, and runs forward over the middle of the Meckelian rod (*mk.*).

At the middle and from thence, forward, that rod is wholly unossified, and in this type the middle of the mandible is its "coronoid region;" there the coronoid bone meets the splenial (*cr.*, *sp.*); they are attached by enlarged ends, the point of one looking forwards, and of the other backwards.

The dentary (*d.*), surangular (*s.ag.*), and angular (*ag.*) are seen in the same figure: the latter on the inside mainly; the other two principally on the outside.

But the backward extension of the huge mandibular arch has thrust it past the hyoid rudiment; this is the cause of the very peculiar position of the stylo-hyal and columella (*st.h.*, *co.*) on the inner face of the quadrate.

The third branch of the 5th nerve, the facial nerve, and the columella, take the same backward direction, as a correlate of the extreme backward extension of the gape.

Notwithstanding the small size of the arrested hyoid arch, it has become segmented into the two normal pieces; the columella (minus the stapedial plate) answering to the hyo-mandibular, whilst the stylo-hyal is the upper part of the familiar "stylo-cerato-hyal" bar.

The true stapedial portion of this compound columella (figs. 4, 5, 7, 8, *st.*) has its posterior margin almost straight, the fore edge being well curved: its inner face is concave (fig. 8).

The shaft (*co.*) is gently sigmoid; the terminal third is unossified: this is the "extra-stapedial part," and it has no supra-stapedial spur.

The form of the original rod (Plate 28) is scarcely changed, but the direction is backwards instead of forwards; the capitular part is below and forwards, the tubercular above and backwards.

There is no distinct *membrana* nor *cavum* tympani, and at present the stylo-hyal cleaves to the columella.

This element is reniform (fig. 8, *st.h.*), and its middle and convex portion is covered with a scabrous ectosteal plate; this and the extra-stapedial are jammed between the skull and the quadrate (figs. 4 and 7).\*

\* This explains what for many years was an enigma to me—namely, that in every ophidian skull I examined there was to be seen a thin scale of bone adherent to or coalesced with the inside of the quadrate, above its middle. The arrested stylo-hyal is stowed away there, permanently; faint, and functionless.

*Seventh Stage. Snakes six weeks old,  $7\frac{2}{3}$  inches long.*

Being informed by Professor HUXLEY that there was cartilage in the distal parts of the Snake's hyoid or lingual region, I made diligent search both in early stages and in the adult: the evidence obtained was negative.

Knowing well that feeble parts are often late in budding forth, and early in fading, I considered it to be the best chance for finding hypo-hyal or hypo-branchial rudiments in the Snake to look for them in well-grown young.

I thus take this for my *seventh stage*: there has been plenty of time for such cartilages to appear, but none for their vanishing: the result is the same; I can find no hyaline cartilage whatever between the distal parts of the mandible and the larynx; all the floor of the mouth with the forked tongue and its sheaths are membranous.

The other parts need have no further notice; there need be no intermediate stage for them between the ripe young and the adult.

*Eighth Stage. Skull of the adult Snake.*

There are several reasons why the skull of the adult Snake should be worked out exhaustively,—in the light of the history of its development.

One reason is, that the "Ophidia" are a large and important order of the Saurosida, and to know one is to know all, so uniform are they, save in easily understood specializations.

Beginning at the Amphisbænæ and Anguians, if we run up the Lacertian Order, we shall find that their skull also can be read off in the light of that of the Snake.

The skull of other groups also, fossil or recent, will be more intelligible when once this kind is known; for the Snake's skull is at once extremely simple, and yet marvelously specialized: some things in it stand almost still, whilst others run to the utmost stretch of their morphological tether.\*

The skull of the adult Snake is irregularly oblong, flat above in its fore part, and sub-carinate below; but the hinder part is gently convex both above and below (Plates 32 and 33).

The orbital and occipito-otic regions are about equal; the nasal region is about half the length of the others.

The gently bi-convex, transverse, occipital cincture articulates with the atlas by a transversely oval condyle (Plate 32, fig. 2, *oc.*, *c.*); above, the arch overlaps the vertebra in an imbricated manner (fig. 1).

\* Most solid in its *cranial*, yet the Snake's skull is, of all others, the most elastic and mobile in its *facial* parts; no foot must bruise its head, for it is doomed to go on its belly all the days of its life, yet its throat must be, practically, "unhidebound;" devouring, as it does, prey, whose girth is many times its own.

The basioccipital (*bo.*) is an irregular lozenge, transversely placed; it is slightly emarginate in front, and mammillate for muscular attachment.

It articulates with the basisphenoid in front (Plate 32, fig. 2, *bo.*, *bs.*), with the exoccipitals postero-laterally; in front of these (Plate 33, figs. 1, 2, *pro.*, *op.*) it receives the prootic and opisthotic.

With the hind part of the basisphenoid (Plate 33, fig. 1), it forms a very considerable hollow for the medulla oblongata.

The strong sides of the arch, the exoccipitals (*eo.*), run their lower angle into the condyle (*oc.c.*), whilst above the foramen magnum they meet and push out the superoccipital wedge (*so.*); they have coalesced with the opisthotics; the 9th, 10th, and 12th nerves pass out (Plate 33, fig. 2) close to the lower line of their ankylosis.

The superoccipital also seems to be much larger than in the young; this arises from its coalescence with the right and left epiotics (*ep.*).

It is now a five-sided, transverse roof-bone, its outer or epiotic angles being somewhat convex (Plate 32, fig. 1; Plate 33, fig. 2).

The parietals (Plate 33, fig. 1, *p.*) scarcely overlap the superoccipital; the junction is by a harmony-suture, exactly where the prootic (*pro.*) begins.

This main auditory bone has also coalesced with a true cranial element—the alisphenoid (*al.s.*); yet the tri-radiate suture between the three periotics is persistent; each element of the capsule is distinct from the other two, and yet each is fused to a neighbour-bone of the skull wall.

Here a distinct cartilaginous sense-capsule is ossified by three centres, which disclaim, as it were, their true affinity to each other, and lose themselves in the cranial wall.

In the Mammals, in sharp contrast with these transformations, the capsule chondrifies with but slight separateness from the cranial wall; and then these three centres ossify the capsule, and completely enucleate it from the skull proper. This is best seen in Shrews, the lesser Bats, and the Whale-tribe.

In the Bird these parts behave as in the Reptiles, but with this difference—namely, that the opisthotic and epiotic are very small, so that the labyrinth of the ear grows into the occipital arch.

The *otic* elements first unite with their *cranial* neighbours, and then everything is ankylosed; all the morphological writing is blotted out in that Class.

These lateral and upper cranio-auditory plates are marked with the form of the enclosed labyrinth, as may be seen by comparing their wavy surface with the form of the earlier cartilaginous capsule.

Infero-laterally, these plates are riddled with holes, mostly for the passage outwards of the cranial nerves.

In the crescentic chink below the opisthotic region (*op.*) the exoccipital is perforated for the 12th, 10th, and 9th nerves; these can be seen on their emerging below, but better in the inside; for externally they are partly hidden by that angle of the opisthotic which contains the hinder ampulla (*p.sc.*).

Above the exit of the 12th there is a small passage for a vessel; this hole is evidently the "foramen condyloideum posticum."

In front, on the inner side (Plate 33, fig. 1; 5), the large foramen ovale is reniform, and the space is large where the Gasserian ganglion gives off the *trigemini*; but a buttress of bone outside (fig. 2), formed by junction of the horns of the alisphenoid into a ring, causes the first and second branch to divide off, and leaves the third to take a recurrent course.

This it does (fig. 2; 5<sub>3</sub>); and in some Snakes, especially the gigantic kinds, the bone is deeply grooved for this large mandibular nerve.

Behind the foramen ovale there are two larger and one smaller passage; the first of the larger holes transmits the facial nerve (7); the largest hole is for the 8th, in its passage to the membranous labyrinth.

A directly lateral view outside (fig. 2) does not show the holes for the 9th, 10th, and 12th nerves; but behind the hole for the facial (7th) we see two rather large passages: these are the fenestra ovalis and fenestra rotunda. In the figure the columella (*co.*, *st.*) is dislocated purposely; it has become relatively small, and its shaft a mere prickle.

As we saw in the ripe young (Plate 31), two spurs of the opisthotic stand upon the edge of the skull floor; the first of these divides the fenestræ from each other, and the other forms the back part of the fenestra rotunda, and is clamped to the fore edge of the exoccipital.

In the *dry* adult skull the fenestra rotunda is seen to have but a slight relationship to the membranous labyrinth; for the cochlear bud does not grow, the stapedial plate closes in the passage to the vestibule, and the fenestra rotunda opens into the cavity of the skull.

The lozenge-shaped alisphenoid forms both a wall and an eave to the second part of the foramen ovale; it also forms a double prop on which the swelling prootic rests, the "wing" itself resting obliquely upon its own base—the basisphenoid (*bs.*).

This latter is now a *compound* bone; it was made from the two proper basisphenoidal centres, and has gained a bulging floor and a large carinate rostrum from the parasphenoid (*pa.s.*).

But neither the parasphenoid nor the basisphenoid directly floor the cranial cavity; the arrest of the chondrocranial elements is correlated with a very curious undergrowth of the *roof* bones (*f.*, *p.*).

The frontal meets its fellow below, and the parietal nearly (fig. 1); the pituitary body is let down through a longitudinal chink between the floor-plates of the parietal, and there it finds a large empty room, "a world too wide" for so small a body.

By reference to the earlier stages this is easily understood, for the roots of the trabeculæ were planted on to the "investing mass" far apart, and no floor existed until the parasphenoidal blade grew backwards beneath the unfloored space.

Not only has the front fontanelle, or false floor, thus gained a good floor of bone, but the hinder gaping space is floored also (see earlier figures, *p.b.c.f.*).

Now, (Plate 32, fig. 2, *bo.*, *bs.*, and Plate 33, figs. 1, 2, *bo.*, *bs.*) the basioccipital and the basisphenoidal plates have supplied what was wanting by periosteal growths; between these two large slabs there is a persistent speno-occipital suture.

The post-pituitary part of the basisphenoid (Plate 33, fig. 1, *bs.*) shelves down behind the post-clinoid ridge, obliquely roofing the sub-cranial cellar; this it does completely, behind.

But in front, as before said, the two parietals fail to meet below the mid brain (fig. 1); they, however, send strong tentorial ingrowths, which run from the front of the auditory mass into the floor.

Above (Plate 32, fig. 1, *p.*), the parietals are completely confluent along the *sagittal* line; there they are somewhat depressed in this small kind, but in the gigantic kinds there is a parietal crest as strong as that of the Hyæna or the Tiger.

Also behind the coronal suture (which is persistent) the parietal grows inwards, filling up the space above, between the mid and fore brain (Plate 33, fig. 1, *p.*).

Above the beginning of the rostral part of the sphenoidal beam there is a large optic fenestra, as in the Batrachia, much larger than the optic nerve, and above this there is a post-orbital fenestra between the orbital regions of the parietal and frontal (Plate 33, figs. 1 and 2).

This is partly filled in by the small trifoliate orbito-sphenoid (*os*), which cleaves to the hind edge of the frontal descending plate.

The parasphenoidal rostrum ascends to meet the orbito-sphenoid in the angle between the diverging optic nerves, then for the rest of its length the crest is lower (Plate 33, figs. 1, 2, 3, *pa.s.*).

Both externally (fig. 2) and in section (fig. 3) the trabeculæ (*tr.*) are seen as unossified rounded rods, as far as the parasphenoid goes, that is, up to the olfactory region.

As in front of the ear-mass the parietals grew inwards, so behind the olfactory walls the frontals do also, but more perfectly (Plate 33, figs. 1 and 4, *f.*), for they are fitted, face to face, at the mid-line.

A recess on each side receives the narrow end of the fore brain, and under these lobes (C<sup>1</sup>) the olfactory crura (1) pass to their destination (fig. 4).

There the frontals spread and articulate with each prefronto-lachrymal (*p.f.*), but further back they completely enclose the brain, as in certain Mammals (Plate 33, fig. 3, *f.*).

The sectional view (fig. 3) shows well the curious architecture of the Snake's skull: the roof and side walls are made by the frontals, the former flat, the latter concave and slanting inwards; the frontal suture (Plate 32, fig. 1, *f.*) is persistent. An eave is formed by the prefronto-lachrymals (*p.f.*), and a strong foundation by the crested parasphenoid (*pa.s.*), burrowed on each side by the trabeculæ (*tr.*): here the whole strength of this strong building is derived from membranous materials external to the endo-cranial elements.

The post-orbital region has an additional eave-tile, a post-orbital scale bone (*pt.o.*),

which cleaves to the post-frontal projection of the large parietal bone—a remarkable state of things certainly, but the parietals are prepotent in the Snake's skull.

The foremost *fourth* of the skull belongs to the olfactory region: the essential parts here are most simple, the superadded things are as curiously complex as anything to be found in Vertebrate morphology.\*

The fore end of the Snake's skull is composed of the following elements, viz.:

- (a.) The coalesced vertical part of the trabeculæ, and
- (b.) The nasal roof-cartilages (sense-capsules) grafted thereupon.
- (c.) The short confluent trabecular cornua,—the rudiment of a terminal visceral arch (first pre-oral).
- (d.) Attached to, or partly coalesced with these cornua, two pairs of upper labial cartilages.
- (e.) Nine membrane-bones, of which the odd one, the premaxillary, is the splint of the cornua, the nasals or splints of the olfactory roof, the prefronto-lachrymals or splints of the postero-lateral region of the nose, and the septo-maxillaries and vomers, which are related to the middle wall of the nasal capsules.
- (f.) Lastly, there are the huge nasal glands, that are encapsuled in the last-mentioned bones.

(a.) The form and relations of the septal portion of the trabeculæ are shown in the lateral view of the bisected skull (Plate 33, fig. 1, *s.n.*), and in the series of transverse sections (Plate 33, figs. 6-14, *s.n.*).

This wall is highest where the olfactory cartilages are united to it, behind, and lowest in front when the roof cartilages overlap it (fig. 6).

(b.) The nasal cartilages (*ol.*) are quite simple; I find no turbinal outgrowths in them whatever.

They are only imperfectly covered by bone (Plate 32, fig. 1); they turn inwards below in some degree, especially behind (Plate 33, fig. 4, *n.f.*), forming at the beginning of the septum a partial floor.

They are baggy in front (Plate 33, fig. 5), and notched externally for the nostril (Plate 32, figs. 1 and 3, and Plate 33, figs. 2 and 5).

(c.) The recurrent cornua are very short and have a median rudiment of the pre-nasal cartilage (Plate 32, fig. 3, *c.tr.*, *p.n.*); I found, in that specimen, the left cornu confluent with the first upper labial (*u.l.*).

\* My study of these structures in the Snake began ten or twelve years ago, during which time I have had frequently to refer to them in the descriptions of their homologues in other types, especially in the Birds, so far above them. The reason of the delay as to this paper has been the slow incoming of embryos young enough for my purposes.

Now, however, I can show a sort of practical standard, towards which the Ganoid and Teleostean Fishes and the Amphibia ascend, and from which the higher Reptiles and the Birds take their start. Of course I speak of the use of this Ophidian standard as an arbitrarily practical matter, and I do not wish to suggest anything except in a general way as to the actual descent of these Vertebrate types.

(*d.*) These labials are shown *in situ* in the same figure, which shows the nasal roofs from below, with the underlying parts.

The first labial is pointed in front: this is free or coalesced with the corresponding trabecular cornu, it then becomes wider, diverges, and becomes pedate and sub-bifurcate.

This first labial keeps along the suture, between the septo-maxillary above, and the vomer below (Plate 32, figs. 2, 3, and Plate 33, figs. 2, and 5-9, *u.l.*<sup>1</sup>, *sm.x.*, *v.*); it reaches the opening between the two bones for the duct of the nasal gland (*n.g.*).

The second upper labial (*u.l.*<sup>2</sup>) is a broader cartilage; its external part, which acts as a valve to the opening for the duct, is oblong, but the band is carried inside the capsule, and then ends in a rounded lobe (Plate 33, fig. 10, also figs. 2, 9, 11, 12, 15, and 16; and Plate 32, figs. 2, 3).

(*e.*) The azygous bone attached to the nasal region is the premaxillary (*px.*): it has a somewhat angular anterior margin, a short, blunt nasal process (Plate 32, fig. 1, and Plate 33, figs. 1, 2), an edentulous edge, and two short, rounded palatine processes (Plate 32, fig. 2).

The nasals (*n.*) imperfectly cover the roof, their upper surface (Plate 32, fig. 1) is roughly triangular, and they send down a vertical plate between the cartilages, the right and left plates lying back to back; these plates are deeper than the septum nasi (Plate 33, figs. 1 and 6-12, *n.*, *s.n.*).

A stout shell of bone, having a lozenge-shaped outline, lies over the outside of the olfactory cartilages; this is the prefronto-lachrymal (*pf.*). It has the character, and supplies the place of both those bones; by this the orbital rim is finished in front, and to the lower process of this bone the maxillary is attached, especially in venomous Snakes.

If this bone had grafted itself upon the cartilage, it must have been called the prefrontal or ecto-ethmoid; it is, however, as free as the ordinary pre-orbital or lachrymal.

Nothing that has come under my notice in cranial morphology shows a more curious or a more elegant architecture than the four *pre-palatal* bones now to be described.

The upper pair are the so-called inferior turbucals of older authors; but the Snake has no inferior turbucals, and when these exist, they are not membrane-bones, but cartilages, soft, or more or less ossified, that grow as outgrowths from the inner face of the nasal wall, and run from the inside of the outer nostril downwards and backwards to the "choana" or "middle nostril."

Those outgrowths are largely developed in Birds and Mammals, and I find a rudiment of them in *Chelone mydas*, and in Lizards.

But these bones form a floor to the nostrils; they are found in both Urodeles and Anourous Batrachia; and if those of the Lizards—the *Varanians* especially—be compared with that pre-orbital bone of Ganoid and Siluroid Teleostean Fishes, which



lies directly beneath the nasal, and above the maxillary, the homology will at once be seen.

There they are mere muco-dermal bones, enclosing part of the net-work of the mucous glands of the head, where the "lateral line series" breaks up into rows. In the Amphibia and Reptiles they are specialized—just as other dermal bones are specialized—and assist in walling-in and flooring the more and more perfect nasal labyrinth.\*

Here, in the Snake all the *slime-glands* appear to be concentrated into one on each side (Plate 33, figs. 9–12, *n.g.*), and these glands find a place under the olfactory pouches—involutions of the antero-inferior regions of the face.

Moreover, the bone which I seize upon in the Siluroid *Clarias capensis* as the fore-runner of the reptilian septo-maxillary is the "os-terminale" of the *sub-orbital* series of slime-bones, as the "nasal" of the fish is the "os-terminale" of the *super-orbital* series.

Seen from the inside (Plate 33, fig. 16, *s.mx.*) the septo-maxillary is a flat wedge, broad behind and pointed in front; this flat inner face is separated from the septum nasi by the thick sub-mucous stroma (Plate 33, figs. 6–14, *s.mx.*, *s.n.*).

Its upper surface is sinuous (figs. 6–15) for at its broadest part, where it forms a lid to the *vomerine dish*, containing the kidney-shaped gland, it shelves downwards, is gently convex and then rises into the nasal wall (figs. 9–11), and also grows round the side of the gland. In front (figs. 6–8) it is a mere splint; behind (figs. 13–15) it is a thick plate.

The vomer is related to the lower edge of the septum (figs. 7–14, *v.*); on its inner face it is flat, but has a larger and more irregular surface than the septo-maxillary (fig. 16, *v.*).

Below (Plate 32, fig. 3, *v.*) it shows three parts: an anterior spike; a middle bowl; and a hinder ear-shaped lobe. The bowl (see also Plate 33, figs. 2 and 15, *v.*) is notched for the duct of the gland and the second labial (see also figs. 10, 11).

Thus in some of the sections (figs. 11, 12) we apparently have two bones; these, however, are only parts without and within the notch.

Where the duct passes out (fig. 11, *d.n.g.*) there the gland is most accurately encapsuled; the septo-maxillary, as a *lid*, with its rising outer and inner edges, covering the gland, which is embraced by the curling laminae of the vomer both without and on the inner side.

The copious illustrations of this pleasing piece of morphology will make the above description quite intelligible.

\* In the Herring and its congeners, the maxillary bone carries two bones on its back; the hinder of these looks forwards, and forms an acute angle with the free end of the maxillary: this is the jugal. The other forms an acute angle with the fore part of the bone, and almost a right angle with the jugal: this is the *pre-orbital*, which takes on the curious specialization in the air-breathers by which it becomes the "septo-maxillary."

(*f.*) The form and relations of the nasal gland (*n.g.*) are involved in the foregoing details :—

The parts remaining to be described are the bones that belong to the maxillo-palatine, mandibular, and hyoid arches; the latter has only two traces, the spike of the columella (*co.*) and the minute style-hyal scale (Plate 32, figs. 1, 2, *st.h.*); but the parts round the mouth are greatly developed and modified.

The palatines, transpalatines, and maxillaries are the three elements of the second pre-oral arch; the first of these (Plate 32, figs. 1, 2, *pa.*) is a slightly inbent rod loosely attached to the sides of the nasal region in front, and overlapping the apex of the pterygoid (*pg.*) behind.

Its ethmoid process (Plate 33, figs. 13, 14, *e.pa.*) is much flatter than in the early stage; it lies over the middle nostril.

The maxillary (*mx.*) is a narrow, arcuate, dentigerous bone; it bounds the gape, running forwards from the pre-maxillary to a point opposite the post-orbital region.

Lying on the jugal end of the maxillary is the blade of a curious hatchet-shaped bone, the transpalatine (*t.pa.*): its handle lies on the outer edge of the middle of the pterygoid.

The mandibular arch is yoked on to the maxillo-palatine by means of the pterygoid (*pg.*): this bone only answers to the bony plate of the Salamander's or Frog's pterygoid; there is no corresponding cartilage budding forth from the quadrate.

This is a long falcate bar, widest in the middle, gently convex below, and slightly scooped above; it is obliquely attached to the under face of the end of the palatine, and then stretches backwards and outwards, clamping the quadrate above and inside its hinge, and reaching to the end of the long angular process of the mandible itself (*ar.*).

In the gigantic types (Python, &c.) there are large "basi-pterygoid processes," on which the pterygoid glides; here these are not distinct.

The suspensorium or quadrate (*q.*) is let down, backwards, by its own splint, the squamosal (*sq.*). This latter bone lies over the auditory mass, reaching to the parietal; it is oblong and rounded in front, and behind it is bevelled and faced, there, with articular cartilage.

The supra-temporal scale is now ankylosed to the squamosal.

The broad, oblique, top end of the quadrate (*q.*) glides over the articular face of the squamosal, and then lessening, this bone becomes a rib-like rod, with a cylindroidal condyle for the excavation in the articulare (*ar.*).

This latter bone has ossified much of Meckel's cartilage, and is invested with the long angular and surangular, both narrow and pointed at both ends (*ag.*, *s.ag.*).

There is a partial hinge on the ramus opposite the end of the maxillary, dividing the bar so as to leave only two-fifths in front and as much as three-fifths behind.

Externally, the dentary (*d.*) overlaps this part by its forks; but, on the inside, the splenial and coronoid (*sp.*, *cr.*)—the latter is the larger bone—meet each by a broad

end, the suture being vertical; this is the anomalous position of the true *coronoid region*; the two bones are very similar, but their points look in opposite directions.

These two bones hide the shrivelled remains of Meckel's cartilage; none of these bones of the mandible are dentigenous except the dentaries, and only the palatines and pterygoids and maxillaries above.

Of the hyoid or second post-oral arch I can only find two rudiments, and these have lost their independence; the antero-superior or hyo-mandibular element is now the small columellar prickle on the oval stapedal plate (Plate 33, fig. 2, *co.*).

The other, or postero-inferior, piece is starved and useless; it is ankylosed to the inner face of the quadrate, towards the back of the upper third (Plate 32, fig. 2, *st.h.*). This is all that remains of the stylo-cerato-hyal bar; at least I have failed to find any cartilage in the distal or lingual region.

#### *Concluding Remarks.*

I have carefully studied the skulls in the ripe young and the adult of Lacertians, Chelonians, and the Crocodiles, but time has not served for working them out from their early stages.

Materials are ready for the Lacertians and their sub-group, the *Anguians*. Early embryos of the Tortoise\* and Crocodile are still wanting; yet this present piece of work, it is to be hoped, will be of considerable use. It will serve me as a lantern with two windows: letting light backwards upon the Ichthyopsida and forwards on to the nobler Reptiles; and it will light up even the winged Fowls that, in their perfectness, seem to have exhausted the possibilities of the Sauropsidan type.†

#### DESCRIPTION OF THE PLATES.

##### PLATE 27.

Fig. 1. First stage. Side view of Embryo of Common Snake (*Tropidonotus natrix*), whose total length was  $\frac{3}{4}$  inch.  $\times 17$  diameters.

Fig. 2. Head of the same, severed and slightly bent back (straightened); lower view.  $\times 17$  diameters.

Fig. 3. Second stage. Side view of the head and neck of an older Embryo, measuring about 1 inch in length.  $\times 16$  diameters.

\* Since the above was written, I have received from Sir WYVILLE THOMSON several *large*, and from Mr. MOSELEY many *small*, embryos of this important type.

† The use which I have made from time to time of the Snake's skull may be seen by reference to various papers on the Structure and Development of the Bird's Skull in the Transactions of the Royal, Linnean, Zoological, and Microscopical Societies. In the Snake's skull, *ichthyic elements* are curiously specialized; in that of the Bird the same parts re-appear, but in most remarkable metamorphic combinations.

Fig. 4. The same from below (not straightened).  $\times 16$  diameters.

Fig. 5. The same from above.  $\times 16$  diameters.

Fig. 6. Palatal view of severed head of same.  $\times 16$  diameters.

#### PLATE 28.

Fig. 1. Third stage. Side view of the head of an Embryo,  $1\frac{3}{4}$  inch long.  $\times 8$  diameters.

Fig. 2. The same dissected.  $\times 8$  diameters.

Fig. 3. The same from above.  $\times 8$  diameters.

Fig. 4. The same; palatal view, with lower arches removed.  $\times 8$  diameters.

Fig. 5. Longitudinally vertical section of the same.  $\times 12$  diameters.

Fig. 6. Palatal view of same dissected.  $\times 12$  diameters.

Fig. 7. Ear-capsule and arches of same, side view.  $\times 12$  diameters.

Fig. 8. Upper view of chondrocranium of an older Embryo, measuring  $2\frac{1}{4}$  inches long.  $\times 12$  diameters.

Fig. 9. Nasal capsule of same, front view.  $\times 12$  diameters.

#### PLATE 29.

Fig. 1. First stage. Vertical section of head of youngest Embryo,  $\frac{3}{4}$  inch long.  $\times 17$  diameters.

Fig. 2. Second stage. Vertical section of head of Embryo, 1 inch long.  $\times 12$  diameters.

Fig. 3. Fourth stage,  $2\frac{1}{2}$  to 3 inches long. Side view of skull with nasal sac removed to show septum nasi.  $\times 15$  diameters.

Fig. 4. Upper view of a skull of a somewhat older Embryo with all the sense-capsules *in situ*.  $\times 12$  diameters.

Fig. 5. Lower view of chondrocranium (same as fig. 3), with eyeballs and nasal sacs not drawn.  $\times 12$  diameters.

#### PLATE 30.

Fig. 1. Longitudinally vertical section of a skull--(fourth stage continued).  $\times 12$  diameters.

Fig. 2. Transversely vertical section of a similar skull through the middle of the nasal region.  $\times 16$  diameters.

Fig. 3. A *second* section through fore part of eyeballs.  $\times 16$  diameters.

Fig. 4. Part of a *third* section through the middle of the eyeballs.  $\times 16$  diameters.

Fig. 5. A *fourth* section between eye and ear.  $\times 16$  diameters.

Fig. 6. A *fifth* section through fore part of ear-capsules.  $\times 16$  diameters.

Fig. 7. A *sixth* section through their middle.  $\times 16$  diameters.

Fig. 8. A *seventh* section between ear-capsules and foramen magnum.  $\times 16$  diameters.

## PLATE 31.

- Fig. 1. Fifth stage,  $4\frac{1}{2}$  to 5 inches long. A horizontal section of the skull showing the floor, from above.  $\times 10$  diameters.
- Fig. 2. The same stage and size, showing skull with palatal bones, from below.  $\times 10$  diameters.
- Fig. 3. Sixth stage. Longitudinally vertical section of skull of ripe Embryo,  $6\frac{1}{2}$  inches long.  $\times 10$  diameters.
- Fig. 4. Hinderpart of same skull, seen from the outside.  $\times 10$  diameters.
- Fig. 5. Part of same view.  $\times 20$  diameters.
- Fig. 6. Same skull, hind part, seen from above.  $\times 10$  diameters.
- Fig. 7. Mandible and columella of same; inner view.  $\times 10$  diameters.
- Fig. 8. Another view of columella.  $\times 20$  diameters.

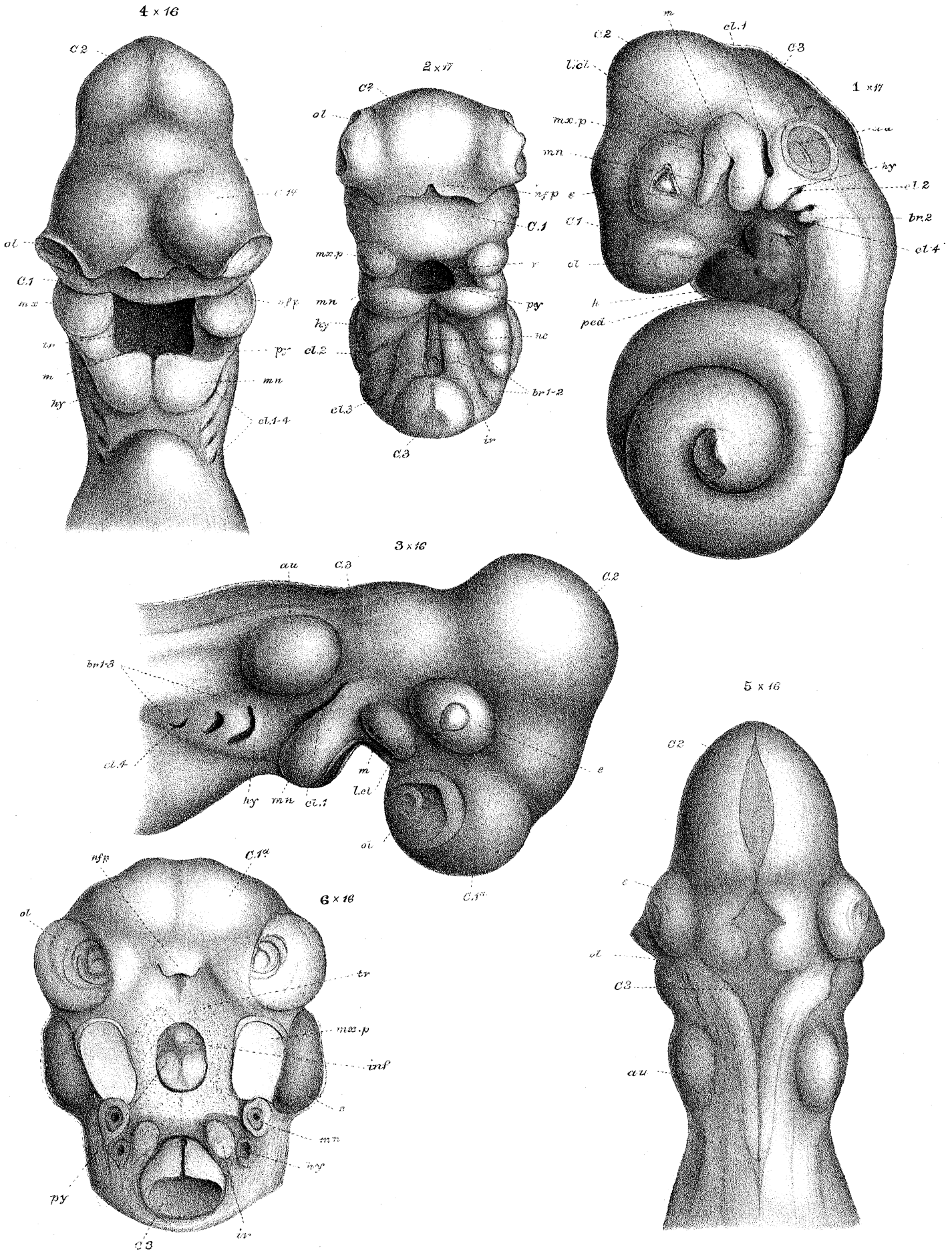
## PLATE 32.

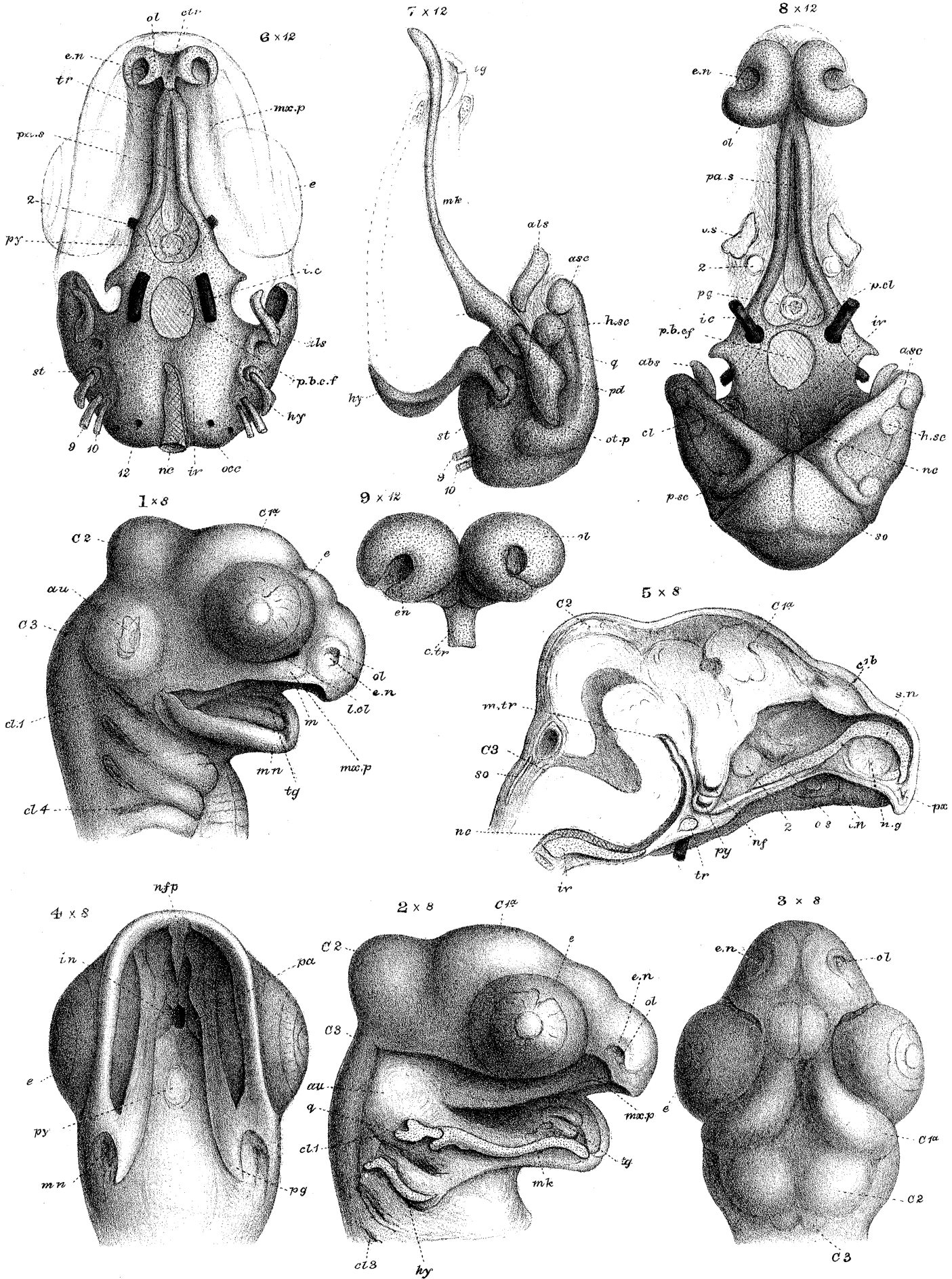
- Fig. 1. Last stage. Adult Snake, upper view of skull and arches.  $\times 5$  diameters.
- Fig. 2. The same from below.  $\times 5$  diameters.
- Fig. 3. Nasal sacs and vomerine bones, from below.  $\times 5$  diameters.

## PLATE 33.

- Fig. 1. Separated cranium of same seen in section.\*  $\times 5$  diameters.
- Fig. 2. Side view of same.  $\times 5$  diameters.
- Fig. 3. Transverse section of same, orbital region.  $\times 5$  diameters.
- Fig. 4. Another section, ethmoidal region.  $\times 5$  diameters.
- Figs. 5 to 14. A series of transversely vertical sections through nasal region of same, from the nostrils to the orbits.  $\times 12$  diameters.
- Fig. 15. Vomerine bones and cartilages of left side, outer view.  $\times 5$  diameters.
- Fig. 16. Those of right side, inner view.  $\times 5$  diameters.

\* The round space seen on *op.*, in this figure, is accidental.



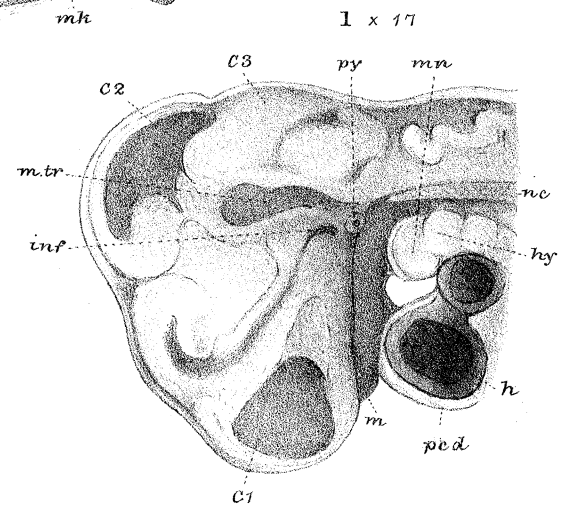
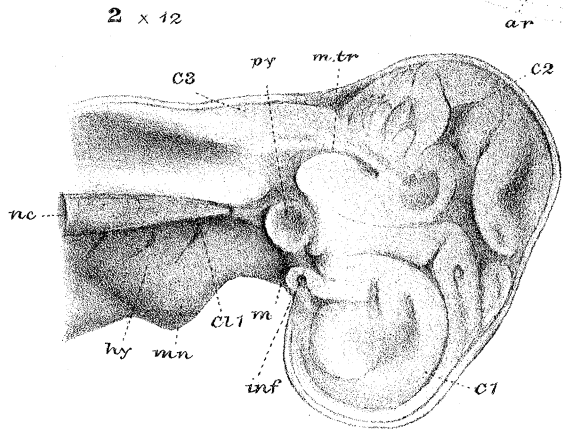
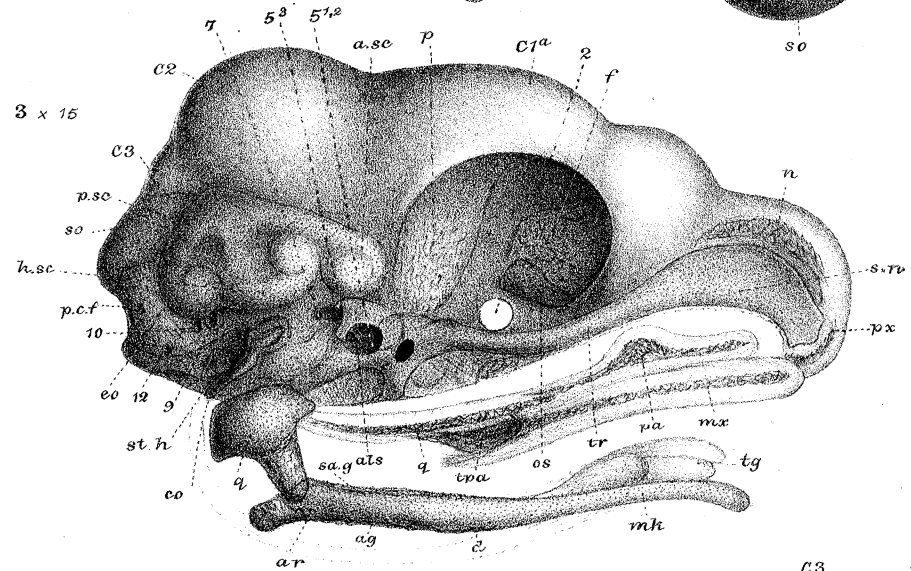
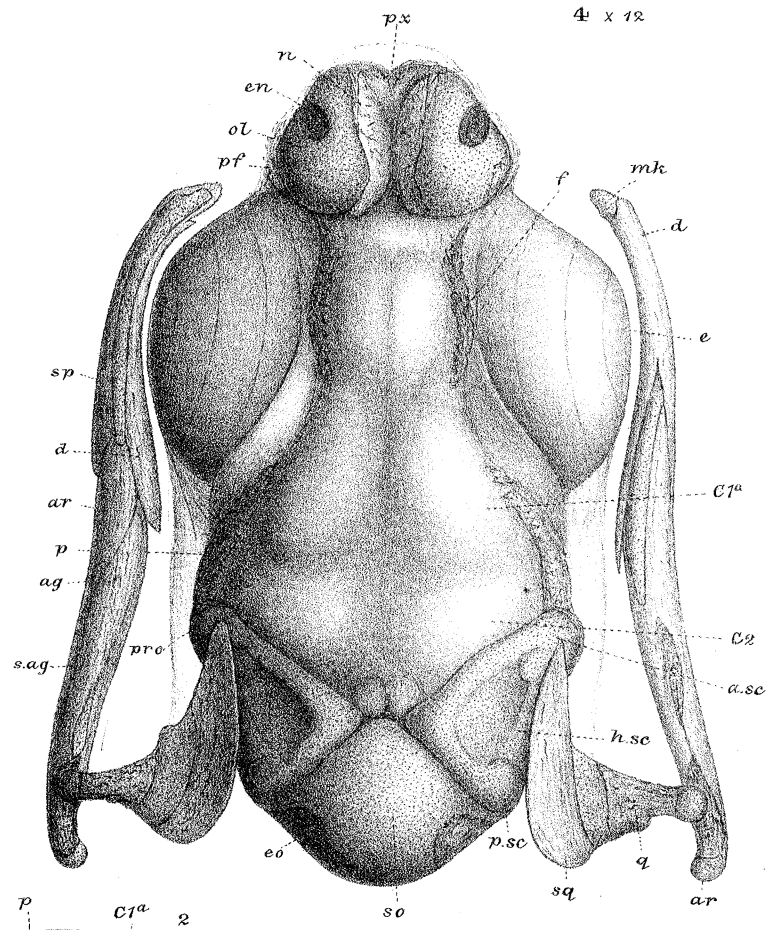
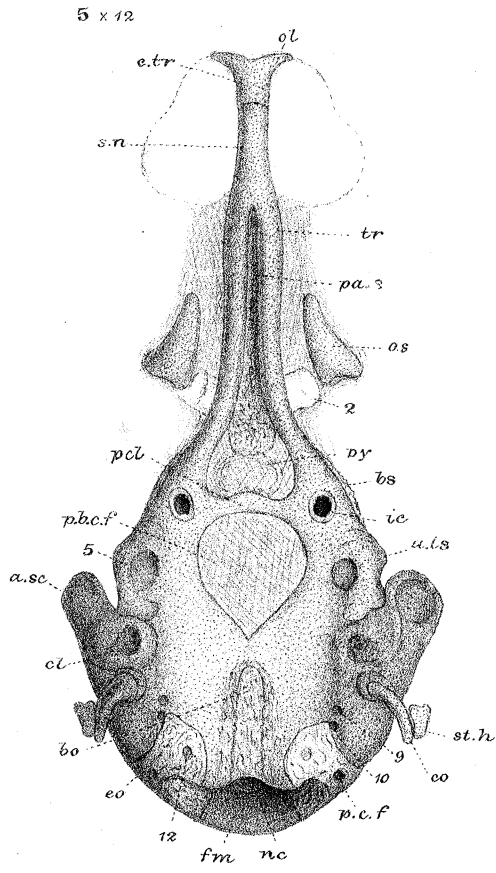


W.K.P. del., ad nat. G. West Junr. lith.

Common Snake.

W. West & Co. imp.



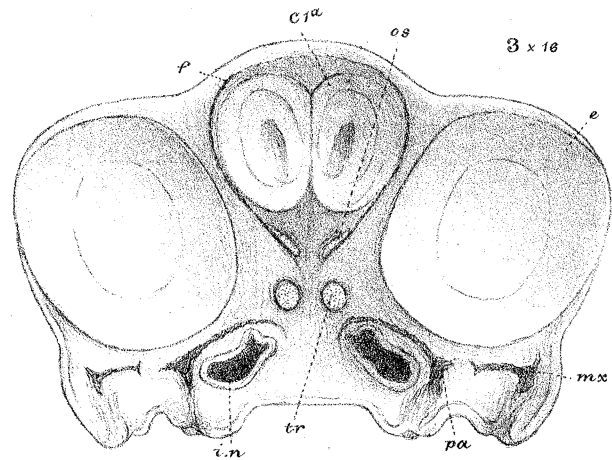
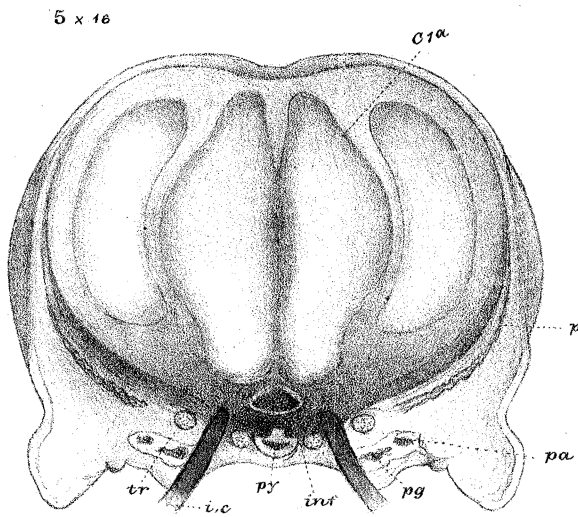
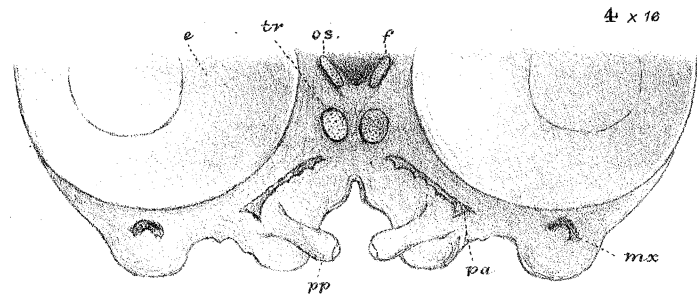
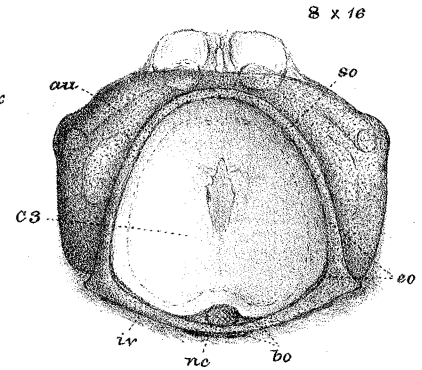
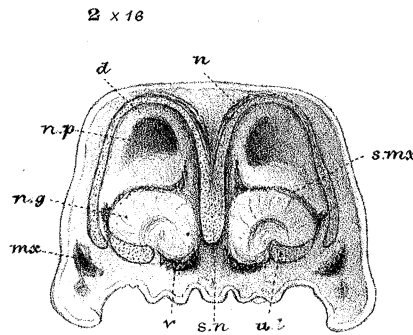
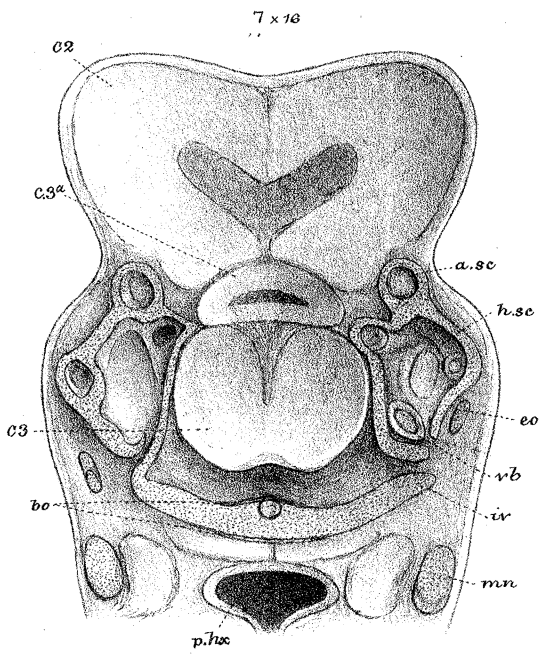
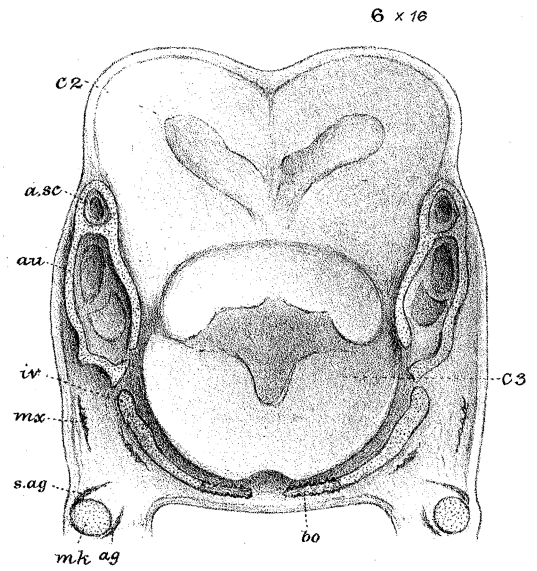
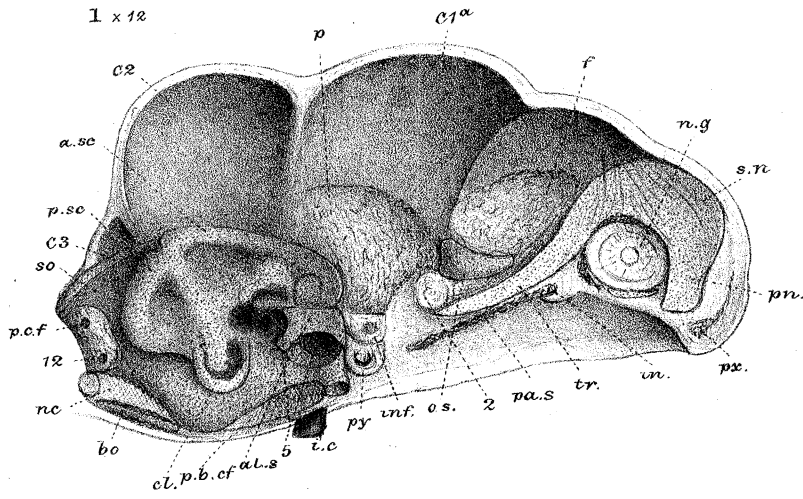


W.K.P. del. ad nat. G. West Junr' lith.

W. West & Co. imp.

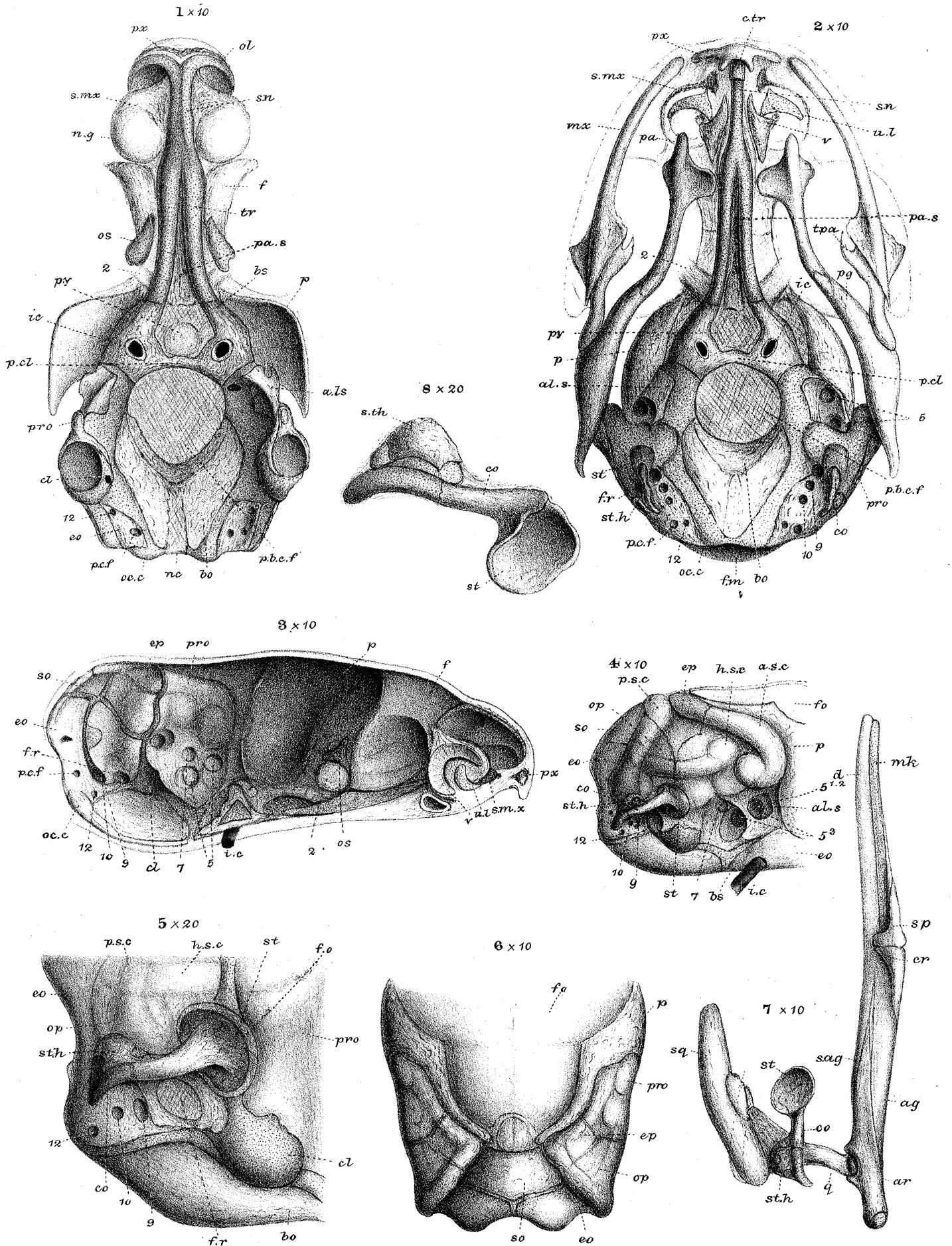
Common Snake.





W.K.P. del. ad nat.  
G. West Junr. lith.

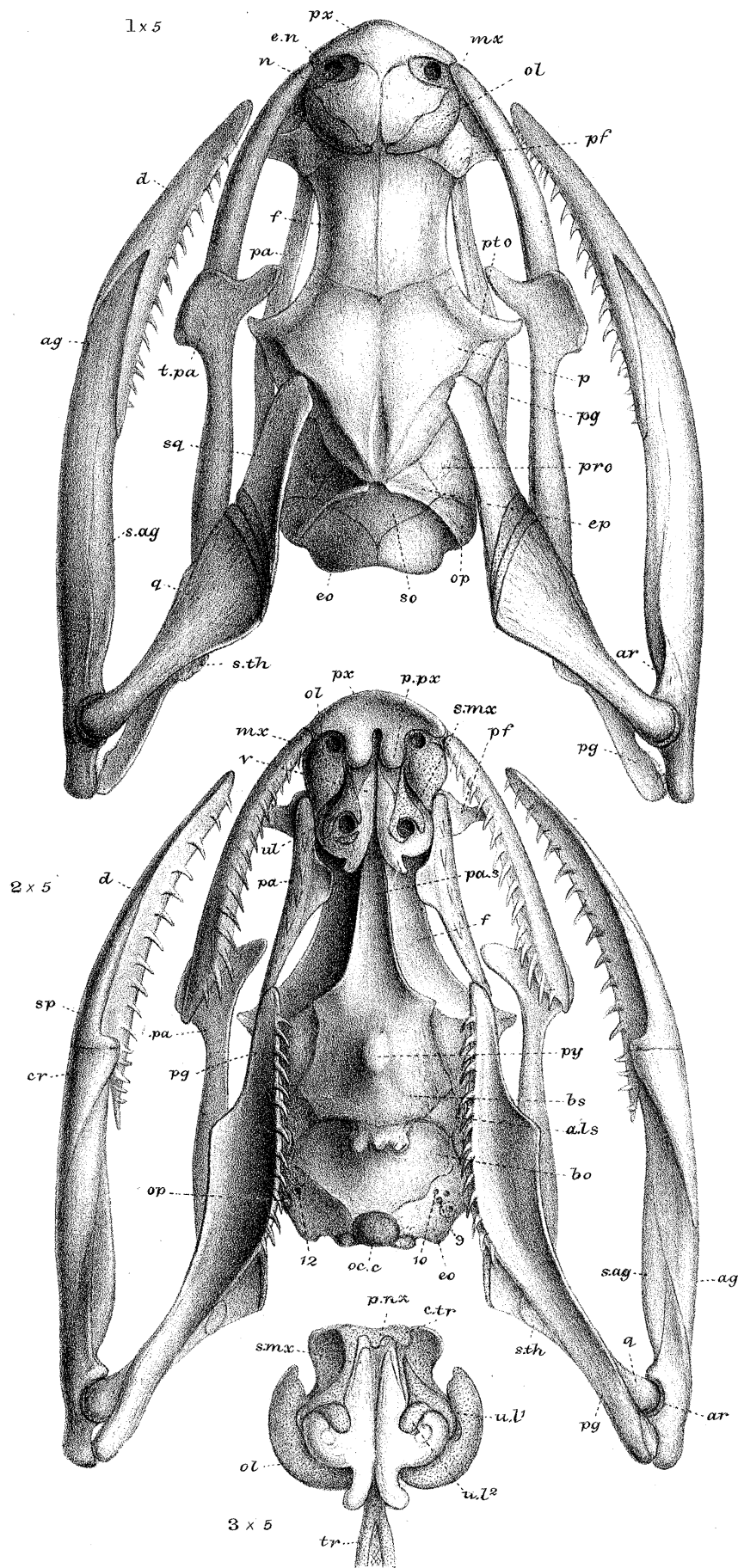
W. West & Co. imp.



W.K.P. del. ad nat. G. West Junr. lith.

W. West & Co. imp.

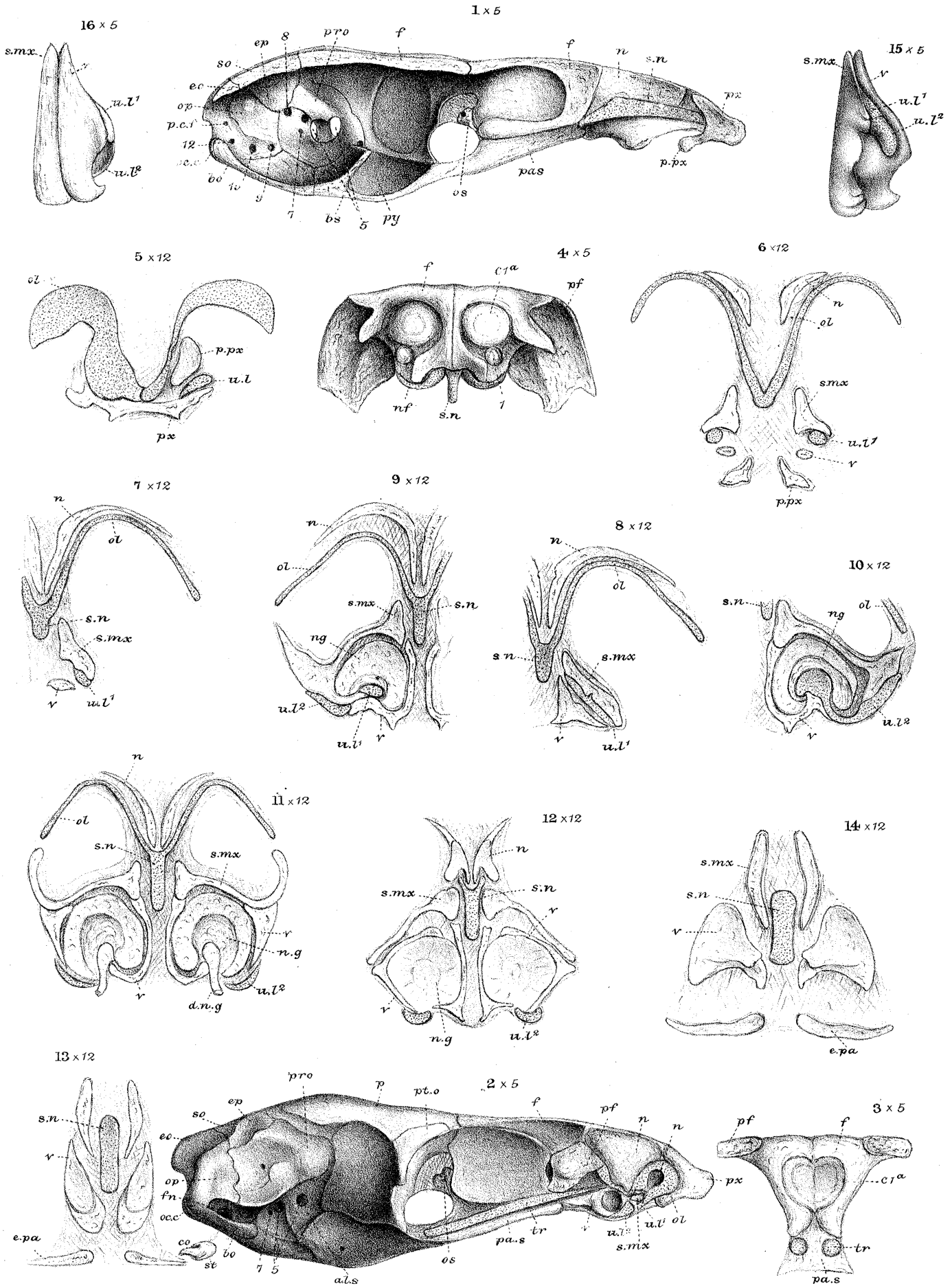
Common Snake.



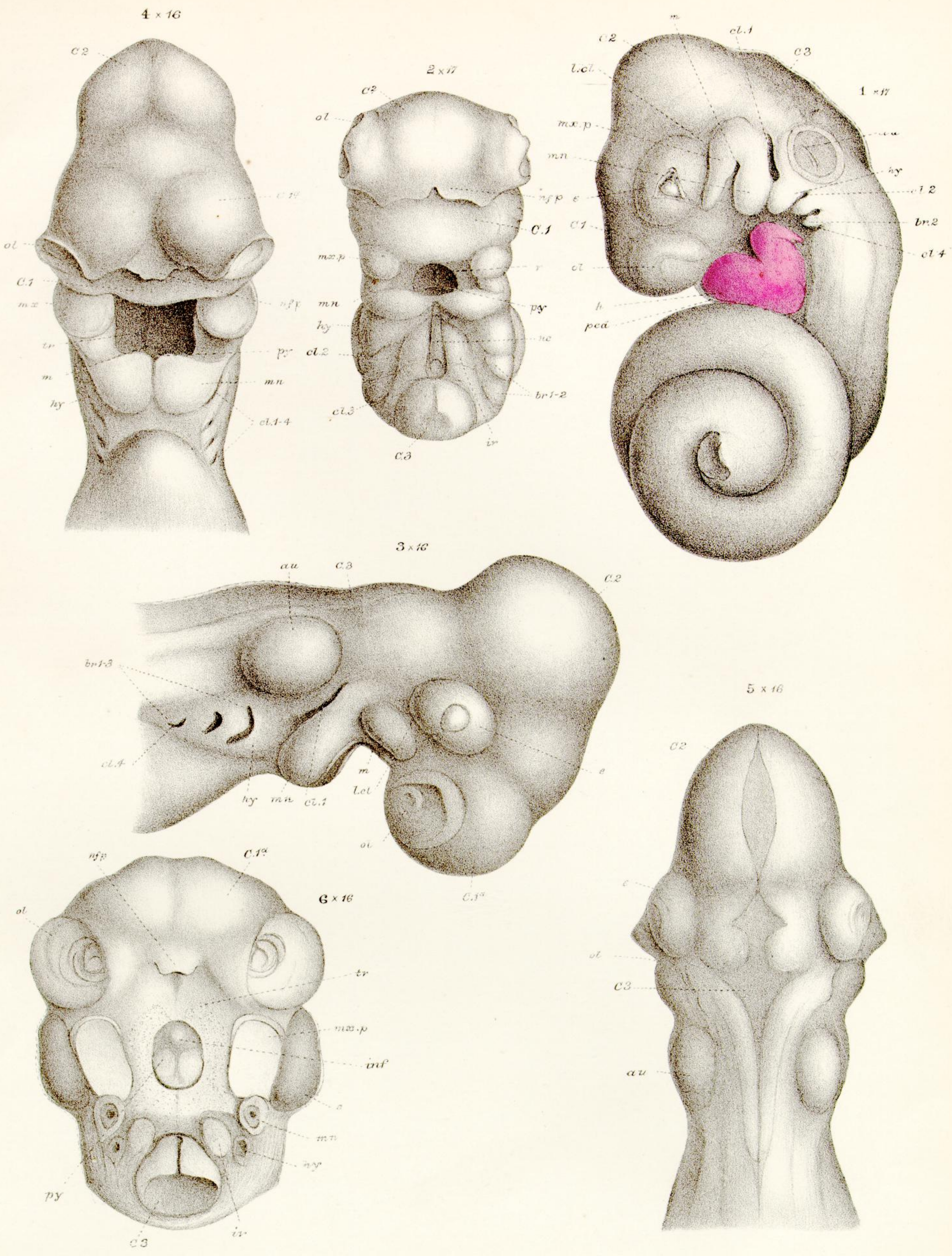
W. K. P. del. ad nat.  
G. West Junr. lith.

W. West & Co imp.

Common Snake.





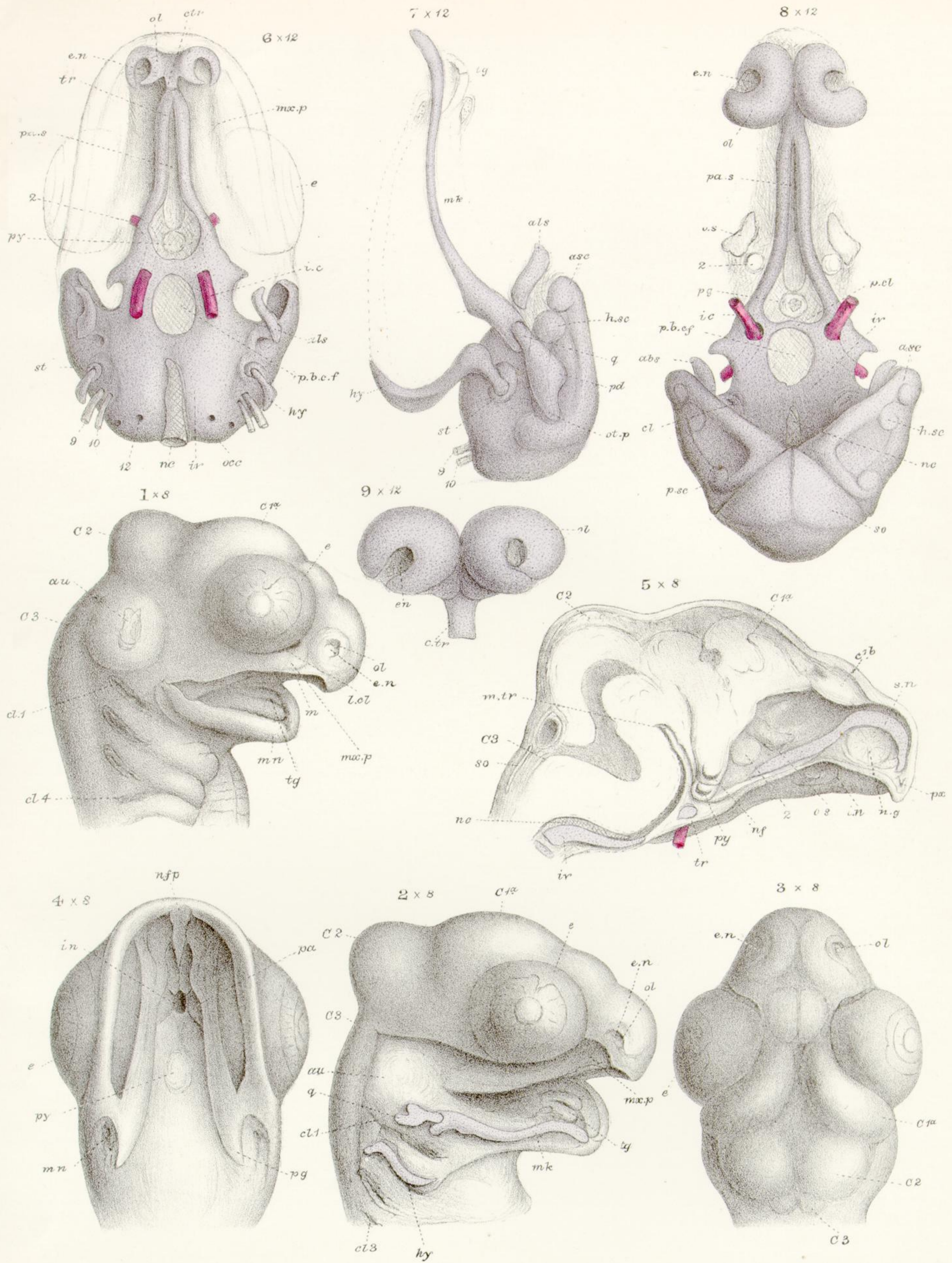


Common Snake.

PLATE 27.

- Fig. 1. First stage. Side view of Embryo of Common Snake (*Tropidonotus natrix*), whose total length was  $\frac{3}{4}$  inch.  $\times 17$  diameters.
- Fig. 2. Head of the same, severed and slightly bent back (straightened); lower view.  $\times 17$  diameters.
- Fig. 3. Second stage. Side view of the head and neck of an older Embryo, measuring about 1 inch in length.  $\times 16$  diameters.
- Fig. 4. The same from below (not straightened).  $\times 16$  diameters.
- Fig. 5. The same from above.  $\times 16$  diameters.
- Fig. 6. Palatal view of severed head of same.  $\times 16$  diameters.



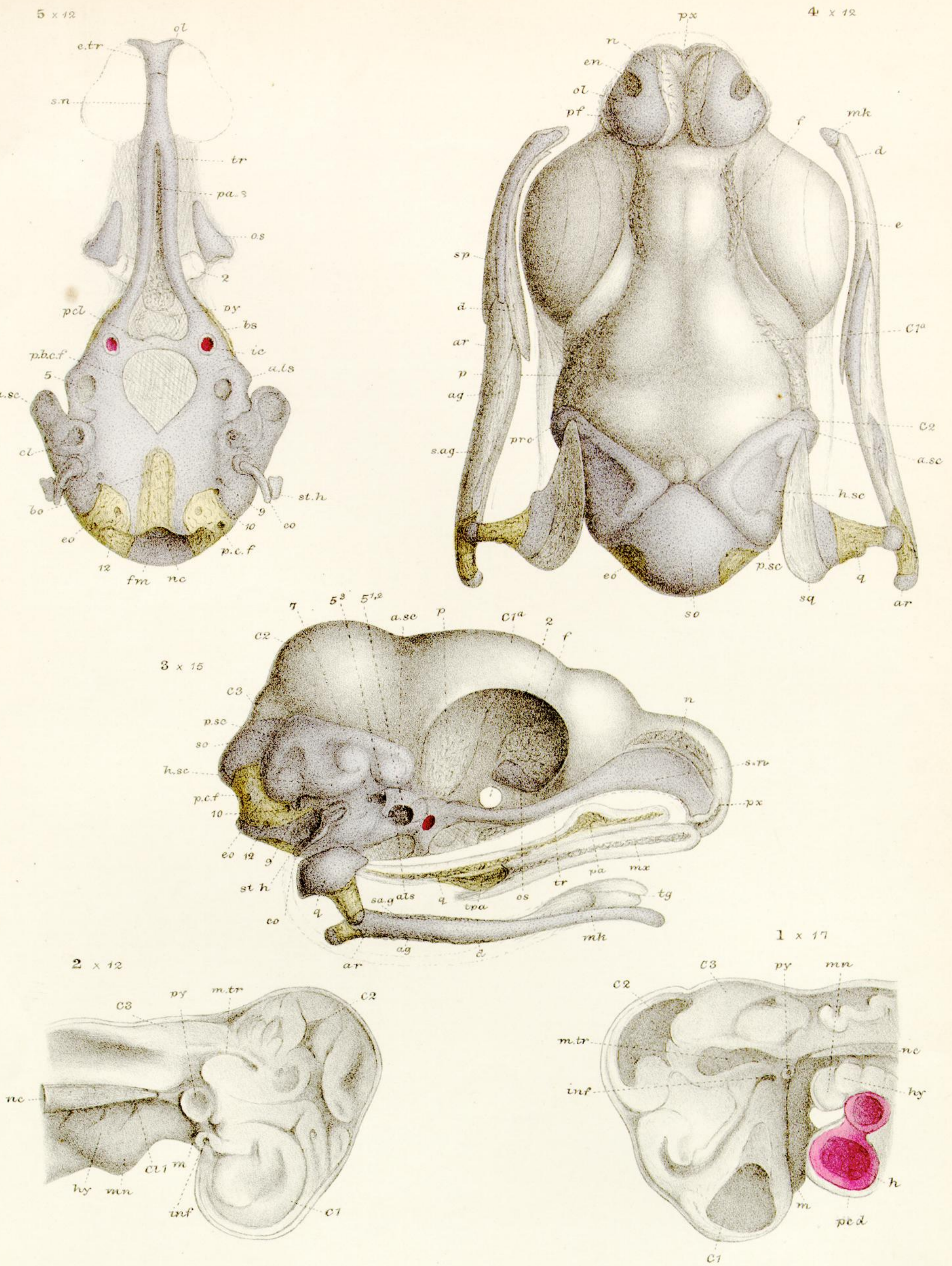


Common Snake.

PLATE 28.

- Fig. 1. Third stage. Side view of the head of an Embryo,  $1\frac{3}{4}$  inch long.  $\times 8$  diameters.
- Fig. 2. The same dissected.  $\times 8$  diameters.
- Fig. 3. The same from above.  $\times 8$  diameters.
- Fig. 4. The same; palatal view, with lower arches removed.  $\times 8$  diameters.
- Fig. 5. Longitudinally vertical section of the same.  $\times 12$  diameters.
- Fig. 6. Palatal view of same dissected.  $\times 12$  diameters.
- Fig. 7. Ear-capsule and arches of same, side view.  $\times 12$  diameters.
- Fig. 8. Upper view of chondrocranium of an older Embryo, measuring  $2\frac{1}{4}$  inches long.  $\times 12$  diameters.
- Fig. 9. Nasal capsule of same, front view.  $\times 12$  diameters.



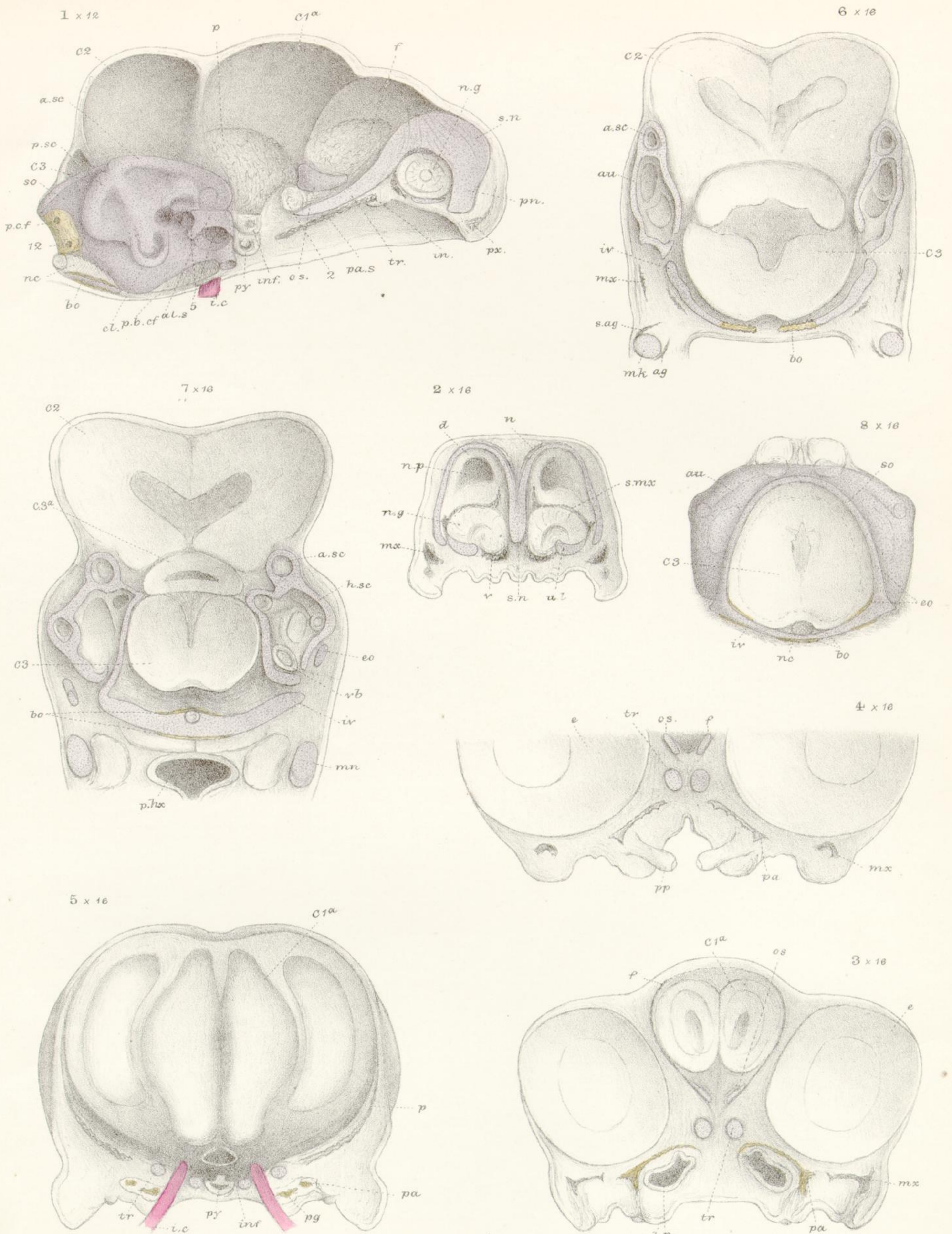


Common Snake.

PLATE 29.

- Fig. 1. First stage. Vertical section of head of youngest Embryo,  $\frac{3}{4}$  inch long.  $\times 17$  diameters.
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Common Snake.

PLATE 30.

Fig. 1. Longitudinally vertical section of a skull—(fourth stage continued).  
 × 12 diameters.

Fig. 2. Transversely vertical section of a similar skull through the middle of the nasal  
 region. × 16 diameters.

Fig. 3. A *second* section through fore part of eyeballs. × 16 diameters.

Fig. 4. Part of a *third* section through the middle of the eyeballs. × 16 diameters.

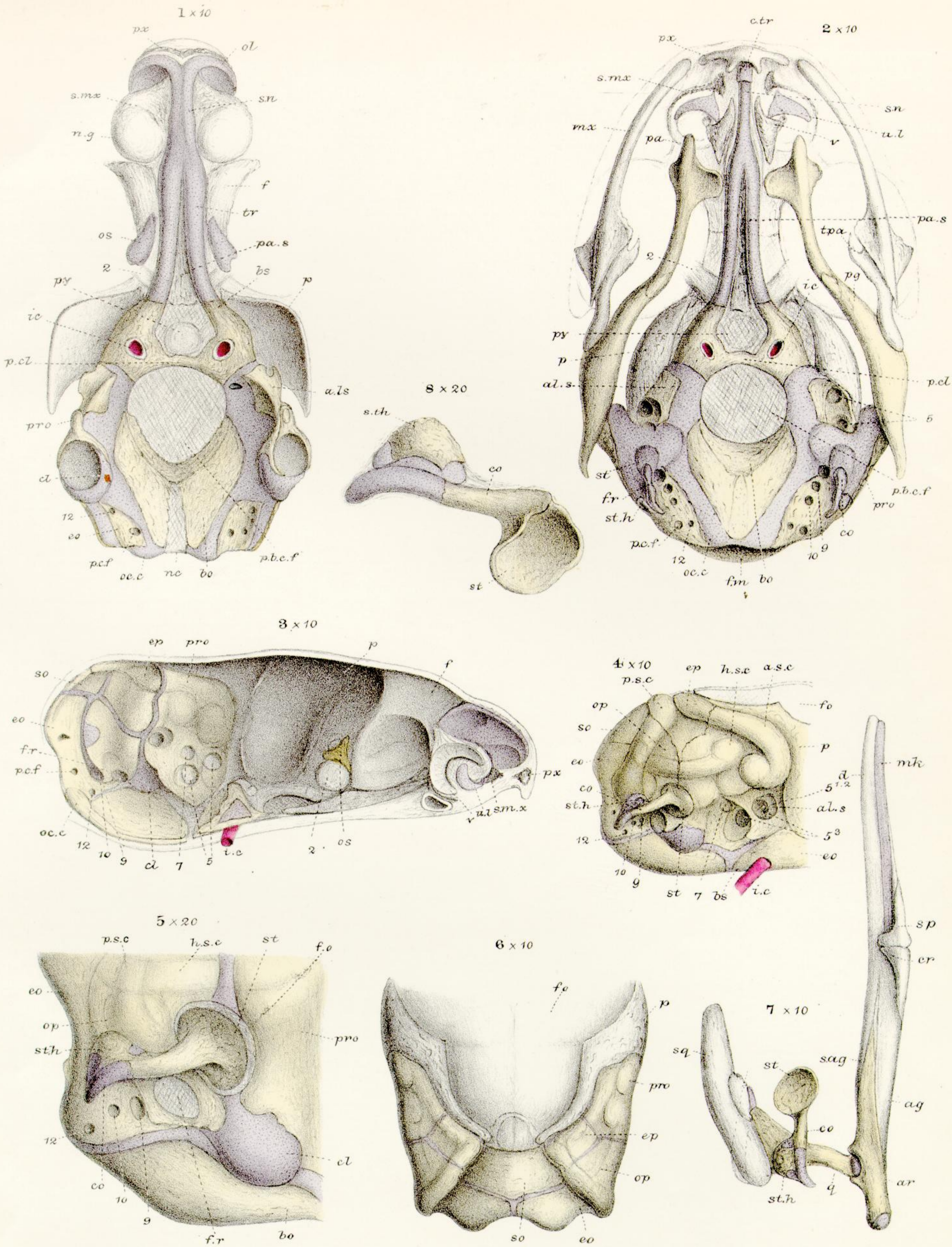
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Fig. 6. A *fifth* section through fore part of ear-capsules. × 16 diameters.

Fig. 7. A *sixth* section through their middle. × 16 diameters.

Fig. 8. A *seventh* section between ear-capsules and foramen magnum. × 16 diameters.



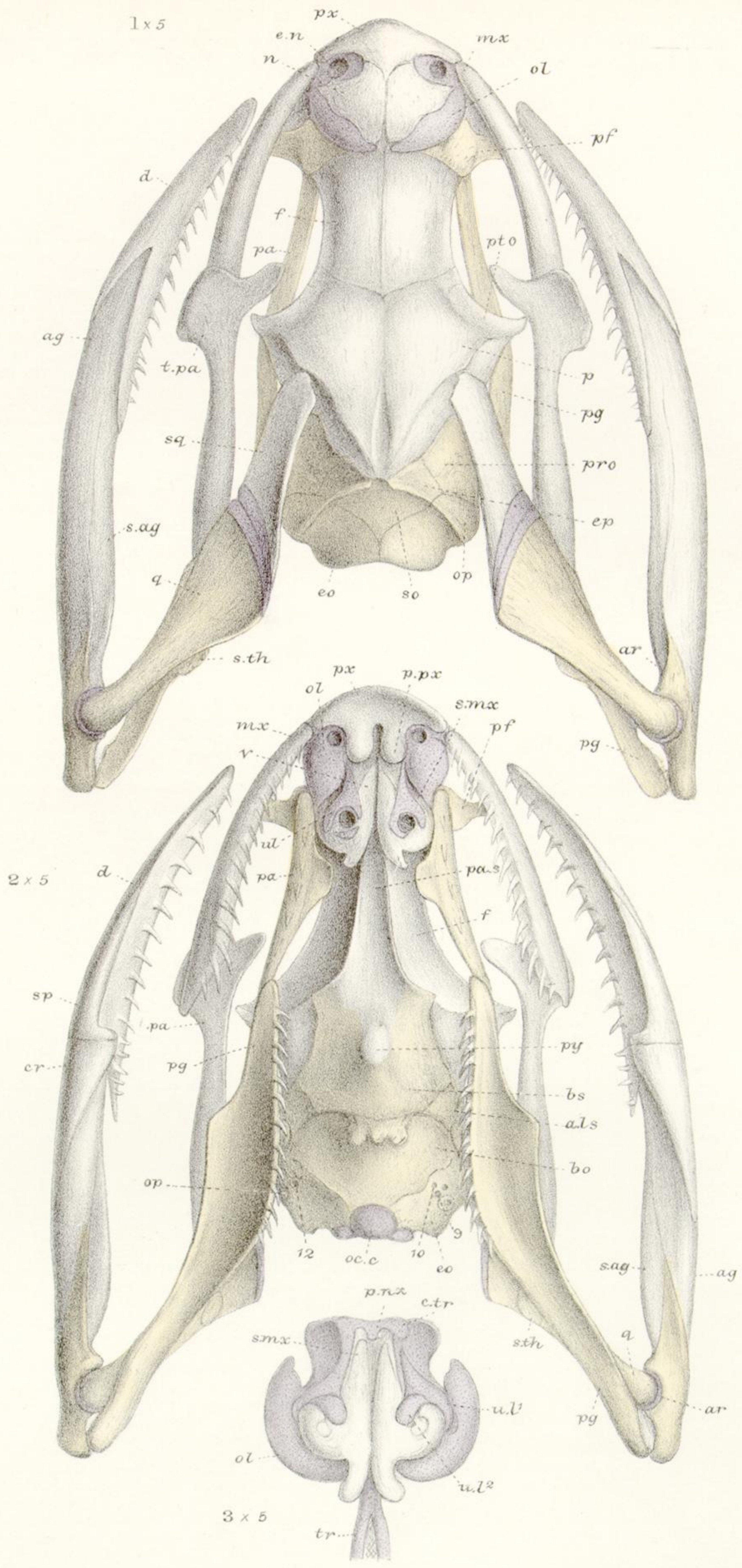


Common Snake.

PLATE 31.

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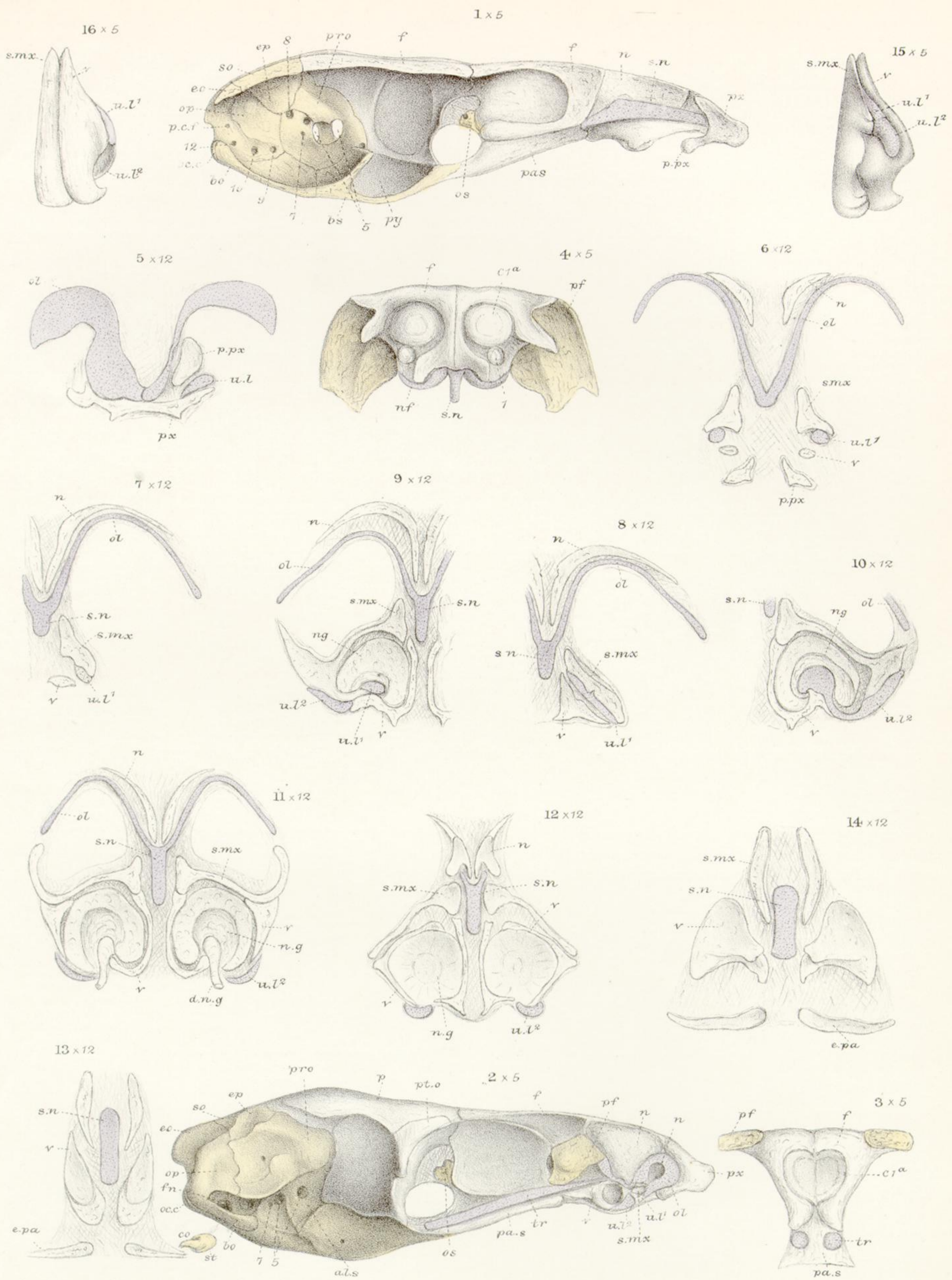


Common Snake.

PLATE 32.

- Fig. 1. Last stage. Adult Snake, upper view of skull and arches.  $\times 5$  diameters.
- Fig. 2. The same from below.  $\times 5$  diameters.
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Common Snake.

PLATE 33.

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\* The round space seen on *op.*, in this figure, is accidental.