A CONTRIBUTION TO THE DEVELOPMENT AND MORPHOLOGY OF THE LOPHOBRANCHIATES; (HIPPOCAMPUS ANTIQUORUM, THE SEA-HORSE.)

(With one plate.)

By JOHN A. RYDER.

During the present summer Mr. W. P. Sauerhoff captured a male sea-horse of our common American species in the Chesapeake, near Cherrystone, Northampton County, Virginia. It was placed in an aquarium some time in the latter part of July and shortly afterwards over 150 young ones were discharged from its distended marsupium, or brood-pouch. One of these young specimens preserved in spirits and handed to me for investigation is the subject of this notice.

There is perhaps no teleostean fish which is more grotesquely and profoundly modified in structure as compared with the ordinary ichthyan type than the sea-horse, and it is for this reason that its development is of especial interest to students of embryology. To briefly indicate in what particular features it differs most widely from other bony fishes may not be amiss.

The caudal fin has completely disappeared and the tail is not even used as a rudder, as in the pipe-fishes, but has become prehensile and serves the animal to hold fast to slender objects in the water. The usual function of the caudal has been assumed by the dorsal and anal; the dorsal is the principal agent used in propulsion, and with its help the creature sculls along with the axis of its body inclined at an angle of about 45° to the horizon; the sculling action is undulatory and the dorsal border of the fin describes in its movements a figure like the number 8. The anal appears to play the part of a rudder as well as assist in propulsion. The dorsal is also used in the pipe-fishes as the propeller; the body is also inclined when in motion; their behavior in the water indicates that they have not been as highly specialized or have not undergone such extensive modifications as their relative the sea-horse, but that it is probable that both have descended from a common ancestral type. In both the eggs appear to be received and carried about by the males during the period of incubation; in the male sea-horse there is a marsupium or brood-pouch situated behind the anal fin; it is comparatively undeveloped except in the spawning season. In some of the pipe-fishes the eggs are carried by the males in an excavation or groove in the under side of the abdomen extending for some distance in front of the vent, and covered over by wide dermal folds which arise from either side of the lower edge of the body and which lap over each other in the middle line; in others, as in *Syngnathus ophidion*, there is a pouch behind the vent as in the sea-horse. In this space the developing eggs are embedded in a firm gelatinous matrix. Impregnation of the ova probably takes place at the time the eggs are transferred from the female to the male.

The most striking feature of all, however, in the organization of *Hippocampus* is the downward flexure or bend of the head, which, together with the shape of the latter, develops a most marked resemblance of the forepart of the body to the head and neck of the horse, whence the common name of the animal. Accompanying this feature the bones of the snout have been prolonged so that the jaws are carried very far forward, while the latter have themselves not undergone so much modification. The gills and opercular apparatus have also been much modified, the former in the adult consist of four pairs of arches with two rows of pinnate, pyramidal, vascular branchial appendages resting on and attached by their apices to their outer borders; these answer to the branchial leaflets of other forms; the opercles articulate with the hyomandibular behind by means of a distinct articular facet, and are swung inwards and outwards on this articulation. At the upper border of the opercle on either side and behind the auditory structures there are placed the gill-openings, which are almost spiracular, and open upwards, the opercles being attached by their borders all round by membrane, except for a short distance at their upper posterior edges, where the opercular efferent openings are placed. In that the water is forced through the gills by the concurrent action of the opercles, hyoid apparatus, jaws, and spiracular openings, it will be noticed in living specimens that these parts together constitute a much more perfect pumping apparatus than is usually seen in the branchial structures of fishes. The gills are specialized beyond what is usual, as indicated by the term *Lophobranchii;* but this is misleading, as the branchial structures are not really tufted, as may be learned by a careful examination; the inferior and superior branchihyal elements of the branchial skeleton are wanting, according to Cope, and the arches, to the number of four, appear to be less strongly developed than in other young fishes of the same relative age. I can discern but four pairs, as in the adults, in my specimen. The bend downwards of the head involves a bend in the axial structures in the neck. Here the notochord is strongly bent upon itself, as the embryo studied by me clearly shows. The spinal cord also bends sharply downwards just behind the medulla oblongata, as necessitated by the sharp bend in the notochord below it. These constitute some of the most salient differences of *Hippocampus* as compared with other types of fishes. The skeletal and anatomical characters which distinguished the Lophobranchs as an order, are given in the following words by Owen (Anat. Vertebrates, I, 12): "Endoskeleton partially ossified, without ribs; exoskeleton ganoid; gills tufted; opercular aperture small; swim-bladder without air duct. Males marsupial." Cope* defines the order as follows: "Mouth bounded by the premaxillary above; post-temporal simple, coössified with the cranium. Basis cranii simple. Pectoral fins with elevated basis; well-developed interclavicles. Ante-

*Report of State Commissioners of Fisheries of Pennsylvania for 1879-80, p. 118. 1881.

rior vertebræ modified; the diapophyses much expanded. Inferior and superior branchihyals wanting or unossified. Branchial processes in tufts." To this the following may be added as complementary and as serving to extend the diagnosis: Opercle a simple plate; mouth toothless; *opercular membrane persistently roofing over the gill-chambers of the embryos.*

The term Lophobranch, it appears to me, is liable to lead to misapprehension, as the gills are in reality not tufted at all, but can be referred to the ordinary pinnate type commonly found in a great many fishes. Yarrell* observes in a foot-note: "The tufted filamentous gills of the Lophobranchs are compared by Milne-Edwards to the filamentous branchiæ of a tadpole; and Rathke, who has investigated their structure, informs us that each is framed of a short, delicate, ligamentous stem, to which the respiratory processes are attached by repeated doublings of the branchial membrane, the folds widening as they recede from the base, so as to form an inverted cone or club-shaped tuft." Filamentous tufts do not exist in the gills of *Hippocampus*, so that the first part of the foregoing quotation is erroneous; the latter part of it, attributed to Rathke, is correct, except the last word, and in this the German anatomist was possibly misunderstood.

The true state of the case is as follows: there is a median stalk or rachis to which the branchial leaflets are attached in a pinnate manner on each side. The leaflets become larger as you go outwards, so that the pyramidal form of the compound branchial leaflets results; this pyramid is fixed by its apex to the outer side of the branchial arch. These inverted pyramidal branchial structures are disposed in two series, usually four-sided. There is therefore nothing at all in these structures which is not represented homologically in the fish's gill of the ordinary type, since the two series of vascular branchial appendages to each arch in *Hippocampus* are perfectly comparable with the bifurcated vascular branchial appendages of such a form as *Salmo*. There is plain evidence that a process of degeneration has taken place in the branchial apparatus of *Hippocampus;* the arches themselves have undergone reduction in length; the mesobranchial bony elements are reduced or aborted, and the number of vascular appendages is reduced very much below what is usual; the greatest number of pinnate vascular branchial appendages ranged in one row on the posterior margin of one arch of *Hippocampus* is about ten, which is exceeded several times by the number found in *Salmo*, or in many other common genera. The reduction in number of these appendages may have called for the extension of the area of the ultimate branchial lamellæ or pinnæ, which is a marked feature in the gills of the sea-horse. In other forms, as in *Brevoortia*, the ultimate vascular pinnæ on either side of the gill filaments, which are the active agents in respiration, being richly supplied with capillary vessels, are very feebly

*British Fishes, II, 395.

developed. It is really these vascular pinnæ which have been exaggerated in development at the expense of the other portions of the branchial apparatus.

EARLY DEVELOPMENT.

From what I have observed of the early stages of development of the pipe-fish, *Syngnathus peckianus*, and from a study of ova taken from the pouch of a male *Hippocampus* preserved in alcohol, I offer the following approximate account of the early phases of the evolution of the latter, depending upon the former on account of its close relationship for the details not actually observed. This will not permit us to develop more than such points as we are warranted to infer from their close affiliation to each other, but even such will be of value.

The egg of *Hippocampus*, like that of other teleosts, is constituted of a yelk and germinal material. The former is a rich orange yellow in color; the latter cannot be described, as it has not been seen. In *Syngnathus* the yelk is of the same color, and embedded in it superficially and all around it there are deep yellow oil globules.

The blastoderm of *Hippocampus* is presumably formed, as in all other known teleosts, by a gradual growth of the germinal disk over the yelk so as to include the latter. The rudiment of the embryo appears at first at the edge of the blastoderm, and develops for some time like other fishes, such as the shad, cod, or stickleback. A segmentation cavity is developed, which probably persists as I have observed in *Syngnathus*, and a vitelline system of vessels is doubtless also formed as in the latter.

Up to the time the tail is about to bud out from the caudal swelling at the end of the body of the embryo there is nothing observable which would be considered remarkably different from the type of development exhibited by less modified fishes. The tail of the embryo Lophobranch buds out, and does not develop the prominent dorsal and ventral natatory folds so characteristic of the first appearance of the tail of the embryos of the spiny and soft-rayed forms. It results from this, that the tail is extended backwards, as development proceeds, as a simple cylindrical prolongation of the hind portion of the body. There is, after a while, in *Syngnathus* a low fold developed where the dorsal and caudal are to appear, but there is nothing like the wide natatory fold apparent, such as we see in the embryos of *Alosa*, *Gadus*, and *Cybium* of the same age. In *Hippocampus* there is no caudal in the adult, and we may therefore expect to find little or no evidence of a caudal fin-fold at any period of its development.

The yelk-sack, I apprehend, is absorbed in the usual way, there being, in all probability, no direct connection of the yelk-sack with the intestine. The period of incubation in the marsupium, from the fact that development is pretty well advanced when the young leave it, I should think would be not less than twelve to fourteen days.

The peculiar elongation of the snout probably begins before the yelk-sack is absorbed, just as I have observed in embryo pipe-fishes. There is also in the latter a more decided downward bending of the head as it becomes free from the yelk; we may expect to see a similar state of affairs in the development of the sea-horse. Beyond this stage in *Syngnathus* an unwonted acceleration in the development in the length of the quadrate cartilage, trabecular cornu (rostral cartilage), pushes the rudiments of the inferior and superior maxillaries forwards so as to lengthen the snout at an unusually early period. In profile, the head of the young Lophobranch now bears a suggestive likeness to that of a pug dog.

From what we know of the early development of the medulla spinalis of *Syngnathus*, according to Calberla,* it is at first solid, as I have found in the case of very young embryos of the shad from a study of transverse sections. This is also probably the primitive condition in *Hippocampus*.

LATER DEVELOPMENT.

The specimen of young sea-horse upon which this notice is based had already left the brood-pouch of the male and had been swimming about for a couple of days; its development had accordingly advanced considerably. We will begin our description with an account of the embryonic skeleton, referring to the plate in explanation of the relations of the parts.

Cartilaginous skeleton.—The axial rod around which the bodies of the vertebræ are developed, and known as the notochord *ch*, still persists and extends from behind the pituitary body *py* to near the end of the tail. At its anterior extremity it is much bent downwards just under the medulla oblongata *mo*. Farther back there is a slight bend in it where the basalia, or basal cartilages of the dorsal fin *df*, almost come into contact with it. In the caudal region it is coiled in conformity with the complete turn which is made by the terminal part of the tail. A sheath appears to be developed around the notochord, and rudiments of the vertebral elements have been developed, but they are not yet segmented and distinct.

The skull.—There are no true bones yet developed in the skull, all of the cranial bones are still represented by cartilage. The anterior end of the notochord *ch* is involved in cartilage which arose primitively as the parachordal cartilaginous masses *p* on either side and a little past the end of the axial element. Beyond this the trabeculæ cranii *t* extend forwards under the brain, the space between them at this stage being slight where the pituitary body *py* lies above it. The cartilaginous basis cranii is extended forwards far beyond the eyes as the trabecular cornu, the olfactory organs or nasal pits *na* lying in an excavation on either side, with an ethmoidal cartilaginous septum, *e*, between them. The tegmen cranii *tc* is developed upwards and backwards so as to roof over the fore brain *ce*. In front of the olfactory pits *na* the trabe-

* Morph. Jahrbuch III, 1877.

cular cornu is prolonged far forwards into a cartilaginous bar, *rc*, which we may designate here as the *rostral cartilage* on account of its great antero-posterior development. The cartilaginous investment of the auditory capsule *au* is still imperfect. From the sides of the trabecular floor upon which the brain lies, the palato-quadrate elements arise to give attachment to the cartilages of the maxillary and hyoid arches. The metapterygoid cartilage *mt* extends outwards and downwards behind and below the eye to articulate with the very long rod-like quadrate *q*, which articulates at its front end with the rudiment of the lower jaw, Meckel's cartilage *mk*. Above the articulation of the quadrate with Meckel's cartilage a curious bent element, *x*, appears to represent the superior maxillary. Just in front of the expanded upper extremity of the maxillary lies the posterior extremity of the upper labial or intermaxillary element *la*, which is continuous with a similar piece on the opposite side; this intermaxillary bar curves over the anterior upward bend of the rostral cartilage *rc*. It constitutes the skeletal boundary of the upper part of the oral opening *m'*, and is not segmented in the median line so as to articulate with its fellow of the opposite side like Meckel's cartilage of the lower jaw.

The hyomandibular *hm* is not well differentiated from the metapterygoid; in fact, the point where the quadrate and metapterygoid are segmented is only faintly indicated, as might be expected from the intimate unions of these bones in later life, amounting almost to synostosis. The symplectic *sy* is a slender rod somewhat impressed into the quadrate externally at its upper end, and almost continuous at this stage with the hyomandibular. The symplectic, like the quadrate, is seen to be enormously elongated, as compared with its homologue in the normal ichthyan skull of the same relative age.

The skeletal elements of the lingual or hyoid arch are also modified considerably. The ceratohyal *cy* is a flat, oval cartilaginous plate lying against the inner side of the lower end of the hyomandibular and the inner side of the upper end of the quadrate. It articulates at its lower end with the rod-like hypohyal *hhy*. There appear to be no mesial hyal elements at all, which also seems to be the case with the adult, the medial skeletal elements of the tongue being suppressed.

The branchial arches *b' b'' b''' b''''* are present at this stage to the number of four, the same as in the adult, and the lower mesial elements appear to be absent, just as in the case of the hyoid elements. The branchial cartilaginous bars themselves are weak.

Shoulder-girdle.—The breast or pectoral fins, at this stage, have a high basis, as stated by Cope in regard to the adults, where, together with the dermal plates of the throat, a firm pectoral arch or shoulder-girdle is developed in which there is sutural or, at least, inflexible union of the coraco-scapular elements. I have only indicated the outline of this arch in the figure at *cs*; the object was too opaque here to make out the contour of its elements. The lower end is coracoid, and has already assumed a horizontal position, the apparently scapular portion is vertical; the pectoral rays seem to arise almost immediately from its hinder border. A powerful azygos muscle originates from the anterior border of the coracoids in the middle line which is inserted by a tendon at the point of junction of the hypohyal cartilages, as shown in the figure. This muscle pulls down the hyoids and increases the capacity of the tubular snout, and is one of the effective agents in the function of respiration; the muscle is represented in its contracted state in the figure.

Structure of the unpaired fins.—These consist of the dorsal and anal. The dorsal *df* has eighteen rays, which rest upon eighteen short intermediary basal pieces, *bc*, cartilaginous in structure, and which articulate by a singular series of link-like structures with the cartilaginous interspinous rays or basalia *ic*, nineteen in number. The muscles which move the dorsal from side to side are arranged in eighteen pairs, and run out radially and parallel with the interspinous basalia, to be inserted just where the intermediary pieces join the latter. In adult specimens, the interspinous basalia which are at this young stage nearly in contact with the notochord by their proximal ends, are pushed farther out and become apposed upon and interposed between the spinous dorsal radii springing directly from three vertebræ. The young, therefore, show that the interspinous basalia of the dorsal are at first more nearly in contact with the vertebral axis.

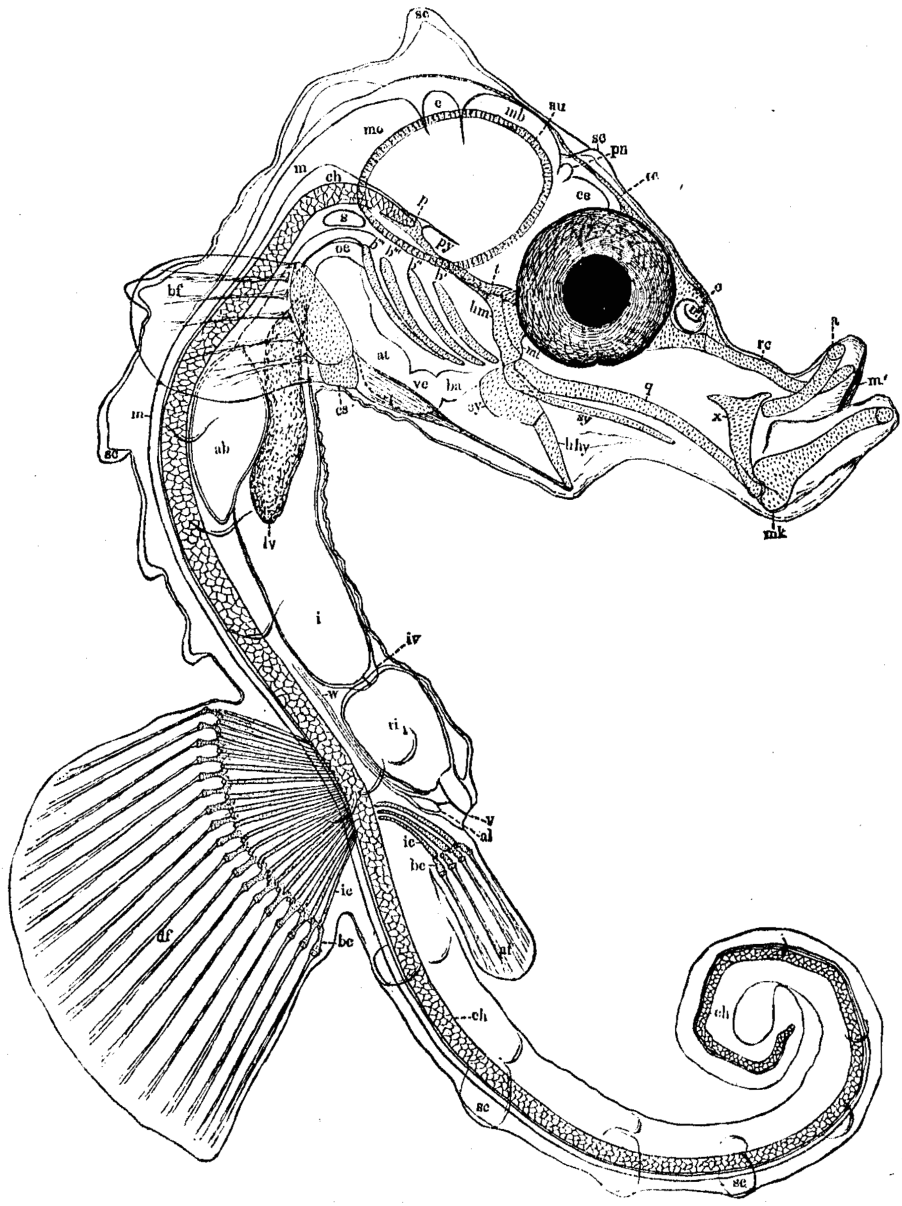
The anal fin, *af*, just behind the vent *v*, has four distal radii unsegmented and hyaline, the same as those in the dorsal, nor are they yet barely more than incipiently cartilaginous in either of these fins. These rest upon four short cartilaginous intermediary pieces, with the same link-like articulations with the interspinous basalia as were noted in the dorsal. The interspinous rays of the anal *ic* are three in number, and are curved towards and nearly in contact with the notochord at their proximal extremities; but in the adult, as the abdomen develops, these are pushed outwards, and between their inner ends and the vertebral axis there is finally a wide interval.

The brain.—Of this there is little to remark, except that its under surface has a direction at right angles to the course of the upper end of the medulla spinalis or spinal cord. The eye is relatively farther forward, as compared with the usual position of the cerebrum *ce*. The eyes on this account are also more approximated than usual, only a very thin interorbital septum separating them, behind which the cerebrum terminates.

Alimentary canal and appendages.—The oral cavity is disproportionately prolonged on account of the length of the intermediary elements of the lower jaw and the length of the trabecular rostrum, and extends from the point *m′* to the pharynx or gill-chamber. The gill-chambers communicate internally in the usual way by clefts with the pharyngeal portion of the alimentary canal. They are essentially closed cavities, except where the interbranchial spaces communicate with the throat, and where the opercular efferent opening *s* is situated behind the auditory capsule. At this point I would call attention to what I believe to be an important embryological character which appears to distinguish Lophobranchiate embryos from those of the normal types of fishes. It is usual to find the gill-openings of embryo fishes more or less uncovered when they first appear. That is, the opercular fold is often so short as to scarcely cover more than the first cleft; this is a very marked feature in Clupeoids, such as the shad, but is less marked in all other types which I have observed. In the Lophobranch embryo the superficial epiblastic layer, which roofs over the gill-chambers, is apparently never broken through until late, and at no time do the clefts and arches come to be completely exposed as in the young shad. The opercular opening appears late as a mere spiracle, and not as in other forms is the opercle developed from before backwards. The simple opercular plate of the Lophobranchiate embryo probably originates as an outgrowth from behind the hyomandibular bone from a tract of mesoblastic tissue, which appears comparatively late, since the opercle is not yet developed in the stage represented in our figure. Of course we cannot yet be sure as to the value of this character until we know more of the development of other forms. The remarkable manner in which the operculum of *Gambusia* is developed warns us to be cautious in putting an estimate upon such features, for here a hollow membranous process from the yelk-sack extends up over the opercula, a feature quite as singular as that noted in the Lophobranch.

There is a sharp bend in the œsophagus *oe*, and a little way below this bend the alimentary canal suddenly widens. Dorsally and about on a level with the middle of the pectoral fin the spacious air-bladder *ab* arises as a diverticulum from the intestine; its connection with the intestine is closed very early. In front of it and at one side the liver *lv* is developed, but I have not been able to make out where it joins the intestine, which, for well-known morphological reasons, it must do; it is therefore represented only in outline.

Nearly opposite the commencement of the dorsal I find a very singular valve in the intestine at *iv*. Nothing comparable to this structure has been observed in fish embryos as young as this except by myself in the posterior portion of the intestine of the larval cod (*Gadus*), but in that form it is only a constriction, and does not completely shut off the anterior portion of the alimentary canal from the posterior. Beyond this valve the intestine of the young *Hippocampus* is continued as a pyriform rectum ending in the vent *v*, around which the rudiment of the sphincter ani muscle is apparent, through which the ano-cloacal canal passes, receiving dorsally a duct from the urinary vesicle or bladder *al*, into which the segmental ducts *w* of each side empty their products. The extent of the development of the segmental ducts and mesonephros or kidney could not be made out from my mounted specimen; this can only be done by the help of transverse sections.



HIPPOCAMPUS ANTIQUORUM, *the Sea Horse.*

The dermal plates are regarded as ganoid by Owen. They appear to me to be of sub-epithelial origin, as they are covered with an epithelial layer of cells in the young, which persists in the adult, as in the case of the outer covering of the scales of true ganoids (*Lepidosteus*), where there is a very thin, soft external organic investment. They are somewhat irregularly conical in the young on the fore part of the body, as shown in section on the head and back at *sc*. They are thickest at their apices, and probably grow in thickness from below. On the top and front of the head there are two pairs, on the back four pairs, on the sides of the body one row of three on each side, and a transverse row of three on each side in front of the dorsal; behind the dorsal on the tail, there are first two rows of four and then one row of two, so that it is clear that a good many must be added to make up the number of plates observed to cover the adult. The ventral row found on the adult is absent in the young. Altogether there are more than three times as many plates developed on the full-grown adult male of the same species as are found in the young of the age here described. How these are added can only be learned by further study of more material representing a greater number of stages.

EXPLANATION OF PLATE.

Young *Hippocampus antiquorum* viewed from the side as a transparent object, enlarged 43 times.

ab, air bladder; *af*, anal fin; *al*, urinary vesicle or bladder; *at*, venous sinus; *au*, auditory capsule; *b′*, *b″*, *b‴*, *b⁗*, first, second, third, and fourth branchial arches of the right side; *ba*, bulbus aortæ; *bc*, basiradial cartilages; *bf*, breast or pectoral fin; *c*, cerebellum; *ce*, cerebrum; *ch*, chorda dorsalis or notochord; *cs*, coraco-scapular arch; *cy*, ceratohyal cartilage; *df*, dorsal fin; *e*, inter-nasal cartilage; *hhy*, hypohyal cartilage; *hm*, hyomandibular cartilage; *i*, intestine; *ic*, interradial cartilages or basalia of fin rays; *iv*, intestinal valve; *la*, labial or inter-maxillary cartilage; *lv*, liver; *m*, medulla spinalis or spinal cord; *m′* mouth; *mb*, mid-brain; *mk*, Meckel's cartilage; *mo*, medulla oblongata; *mt*, metapterygoid cartilage; *na*, nasal pit; *œ*, œsophagus; *p*, parachordal cartilage; *pn*, pineal gland; *py*, pituitary body; *q*, rod-like quadrate cartilage; *rc*, rostral cartilage or prolongation of the trabecular cornu; *ri*, rectal portion of intestine; *s*, spiracular outlet of the gill-chamber; *sc*, dermal scutes or plates; *sy*, elongated symplectic; *t*, trabeculæ cranii seen from the side; *tc*, tegmen cranii; *v*, vent or anus; *ve*, ventricle of heart; *w*, Wolffian or segmental duct; *x*, supra-angular cartilaginous element, the rudiment of the supra-maxillary.