

## A CONTRIBUTION TO THE ANATOMY AND PHY- LOGENY OF *AMPHIUMA MEANS* (GARDNER).<sup>1</sup>

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THE anatomy of the adult skull of this eel-like Amphibian has been well described by Wiedersheim (1). Osborn (8) has given a most excellent description of the central nervous system. Hay (2) has given an interesting account of the finding of its eggs in an Arkansas swamp in September of 1887, and subsequently published the results of his study of the embryos contained in these eggs, and also of the skull of a small specimen six inches long. Cope has furnished a general description of the species, and endeavored to trace out its phylogeny by means of the insufficient data at hand. Kingsley (5), through a study of Hay's embryos, for the most part confirmed the latter's account, and also added to our sparse knowledge some important points, especially along the line of phylogeny. The writer has published a description of the conical arrangement of the muscles (6), and in a later article the manner of the fertilization of the eggs (7). No other investigations of any importance than the above mentioned have been made on this peculiar Amphibian, owing undoubtedly to the fact that the embryological material is so difficult to secure. The animals will not breed in captivity, and the batches of eggs laid are so few and so well concealed as to escape the sharp eye of the naturalists. Since the eggs are fertilized internally, a comparatively short period of external incubation is necessary, thereby limiting the probability of being discovered. Previous to February, 1894, no one had secured a specimen of the young less than six inches in length. In that month I was so

<sup>1</sup> I was very materially aided in making these investigations in the Princeton Biological Laboratory by Mr. C. W. F. McClure who placed at my disposal a large number of Amphibians and gave me numerous valuable suggestions.

fortunate as to have sent me, by a North Carolina dealer in embryological supplies, several very young specimens varying in size from seventy-eight to ninety millimetres in length.

In this paper it is my intention to give a detailed account of the anatomy of these very young specimens, and by comparisons with the adult structures as well as with other Amphibians to deduce a few new points in phylogeny. Since there has never been published any complete and reliable account of the anatomy of the adult, it will be necessary for me to begin at this point.

#### *External Features of the Adult.*

The general form is serpentine, having the same proportions as the body of a teleost eel. The circumference of the largest specimen I have seen was 150 mm., and its length almost one metre. The tail occupies about one fourth the length of the animal, and is laterally compressed in such a manner that the area of a cross-section is triangular with the apex at the dorsum. The body is slightly contracted just anterior to the fore limbs forming the so-called neck. The head is twice as long as it is broad, and vertically compressed. The snout is obtusely rounded, but is more pointed than in other urodeles, and extends from six to eight millimetres beyond the lower jaw. The lips of the upper jaw overhang for the most part those of the lower, thus preventing the mud from entering its mouth during its subterranean excursions. The eyes are one and a half millimetres in diameter, have no lids, utilize the epidermis as a cornea, and are situated along a transverse line cutting off the anterior third of the head. The anterior limbs are from fifteen to twenty millimetres in length, and support two or three diminutive digits. The posterior limbs, situated just anterior to the vent, are from fifteen to twenty-five millimetres long, and also have two or three digits. Cope (4) says that specimens have been found having two digits on the anterior limb and three on the posterior.

A few millimetres anterior to the fore limb is the branchial fissure, securely guarded by two membranous flaps. The skin is smooth, silky, and of a dark brown color dorsally, and of a

slate gray ventrally. The head is covered with mucous pores, arranged in several rows which unite in the region of the neck so that only two distinct rows are seen on each lateral area of the body. Cope (4) errs in saying none are present on the body.

#### *Bones of the Head.*

The head of *Amphiuma* is long and narrow, the general outline being somewhat like that of the skull of the *Proteus* except that the snout is not so pointed. While in the majority of *Amphibia* the skull is as broad as long, in *Amphiuma* it is twice as long as it is broad. It is composed of twenty-eight distinct bones: two maxillaries, a premaxillary, two nasals, two frontals, two prefrontals, two orbitosphenoids, two vomeropalatines, two parietals, two exoccipitals, two prootics, two pterygoids, a parasphenoid, two stapes, two quadrates, and two squamosals. The maxillary is an irregular, oblong bone with a triangular cavity beneath, along one side of which are attached twenty-two conical teeth. This bone is not curved as in the majority of amphibians, but presents a straight alveolar edge. The foramina (Fig. 1, *c*, *b*) are seen on its dorsal surface, the anterior of which gives passage to small blood vessels and nerves. Cope (4) believes that the larger foramen is prophetic of the tentacular canal of the *Gymnophiona*. The maxillary articulates dorso-laterally with the prefrontal and nasal, ventro-internally with the vomero-palatine, and anteriorly with the premaxillary, which in *Amphiuma* is a single bone. This very irregular bone is composed of three parts: the alveolar portion (Fig. 11, P) bearing ten teeth, the dorsal wedge extending backwards between the nasals and frontals to a line joining the orbits, and a ventral wedge lying in the roof of the mouth between the vomero-palatines and parasphenoids. The greatest width of either of these wedges is one millimetre, and the length of each is about one third that of the skull. The nasals are small bones very much pitted, and serve to roof in the anterior part of the nasal chamber. The frontals are the longest bones of the skull, and bound the fore brain both dorsally and anteriorly. They extend underneath the posterior edge of the

dorsal wedge of the premaxillary, and the union of the descending plates at this point functions as a nasal septum, as seen in Fig. III. Through this portion of the bone is the canal for the passage of the olfactory nerve. Hay (2) does not believe that such a canal exists, though Wiedersheim (1) has correctly described it. Cope (4) has called the descending union of the frontals the ethmoid. In this he is wrong, as embryonic investigations (3) have clearly shown. I think the Sarasins (9) have followed Cope in this error, and together with him have sought to show relationships which do not exist. The frontals are in contact with the nasals and premaxillaries anteriorly, and laterally join the prefrontals and orbitosphenoids. Upon reaching the frontal bone the sagittal crest of the parietals divides, each fork running to the outer side of the former bone. In the groove thus formed lies the temporal muscle. The prefrontals take part in roofing the nasal chambers, have a rough surface and an irregularly oblong outline. They join the maxillaries laterally and form part of the orbit. The orbitosphenoids are small, taking part in the lateral boundaries of the brain cavity. They articulate with the parietals, parasphenoid, and vomero-palatines. They are almost separated from the frontals by the interposition of a narrow wedge of the parasphenoids. The vomero-palatines bear the inner concentric row of teeth, which number about forty-four. *The number of premaxillo-maxillary teeth is never less than fifty.* The number is wrongly stated by Cope as thirty-one. The vomero-palatines, together with the ventral wedge of the premaxillary, form the roof of the mouth. This pair of bones unite anteriorly, and are nowhere separated more than two millimetres from each other. Their backward extent ceases slightly posteriorly to the beginning of the parasphenoid. The parietals are the largest bones of the skull, and form the roof of the greater part of the brain cavity. Their median juncture is the sagittal crest. Their external borders are deflected upwards to form the temporal crests, thus giving rise to a broad groove for the reception of the powerful temporal and masseter muscles. The proötics and squamosals lie lateralwards of these bones, and posteriorly are joined by the exoccipitals which bear the two

pedestals for articulation with the axis. The exoccipitals join each other only in a very small part of their length, being separated by a V-shaped opening which is the foramen magnum. Immediately within this aperture, on either side, is seen a small facet for articulating with the prezygapophyses of the axis. The large foramina seen at the external sides of the bases of the pedestals give passage to the vagus and hypoglossal nerves. The exoccipitals are in apposition laterally with the squamosals and stapes. They do not reach the proötics, which lie anterior to the squamosals and external to the parietals, with which they join in such a manner as to form the anterior parts of the temporal crests.

The pterygoids are wing-like bones extending from the quadrates forward along the parasphenoid to near where the vomero-palatines arise, at which point the bone gives way to cartilage. The parasphenoid is the broad basal bone of the skull, extending throughout more than half its length. It is broadest in the otic region, and narrows in either direction. Its posterior part is bounded on three sides by the exoccipitals. Anteriorly, it extends beneath the ventral wedge of the premaxillary. The stapes is an orbicular bone, scarcely three millimetres in diameter, articulating with the parasphenoid, the exoccipital, and quadrate. It does not form a part of the suspensorium. The quadrate is a comparatively small bone, lying on the inner side of the descending squamosal, and joins the pterygoid, stapes, and parasphenoid. This bone, with the squamosal, forms the suspensory apparatus. It bears the facet for articulation with the mandible. The squamosal is another peculiar bone in the *Amphiuma* skull. *Whereas in most of the Urodeles it is directed forwards and slightly outwards, in Amphiuma it is directed outwards and downwards, and but very slightly forwards.* It is an exceedingly strong bone, and is firmly adherent to the exoccipitals, parietal, and proötic above, and joins the quadrate and stapes beneath. The possession of this bone, according to Cope (4), allies the families *Amphiumidae* and *Coeciliidae*. The bone which Cope has called squamosal in the *Coecilians* is quite differently located, being directed forwards and inwards in such a manner as to form

part of the orbit, and therefore deserves the name quadrato-jugal, as some authors have already called it.

The mandible is a simple structure, each ramus being composed of these bones, *viz.*, the dentary, the angular, and articulary. The dentary supports twenty-two teeth, and forms the whole external portion of the ramus, and appears for some distance in front on the inner side. The external surface presents a foramen for the mandibular nerve. The angular and articular are so well coössified for the most part that their boundaries cannot be clearly defined. Anterior to the facet for articulation with the quadrate, the articular abruptly rises into a prominence, to which the temporal muscle is attached. The angular lies beneath the articular, and forms a projection behind it, in which the digastric muscle is inserted. Immediately anterior to the condyle is a notch for the insertion of the masseter muscle. The rami are not anchylosed in front, but are held together by cartilage.

The hyoid apparatus of *Amphiuma* is quite unlike that of any other Amphibian (Fig. XV). There is but one basibranchial to which are joined two ceratobranchials bound by cartilage. There are four epibranchials. The basihyal is cartilaginous, as are also all the epibranchials except the first. The hypohyals are very short, being scarcely more than one-half as long as the basibranchial. The ceratohyals are longer than the ceratobranchials. The few cartilaginous formations of the skull not already described will be discussed later.

### *The Limbs.*

The limb bones of *Amphiuma* are characteristic of reptilia in some respects. The fore limb consists of a humerus, ulna, and radius, carpus, metacarpus, and phalanges. These bones are proportioned with reference to each other, as in mammalia. The humerus of a specimen one metre long is about one centimetre long. Its head is of cartilage. Immediately below the head, on the anterior side, is a prominence for the insertion of the biceps muscle. The distal third of the shaft is slightly flattened to afford a more advantageous surface for the articu-

lation of the two bones of the forearm. These bones are approximately of the same length, but the radius is the stronger. The carpals are not ossified. They are five in number. The ulna articulates with the ulnare only, but the radius articulates with both the ulnare and radiale. There may be either two or three metacarpals. Formerly this difference in number served as basis for the specie classification, didactyla and tridactyla. Professor Ryder has since demonstrated the identity of the two forms. The second and third digits have two phalanges each. The fourth digit has only one.

The hind limb of *Amphiura* is fully one-third longer than the fore one. The femur has a well developed, cartilaginous head and a prominent trochanter. It broadens gradually from the middle to the distal end. The tibia and fibula are a trifle over one-half the length of the femur, and are approximately equal to each other in strength. The tibia is largest at its proximal end, but the two ends of the fibula have equal surfaces. These bones articulate with the tibiale and fibulare of the tarsals. The third tarsal supports the third and fourth metatarsals, and the tibiale supports the second metatarsal. The second and third metatarsals have each two phalanges, but the fourth has only one. All the phalanges and metatarsals are well ossified, but the tarsals are cartilaginous. The girdle bones are less perfectly formed than the limb bones. The shoulder girdle consists of a cartilaginous coracoid, a bony scapula, and a cartilaginous suprascapula. There is no evidence of true sternal elements. The pelvic girdle is more complete, having an ischium, ilium, and pubes. The ischium and pubes are united to each other and also to their fellows of the opposite sides, so as to form a shield-like plate, which is composed of cartilage, with the exception of two discoid ossifications in the posterior parts. The acetabulum is entirely cartilaginous. The ilium proper is well ossified, very slender, and surmounted by a cartilaginous style which is attached to the sacral rib of the sixty-third vertebrae on the right side and the sixty-fourth on the left. I think Mr. F. A. Lucas of Washington was the first one to observe this asymmetrical disposition of the iliac bones.

*The Vertebrae.*

Three divisions of the vertebrae may be recognized: cervical, trunk, and caudal. There is only one bone in the first division known as the axis, the atlas being ankylosed with the skull. The anterior face of the axis presents two concavities for articulation with the occipital condyles. There are also two slight projections between the concavities, which may be called prezygapophyses, as they are applied to the internal facets of the condyles. On the posterior aspect are seen the postzygapophyses descending from the backward extension of the neural arch. The neural spine is only slightly developed, and there are no transverse processes. This vertebra as well as all the others is amphicoelous. The trunk vertebrae number sixty-two. All have prominent transverse processes and high neural spines. The transverse processes of the first seven or eight vertebrae are laterally sulcated in their distal regions, and have short ribs attached. The neural spines bifurcate posteriorly and send their prongs outward on the postzygapophyses. The course of each prong is V-shaped, with the apex directed anteriorly. From this apex a small diapophysial spine extends forward to near the anterior base of the neural spine. This process serves a special purpose in *Amphiuma*, as I shall show later. The faces of the zygapophyses are in a symmetrical plane, extending in an axial direction. All the trunk vertebrae except the first two have small hypapophyses attached to the anterior part of the body, which project anteriorly. The middle two-thirds of the body of each vertebra is so constricted laterally as to form a rather sharp spine viscerally.

There are two sacral vertebrae. Their processes are the same as the trunk vertebrae. The caudal vertebrae number thirty-seven, making a total of one hundred and one bones in the spinal column. All the caudal elements except the first two have prominent chevron bones. The neural spine, which is so high in the trunk region, is very much depressed, and the posterior bifurcations of this spine are more extensive. The transverse processes are declivous and decrease in length posteriorly as far as the mid-tail region, where they entirely dis-



appear. The parapophysial spine remains constant for the important muscular attachments. The many processes and depressions characterizing the bones of *Amphiuma* present but slight genealogical significance until we have made a careful study of the muscular system.

*Muscular System.*

During the past six months I have searched carefully for a description, or even a few words of introduction, to the muscular system of this strange animal, but have been able to find only a very terse discussion of the subject. This is given by Dr. Bronn (10), and consists of a few words concerning the muscles of the head. A brief account of the dorsal muscles was published by the writer (6) in April, 1894. A satisfactory dissection of the muscles requires considerable and careful preparation of the tissues, owing to the fact that the muscular arrangement is so complex and many of the muscles are so minute and massed together. After much experimenting I found the following fluid a most admirable agent for the maceration and differentiation of the muscular elements: one part of one-fourth per cent chromic acid, two parts of ten per cent nitric acid, two parts of seventy per cent alcohol, and three parts of water. The specimen may be left in this fluid a week, at the end of which time it must be thoroughly washed in running water for several hours. Then the muscle-fibres will be found stained a bright red, while the fascial envelopes will remain uncolored and the tendinous origins and insertions will be swollen so as to be readily seen.

Great difficulty is experienced in neatly separating the skin from the underlying muscles, since the two are indissolubly connected by an exceedingly tough fascia. This fascia consists of a dense sheath of tissue arising from the neural spines in two plates, which, scarcely separated at their origin, diverge gradually as they rise to the dorsal surface, thereby bounding laterally an area whose cross-section is triangular. This area is filled with a loose connective tissue and fatty substance. Each plate of fascia is reflected over the external surface of

its respective side. *At a distance of one-fifth of the circumference from the dorsal line, a cleavage into two membranes takes place, one of which descends almost vertically through the body-wall to the cavity where it gives rise to the transversalis abdominis muscle.* This muscle continues ventralward until within about one centimetre of the mid-ventral line, where it becomes fascia. The other reflected plate of fascia extends subcutaneously around the body to the mid-ventral line, where it comes in contact with the internal plate, since no muscle takes part in the formation of the body-wall in the mid-ventral region. This tough fascial sheath also envelopes the head, being strongly attached to the median keel in the posterior region, and broadly adhering to the anterior portion of the frontal, the prefrontal, nasal, and premaxillary bones.

#### *Muscles of the Head.*

*Amphiuma* has four dorsal head-muscles : pterygo-maxillaris, masseter, temporal, and cervico-parietalis. The pterygo-maxillaris arises mainly from the median juncture of the parietals and the fascia covering the horizontal surface of the frontal. A small portion of the muscle is a continuation of the cervico-parietalis. Its insertion is on the dorsal side of the pterygoid bone and cartilage. It is clear to be seen that this muscle in *Amphiuma's* ancestors must have been the anterior part of the cervico-parietalis. The tendons of the temporal, through enlargement and continual activity have usurped almost the entire space of the parietal groove, thereby causing the unused muscle to dwindle. The masseter is an exceedingly strong muscle, and arises in two parts. One part originates from the lateral area of the proötic, the other from the anterior curved keel of this bone. The two unite almost at their origin, and extend as a thick, muscular mass to its insertion on the mandible external to the coronoid process. The temporal is the long and strong elevator of the lower jaw. It arises from the neural spines of the fifth, fourth, third, second, and first vertebrae. It is inseparably joined with its fellow as far as the parietal bone. At a distance forward of this equal to the interorbital space, the

muscle is transformed into two tendons which, passing along the parietal groove, descend anterior to the proötic, and are inserted together in the coronoid process. The arrangement of this muscle is such as to give great strength and yet preserve the flat attenuate condition of the head in the proötic region. The cervico-parietalis muscle arises from the second and first vertebrae, and is attached to the posterior part of the parietal and the dorsal area of the exoccipital bone. The lateral head-region presents five muscles: cucularis, digastricus-maxillae, interbranchiales constrictores arcuum branchiarum, levatores arcuum, and adductores arcuum. The cucularis arises from the fascia of the transverse processes and descends a narrow band of muscle anterior to the forelimb to its insertion in the walls of the oesophagus. The digastricus maxillae is a large flat muscle arising in three portions. The first portion is attached to the neural spines in the shoulder region and is a continuation of the superior dorsal muscle. The second portion arises from the summit of the first epibranchial and mingles inseparably with the first. The third portion is the strongest, and arises from the posterior otic region, joining the other two immediately, whence the entire mass passes downwards and forwards to a firm insertion in the posterior angle of the lower jaw. Bronn's *Their-Reichs* (10) describes only two portions as origins of this muscle. The writer has detected several errors in this work in the descriptions of the muscles of the head of *Amphiuma*. The interbranchialis constrictores arcuum branchiarum exist as thin oblique bands of muscular fibre between the first, second, and third epibranchials, but no fibre joins the third and fourth, between which the gill slit persists in the adult. The levatores arcuum arises from the inferior side of the posterior portion of the digastricus and descends as a flat band of fibres to its insertion on the summits of the epibranchials. The adductores arcuum consist of a tendinous band connecting the summits of the four epibranchials, whence it extends downwards and backwards to a point above the forelimb, where its course becomes transverse, forming the third inscriptio tendinea. The ventral head-region presents eight

muscles : thoracico-hyoideus, omo-humero-maxillaris, genio-hyoideus, mylo-hyoideus, stylo-hyoideus, genio-glossus, cerato-hyoideus externus, and trachealis arcuum. The thoracico-hyoideus is a large muscle extending from the median extremity of the cerato-branchial backwards until it is inseparably mingled with the rectus abdominis. Its fibres are interrupted by several inscriptiones tendineae, which are present as far forward as the gill slit. The omo-humero-maxillaris is well developed, arising from the fascia ventralward of the fore limb, and increasing in strength as it runs forward to its insertion on the angle of the maxillary. The genio-hyoideus is a thin band of muscle, arising from the symphyseal region of the mandible, and is inserted in the fascial sheath of the thoracico-hyoideus. The mylo-hyoideus forms a thin sheet of muscular fibre extending transversely between the rami. The stylo-hyoideus lies posterior to and deeper than the former muscle, and extends from the cerato-branchial to the cerato-hyal and hypohyal bones and basi-hyal cartilage. The genio-glossus lies in the floor of the mouth parallel with the ramus connecting it with the hypohyal. The cerato-hyoideus-externus lies immediately beneath the stylo-hyoideus. The trachealis arcuum is composed of a transverse band of fibres extending from the fascia of the tracheal region to the tendon joining the summits of the epibranchials. Its function I believe to have been the retraction of these arches. Fischer, Duges, Humphry, Schmidt, Goddard, and Van der Hoeven disagree to such an extent upon the names of the muscles of the Amphibian head that I have not adopted any one man's nomenclature, but have retained the name which seemed most proper for the muscles of *Amphiuma*.

#### *Muscles of the Limbs.*

So far as I have been able to learn no one has yet attempted to describe the muscles of *Amphiuma's* limbs. The minuteness and massing together of the muscles render it a most difficult undertaking. On the ventral aspect of the fore limb are seen four muscles. The largest one, representing the

pectoralis major, arises from the fibres of the omo-humero-maxillaris posterior to the limb, and extending distalward as a radiate muscle, is inserted in the fascia of the muscles of the arm. Immediately beneath this muscle, which covers the entire coracoidal region, is found the supracoracoideus, a radiate muscle arising from the ventral surface of the coracoidal cartilage and extending to its insertion in the head of the humerus. Its function is that of depressing the fore limb. The slender fascia-like deltoideus arises insensibly from the fibres of the omo-humero-maxillaris, and runs along the anterior side of the arm, being slightly inserted on the distal end of the humerus, but continuing as a flexor carpi radialis to its final insertion in the carpal cartilages. The coraco-humeralis is a mere branch of the omo-humero-maxillaris, and is strongly inserted in the anterior proximal region of the humerus. It draws the limb cephalad. The flexor digitorum communis is a greatly degenerated muscle arising from the middle part of the humerus and extending downwards to the carpal region. The dorsal aspect of the fore limb presents four muscles very closely bound together by dense fascia. A slender muscle representing the triceps brachii arises from the fascia posterior to the branchial arches, and appears to be attached slightly along its entire course down the arm to the phalanges. From the obliquus externus a band of fibres runs forward to its insertion in the upper part of the humerus, serving to draw the arm backward. This muscle corresponds to the latissimus dorsi. Another muscle arising in common with the last mentioned is inserted along the middle portion of the humerus, sending fibres onward to the phalanges, and is probably the atrophied remains of the infraspinatus. Owing to the fact that *Amphiuma* seldom bends its arm at the elbow, the muscles arising from the shoulder region in many instances continue to the forearm and hand. This is the primitive condition of limb muscles. *In fact, I do not think this animal is capable of flexing the forearm or the arm, as the muscles are so bound together by dense fascia and continuous at the elbow joint. My anatomical inference on this point was confirmed by observing a large specimen moving across the floor. The limbs did not touch the floor, but*

*they were moved quite vigorously backward and forward, and were not bent at the elbow or knee joints.*

The muscles of the hind limbs are larger and more distinct than the foregoing. On the ventral aspect are seen three muscles. The large muscular mass arising from the ischio-pubic symphysis and taking its course down the posterior side of the limb to the phalanges appears in the reptilia as the adductor and gracilis muscles. Immediately beneath this mass a radiate muscle arises from the ischio-pubic plate, and is strongly inserted in the greater trochanter. The femoro-caudal arises from the third and fourth caudal vertebrae, and descends forward in two parts, one of which is inserted in the upper part of the femur; the other joins with the semimembranosus extending down the posterior side of the leg to the insertion into the phalanges. The ischio-caudal is a well developed muscle originating on the posterior margin of the ischium and extending posteriorly to an insertion on the vertebrae of the anterior third of the tail. The pubo-tibialis is a strong adductor arising from the coelomic aspect of the ischio-pubic plate and extending across the middle part of the femur down the front side of the tibia to an insertion in the phalanges.

The dorsal aspect of the hind limb presents two muscles. The rectus femoris is a heavy muscle arising from the fascia in the region of the ilium and extending to the distal part of the femur, where it is attached, thence continuing to the aponeurosis of the foot. The ilio-peroneal arises from the ilium, and extends to the distal bones of the leg. Thus it will be seen that many of the muscles of this limb pass over two joints, thereby indicating very restricted movements, if any, in the knee joint. The phylogenetic significance of these facts will be discussed later.

#### *Muscles of the Trunk.*

The muscles of this region furnish a most intricate as well as a most interesting study. This portion of *Amphiuma's* muscular system had not been described prior to my paper in the *Anatomischer Anzeiger* of April, 1894. As was stated in

the early part of this communication, the trunk muscles are separated into two regions, *viz.*, the dorsal and abdominal, by the fascial lamina split off from the external dorsal sheath. This lamina extends through the wall to the body cavity. A similar disposition of the fascia occurs in *Cryptobranchus japonicus*, van der Hoeven, as described by Humphrey (11). The dorsal mass of *Amphiuma* is not differentiated into separate muscles, but for the sake of convenience may be considered as composed of two parts: the superior, lying above the transverse processes, and the inferior, lying beneath these processes. The former corresponds to the erector spinae of some authors. The latter is called rectus trunci internus by Schmidt, Goddard and van der Hoeven in a description of other Amphibia of this order. Mivart (12) speaks of a similar muscle in *Menopoma* as being a part of the retrahens costarum. The anterior portion of this muscle in *Amphiuma* undoubtedly functions as a retrahens costarum, being attached to the minute ribs found on the first seven or eight vertebrae of the trunk. The skin having been carefully removed from the back, and the muscles well stained and macerated by the fluid mentioned previously, there will be seen lying along the axis longitudinally-disposed rows of cones, the enveloping fascia of which appears, at first sight to form a kind of network.

In the superior dorsal mass there are three rows of cones lying side by side. The apices of the row adjacent to the axis are directed posteriorly, those of the next row anteriorly, and those of the third row posteriorly. *Thus it is seen that the apical direction of the cones varies alternately in the different rows.* Each cone is introduced into the preceding one about one-third of its length, as shown in Fig. 10.

From the exterior apex of each cone in the two distal rows a tendinous cord extends to the interior apex of the following cone, thus serving to hold the apices in position. The row most distant from the axis has the deep part of the base of each cone firmly attached to the outer half of a transverse process. That part of the base distal from the axis is reflected to form an inscriptio tendinea extending transversely to the mid-ventral line. The superficial base of the cone blends with

the fascial body investment. That side of the base proximal to the axis is continued forward as the distal side of a cone in the adjacent row. Therefore it is seen that a transverse line through the apex of a cone in one row will pass through the base of a cone in the adjacent row.

In the middle row the deep sides of the bases are attached to the post-zygapophyses and their spines. The distal and proximal sides of the bases are continued as the lateral boundaries of cones in the adjacent rows. The superficial sides of the bases have the same insertions as those in the row previously described. The cones in the row adjacent to the axis are somewhat flattened laterally by their close apposition to the neural spines. The deep side of the base of each cone is securely inserted on the postero-lateral division of the neural spine. The distal side of each base takes the same course as the corresponding side in the adjacent row. The proximal sides are fastened to the neural spine and also to the fascia arising from the neural spines to serve as the body investment. The superficial sides of the bases and also one-half of the superficial lateral boundaries of the cones are blended with the external fascial envelope. The apices of the cones in this row give off ribbon-like tendons which extend to the interior of the following apices. Such is the general arrangement of the cones in the superior dorsal mass.

The size of these cones varies. Those of the distal row are all of the same size, and are somewhat larger than those of the other two rows, the length being fully three centimetres, and the diameter of a base about one and a half centimetres. The length of a cone in the proximal row is scarcely two centimetres, and its base is about one-half a centimetre. The preceding measurements were made on an animal almost one metre long.

Since the arrangement of these cones is so regular, it is easy to estimate their number, which I have calculated to be three hundred and seventy-two in the superior dorsal mass.

A view of the inferior mass from within the body cavity reveals no evidence of a conical arrangement, but instead are seen, very prominently marked, the transverse septa at regular



intervals, corresponding to the lengths of the vertebrae. It will be noticed, however, that the septa appear to cease very abruptly at a distance of two-thirds of a centimetre from the axis. A careful dissection of a well stained specimen along this line brought to view the same conical arrangement observed in the superior mass. The cones in the distal and middle rows are quite perfectly developed, but those of the proximal row are very imperfectly formed, being too closely apposed to the spinal axis. The direction of the apices in these rows is exactly opposite to those in the superior mass; that is, the proximal row of cones has its bases pointing anteriorly, whereas in the corresponding row of the superior mass the apices pointed posteriorly. The cones are much smaller, being scarcely half as large as the overlying ones. The superficial sides of the bases, as well as a large part of the superficial lateral area, are inseparably united to the dense fascia lining the body cavity. The outer sides of the bases in the distal row are reflected to form the transverse septa, while the deeper sides of the bases are firmly attached to the lower side of the outer half of the transverse processes. The inner sides of these bases are continued to form the lateral boundary of a cone in the adjacent row. The attachments of the middle row are so similar to those of the same row in the superior mass that I will not give them. The apices of these two rows are connected with the interior part of the apices of the cones following by a ribbon-like tendon.

In the row adjacent to the spinal axis the deep sides of the bases adhere to the hypapophyses of one vertebra, and the apices are inserted on the hypapophyses of the vertebra following, so that each hypapophysis serves for the attachment of an apex and the deep side of a base. From this brief description it can be readily seen that the general plan of the cones is the same in both dorsal masses.

The conical arrangement of the muscles prevails not only in the dorsal portion of the tail of *Amphiura*, but also in the ventral portion. The disposition and attachments of the cones here are so very similar to those of the trunk region that it would be unprofitable to describe them. The number of cones

in this region is approximately four hundred and sixty-eight, though some of them near the extremity are rather imperfectly formed. The whole number in the trunk, counting twelve to each vertebra, equals seven hundred and forty-four, which, added to the four hundred and sixty-eight in the caudal region, gives a total of one thousand two hundred and twelve cones. *In other words, the dorsal and caudal muscles of this animal have over one thousand strong fascial attachments.*

Having discussed the general structure of these muscles, it is now in order to determine the direction of the fibres. These are not parallel to a line through the apices of the cones, as we should expect, but are so directed as to form an angle of about ten degrees with that line. Since there are no cones found in the outer half of the dorsal muscle, the direction of the fibres there is exactly parallel with the axis, being, however, completely interrupted by the inscriptions tendineae.

So far as I have been informed, this peculiar conical disposition of the fibres of the dorsal muscle has been observed in only two other vertebrates and in no other Amphibians. Dr. Hair (13) describes similar cones in the alligator, and I have noticed the same structure prevalent in *Sphoenodon* (*Hatteria*), the peculiar New Zealand lizard. The genealogical significance of this muscular arrangement will be discussed later.

The ventral trunk muscles are, as in other Urodeles, composed of four sheets of fibres: the transversalis abdominalis, the obliquus internus, obliquus externus, and rectus abdominis. The first named is a mere continuation of the descending lamina of the external dorsal fascia. It may therefore be said to arise from the neural spines, and with its fellow, form a tube inclosing the viscera and dorsal muscles. In other words, the lamina may be considered as an aponeurosis, the muscle-fibres originating just before the aponeurosis emerges into the body cavity. The muscle passes transversely around the ventrum, dwindling again to fascia about one centimetre before joining its fellow along the mid-line. *The striking feature in this muscle is that it is unaffected by the inscriptions tendineae, a condition not present in any other Amphibian. The obliquus internus and also the obliquus externus are thicker on the left*

*side of Amphiuma than on the right. The left dorsal mass is also considerably stronger than the right.* This asymmetry is probably due to the manner in which the animal lies coiled, though I have not had opportunity to demonstrate that fact. The obliquus internus muscle is composed of fibres taking origin from the tendons of the transverse processes, and extending obliquely anteriorly between the inscriptiones tendineae. External to this muscular plate lies the obliquus externus, readily recognized, as the fibres extend obliquely posteriorly between the inscriptiones. As the fibres of these two oblique muscles approach the ventral line they gradually change their direction, becoming finally parallel with the axis of the animal, and thus form the rectus abdominis. In all other Amphibians except *Amphiuma* this muscle is continuous over the ventral line. Its fibres are completely interrupted by the inscriptiones. Anteriorly it is continuous with the thoracico-hyoideus and omo-humero-maxillaris. Posteriorly it is attached to the pelvic elements, but continues as the ventral caudal muscle. Thus it will be noticed that the trunk and head muscles of *Amphiuma* are more highly specialized than those of other Urodeles, while the limb muscles are less specialized.

#### *Digestive System.*

The food of this Urodele consists of crayfish, small teleosts, and other similar aquatic life. The lining membrane of the buccal cavity is tough and smooth, but its continuation into the pharyngeal and oesophageal region is loose and somewhat corrugated longitudinally. On the ventral side are numerous ciliated columnar cells. The stomach is a slight enlargement of the oesophagus, beginning at a distance behind the shoulder girdle, equal to the distance of that girdle from the tip of the nose. The mucous lining of the stomach is thrown into small longitudinal ridges in the anterior portion of the organ, these ridges increasing in prominence as they extend posteriorly. The walls of the stomach in its anterior parts are but little thicker than those of the oesophagus, but posteriorly they become nearly twice as heavy. The length of the stomach is

equal to almost one-third of the distance between the fore and hind limbs. The transition from stomach to duodenum is readily recognized by the vast difference in the thickness of the wall, that of the latter being very thin. The membranous vascular folds increase in prominence and continue throughout the entire intestine to the rectum. The intestine is for one or two centimetres folded upon itself at two or three points in its course. The pancreatic gland lies dorsalward of the posterior half of the stomach, and for an equal distance along the duodenum. The liver extends from the region of the tenth to the thirty-eighth vertebra, being almost twice as long as the stomach. It is entire. The gall bladder lies near the caudal termination of the liver. The rectum consists of an abrupt expansion of the digestive canal at a distance of four or five centimetres from the cloaca. The internal wall of the rectum is quite smooth. This portion of the canal passes gradually into the cloaca, recognized only by its location and smaller diameter. The cloacal region will be described in the discussion of the urogenital apparatus.

### *The Circulatory System.*

This system in *Amphiuma* is very much the same as in the salamanders. The heart is surrounded by a very large sac, through which may be seen the ductus cuvieri entering the large auricle. The bulbus arteriosus is long, giving off an aorta bow on each side. The carotids are exceedingly large. The iliac arteries and veins are very prominent. The venae revehentes are clearly visible in the kidneys. The portal vein lies along the dorsal side of the liver, receiving its numerous tributaries from the intestines, pancreas, and liver. The pulmonary vein is distinctly visible, passing to the apex of the lung on the external wall. Other features of the vascular system are in common with the order of Urodeles.

I shall not attempt a description of the nervous system, as that has been admirably discussed by Dr. Osborn (8).

*The Genito-urinary System.*

The kidneys are leguminoid bodies located immediately anterior to the hind limbs. In my largest specimens they measured four centimetres in length. The ureter is very short. The urinary bladder is exceedingly elongated, extending from the termination of the liver to the cloaca. *Cope has asserted that Amphiuma has only one testis, but I find paired testes extending from the liver half way to the vent.* In alcoholic specimens they are of a brownish spongy texture. They are attached to the body wall by folds of the peritoneum. A mesonephric or Wolffian duct is present as a thick-walled tube running in a straight course from a point near the gall bladder to the urogenital sinus. The vesicula seminalis is a thin-walled tube ending blindly in front near the gall bladder and extending in a convoluted course to a common opening with the mesonephric duct into the urino-genital sinus. The vasa efferentia are present as delicate tubes arising from the testis and emptying into the Wolffian duct, which acts as a vas deferens. The ovaries are very slender bodies lying a short distance posterior to the liver. The oviducts extend along the dorsal side of the body wall, terminating in the urogenital sinus. It has for a long time been a question whether the eggs of *Amphiuma* are fertilized internally or externally. I published a short article relating to this subject last April (7). I am now fully convinced that internal fertilization takes place.

In the early part of the spring of 1893 I secured a male specimen of *Amphiuma* a trifle over a metre in length in Northern Tennessee. This animal was the largest of its kind on record, and was found farther north than any previously discovered. On examining the vent I found exuding a viscid substance which, when placed under the microscope, revealed numerous spermatozoa. The inner walls of the vent were covered with dense papillae on their posterior parts. These papillae under the microscope proved to be the orifices of numerous glands which secreted the almost colorless waxy substance in which the spermatozoa were lodged. *The anterior parts of the internal vent walls are furnished with from fifteen*

to twenty membranous laminae extending obliquely from within outwards and backwards in such a manner as to transfer the generative products slowly from the cloaca to the external lips of the vent. When these lips are placed in apposition to the lips of the female vent, the reproductive agents are induced within the cloaca of the latter by means of a series of capillary tubes (Fig. XI, C) arranged on the inner walls of the vent and extending from without inwards and forwards. I do not see how these different features in the vent structure of the two sexes can serve any other purpose than that which I have described. Furthermore, the fact that the male was so filled with spermatozoa as to cause them to exude indicates that that month, May, was the natural time for their evacuation; and, inasmuch as the eggs are not deposited until August or September, fertilization must occur within the body of the parent. This theory of internal fertilization is further strengthened by the fact that *Ichthyophis glutinosus*, the blind-worm of Ceylon, an animal closely related to the family Amphiumidae, is reported by the Sarasins (9) to have its eggs fertilized internally.

#### *The Respiratory System.*

The anatomy of the respiratory apparatus in this animal is very simple. The external apertures of the nostrils are exceedingly small, being situated near together on the forward aspect of the fascial region. The internal nares appear lateralwards of the posterior limit of the vomero-palatine series of teeth. *The trachea is very long, being in my largest specimen nearly six centimetres.* The glottis is a small longitudinal slit on the ventral side of the pharyngeal region. There is no epiglottis. The trachea is thin-walled, without any cartilaginous formations. The lungs are annexed to the trachea dorsalward of the heart. Cope has greatly erred in saying the lungs are subequal. *The left lung is coextensive posteriorly with the liver, but the right one extends within three or four centimetres of the vent.* The diameter of the left is much smaller than the right also. The walls of these respiratory sacs are quite thick anteriorly, and grow thinner as they pass caudalward.

The transverse trabeculae in the cardiac region are ten millimetres apart, and are thrice as heavy as the longitudinal trabeculae. Immediately anterior to the front limbs is seen a spiracle guarded by membranous flaps to exclude the mud. This aperture is in communication with the pharynx, and is supplied with special muscles for closing it, as previously described.

Having now called attention to the important features of the adult, it is in order to make a brief examination of the young.

#### *The Young Amphiuma.*

For a long time embryologists have been seeking a good supply of specimens representing the development of this peculiar Amphibian. Hay (2) was successful in finding the eggs of *Amphiuma* in an Arkansas swamp in 1887. This material furnished important information. Last February I was so fortunate as to secure a number of very young specimens from a North Carolina dealer. They ranged in length from sixty-eight to ninety millimetres. They were found in a damp locality under some large rocks. Hay's embryos were 45 mm. long. It is probable that my specimens were hatched in November or December. The general shape of the young (Fig. 12) is very much the same as the adult. There are no signs of gills, and only one gill-opening persists on each side. The eyes are rendered useless by the heavy shields of epidermis, as in the adult. *The dermal glands are more prominent than in the old.* The caudal fin is less atrophied. The lower jaw is correspondingly shorter than the adult's. The projecting dermal folds of the upper jaw are little developed. *The legs are relatively longer than in the adult, but the digits are imperfectly formed, those on the hind limb being quite distinct, while there are no signs of any on the fore limb.* Hay (3) states the reverse of this to be true in his embryos, viz., that the digits of the fore limbs are better differentiated than those of the hind. A gross dissection of this small specimen showed that the internal structure accorded with that of the adult, except in the case of the left lung, which did not extend to the caudal

termination of the liver. The most important information was gained from the study of the heads of several specimens stained *in toto* in borax-carmin and cut serially into sections one-fiftieth of a millimetre in thickness. Horizontal as well as sagittal and transverse sections were made.

*The Skeletal Anatomy of the Head.*

The skeleton of the head is shorter and broader than in the adult. The ossifications are, of course, vastly different. There are but sixteen fully ossified elements in the cranium: premaxillary, nasals, frontals, prefrontals, parietals, squamosals, maxillaries, vomero-palatines, and parasphenoid. The following elements are partially ossified: orbitosphenoids, prootics, and exoccipitals. The pterygoids, quadrate and stapes are wholly cartilaginous. The premaxillary is quite the same as in the adult, and needs no further description than to state that the interosseus septum is not derived from the nasal roofing cartilage, as Wiedersheim (1) has suggested. The two elements, though in contact, present no transition from one to the other. The enveloping cartilage of the nasal sac is incomplete where the osseous septum is present. The union of the cartilaginous floors of the nasal sacs medially extends beneath the anterior part of the brain for a short distance, when the middle portion of the cartilage passes into connective tissue, leaving two lateral bars. Hay (3) speaks of an unpaired piece of cartilage lying in the roof of the mouth of the adult between the anterior ends of the vomero-palatines, and states that it is not found in his embryos. Wiedersheim speaks concerning the same as follows: "Da wo die Vorderenden der Vomero palatine in der Mittellinie zusammenstossen, ragt ein conisch gestalteter Knorpelzapfen vom Boden der Nasenhöhle in die Schleimhaut des Mundes herab, von welcher er einen Ueberzug erhält."

Hay believes that this nodule of cartilage has been cut off from that forming the floor of the nasal sacs by the union of the bones in the roof of the mouth. Fortunately my specimen is of just the proper stage to settle the question. *The roofing*



*bones of the mouth are fully ossified before the nodule is formed. In a specimen eighty-eight millimetres long the cells of the dense connective tissue are concentrically arranged preparatory to the formation of the true cartilage, which in a specimen ninety millimetres long has made its appearance.* The frontal bone, though completely ossified, differs from the adult in the manner of giving exit to the olfactory nerve. Hay implies that Wiedersheim has erred in the following description: "Es handelt sich nämlich, wie am besten aus der Figur 20 F ersichtlich ist, um eine an der Unterfläche der vorderen Stirnbeingegend auftretende Knochenzwinge, deren mediale Circumferenz vorn und einwärts, und deren laterale mehr nach hinten auswärts gelagert ist. Beide stehen parallel zum Medianebeine und sind unten gegen die Schädelbasis zu durch eine schmale knöcherne Commisur in Verbindung." *This description is exactly correct for the adult (Fig. III h), but in the young there exists only an unmodified aperture in the frontal for the exit of this nerve.* Cope (14) attaches great importance to the free margin of the frontal bone in the adult. The frontal in the young has no such margin, the surface being slightly depressed in the middle and regularly convex laterally.

The frontals overlap the parietals to a considerable extent posteriorly. A cross-section through the posterior part of the parietal of the adult presents the curve of a quarter circumference, the depression being external for the temporo-cervical tendon. In the young this bone slopes from the median line outwards at an angle of thirty degrees, and is but slightly depressed in the middle of the distal half.

The orbito-sphenoid confirms Hay's account, being higher in front than behind. Its ossification is almost complete. The exoccipitals remain almost entirely cartilaginous, being invested with a thin parostosis. The ossification of the condyles is beginning. The pterygoid is represented by a bar of cartilage, free anteriorly but attached to the quadrate posteriorly. The otic capsule is quite surrounded by cartilage. The otolithic deposit is extensive. The proötic is cartilaginous to a considerable extent. The stapes shows no evidence of ossification, as is likewise the case with the columella. The quadrate

is perfectly formed in cartilage. The squamosal is the only otic element entirely ossified. A thick plate of basioccipital cartilage lies beneath the hinder portion of the brain. The parasphenoid forming the floor of the brain-case is somewhat convex in its anterior part, but markedly concave in the posterior region. The lateral walls of the brain-case in the pituitary region posterior to the orbitosphenoid are of cartilage, as in the adult. The other features of the cranium are so similar to the descriptions of Hay and Kingsley that I deem it useless to give them.

#### *The Visceral Skeleton.*

The mandible is quite the same as in the adult. The rami are united anteriorly by strong connective tissue. Meckel's cartilage lies in the groove of the ramus as far forward as the point just below the eye, and extends backwards so far as to be in contact with the quadrate. The dentary and angular are well ossified. The teeth are fully developed. The hyoid apparatus is unlike either the adult or Hay's embryo. It is for the most part cartilaginous. The middle third of the basibranchial appears quite well ossified. Thin parostoses invest the ceratohyal and ceratobranchial. The following elements compose the apparatus: one basihyal, two hypohyals, two ceratohyals, one basibranchial, two ceratobranchials, and eight epibranchials. Hay found no basihyal in his embryos. A distinct nodule of cartilage is present at the juncture of the hypohyal and ceratohyal on the external side. Its significance is unknown to me. The ceratohyals extend outwards rather than backwards, as in the adult. The larynx is an exceedingly simple structure, consisting of a fibrous connective tissue tube, strengthened by two lateral bars of cartilage. The external orifice is a longitudinal slit. The trachea has no rings or partial rings of cartilage.

#### *Soft Parts of the Head.*

The disposition of the muscles is approximately the same as in the adult, with the exception that the place of the temporo-cervical tendon appears to be filled by muscular tissue. Ven-

trally the first inscriptio tendinea is seen just below the basihyal. The remnants of some nasal glands are present along the olfactory sac. Hay found these glands better developed in his specimens. The most important and interesting structure is found below and external to the eye in my smallest specimen, seventy-eight millimetres in length. *There appears in this region a canal (Fig. 15) one-tenth of a millimetre long, which is walled by columnar epithelial cells extremely regular in outline. External to the epithelial wall there is seen a thick layer inferiorly of degenerated tissue, which is bounded by a thin layer of fibrous connective tissue. In three other specimens, eighty-eight, ninety, and ninety-two millimetres respectively, no trace of this degenerate canal could be discovered, and in the smallest specimen I was able to detect it on the right-hand side only.* Here it was very clearly seen, as shown in Fig. 15. The significance of this atrophied element will be discussed later. Hay (3), Kingsley (5), and Osborn (8) have to a limited extent described the nervous system of *Amphiuma*. Owing to the fact that my tissue was not prepared for the demonstration of the nervous elements, I can add only one or two points of interest. The brain (Fig. 14) is much shorter than in the adult, caused mainly by the wedging in of the middle brain between the hemispheres of the great brain. The brain viewed dorsally, excluding metencephalon, presents the outline of a longitudinal section of a hen's egg, the anterior end corresponding to the smaller end of the egg. The olfactory lobes are not marked off as in the adult. The brain of *Siphonops annulatus*, as figured by Wiedersheim, resembles to a considerable extent the brain of young *Amphiuma*. The latter, however, is not so elongated as the former. The pineal gland and pituitary body so prominent in the adult are scarcely distinguishable. Hay and Kingsley have described the origin and distribution of the cranial nerves sufficiently for our purpose. My sections clearly corroborate the statement by Hay that the facial nerve passes beneath the columella. Kingsley failed to find the roots of the fifth nerve. *My sections show but one root.* The dorsal ganglion in connection with the twelfth nerve is quite large, being at least one-third the size of the gasserian ganglion.

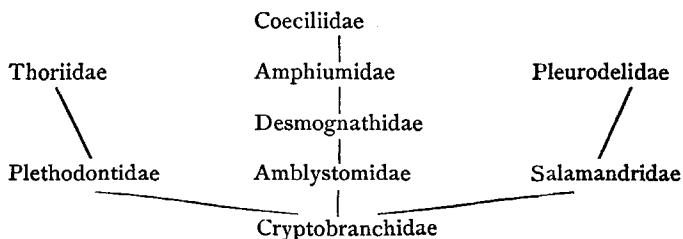
*Axial Skeleton and Appendages.*

The vertebrae are only partially ossified. The transverse processes are wholly cartilaginous, and a portion of the internal part of the body of the vertebrae is unossified. The cartilaginous posterior projection of the roof of the spinal cord is invested with a thin parostosis. The cartilaginous intercentra are present. The ribs are present as cartilage. The neural and diapophysial spines are imperfectly developed. The hypapophyses are well marked. The shoulder girdle is wholly cartilaginous, and presents elements of scapula, coracoid and pre-coracoid. The scapula is exceedingly thin, being only two cells in thickness. The other elements are correspondingly slender. No sternum is present. The humerus is covered with a thin layer of bone, except in the regions of the extremities. The radius and ulna are also ossifying externally. The carpus is present as pure cartilage, and the phalanges remain as hyaline tissue also. The pelvic girdle is entirely cartilaginous. All the elements are present as in the adult, but there is no evidence of the posterior bony disc. The femur is invested with a very delicate ectostosis in the shaft region. The future prominent trochanter process is indicated by a slight flexion of the cartilage at that point. The two abductor, the adductor and two rotator muscles have the same locations as in the adult. The tibia, fibula, tarsus, metatarsus, and phalanges show no signs of ossification. This affords weighty evidence that the formation of the anterior limbs is in advance of the posterior.

I have not been able to discover any conical arrangement in the fibres of the dorsal muscles. The abdominal muscles have the same relative dispositions as in the adult. The transversalis is unaffected by the inscriptiones tendineae, and arises from the internal plate of fascia, originating in common with the external plate on the neural spine. The digestive, respiratory and excretory systems correspond with those of the adult. Having described the anatomy of these different individuals, it remains to determine the genealogical status of *Amphiuma* among vertebrates.

*Phylogenetic Conclusions.*

*Amphiuma* has always been considered a degenerate form. Cope (4) says that *Amphiuma* is the annectant type which Wiedersheim sought for in tracing the ancestry of the *Coeciliidae* to the Stegocephali of the Carboniferous period, and then adds that he derives the *Coeciliidae* from the Urodela direct through the *Amphiumidae*, and adds the following table of affinity:



It is evident to all phylogenists that this table presents an absurdity, since representatives of each of the five families in the direct line of descent are existing at the present time. That these families are closely related cannot be denied. Cope bases his strongest point of relationship between *Coeciliidae* and *Amphiumidae* on the common possession of an ethmoid, when in fact the latter family does not possess an ethmoid. Sections of my young specimens clearly demonstrate this. *What Cope has called the ethmoid are merely the descending processes of the frontals.* Kingsley (5) believes that the many peculiar resemblances of *Gymnophiona* and *Amphiuma* are those of homoplasy. The recent information gained by the examination of the young specimens in my possession, enables me to prove that these resemblances are due, in part at least, to relationship. The *Ichthyophis glutinosus* of Ceylon, as described by the Sarasins (9), is undoubtedly closely allied to *Amphiuma*. It is now known that the eggs of the former are fertilized within the body of the parent. In my description of the reproductive organs of *Amphiuma* I have demonstrated that in this genus also internal fertilization takes place. Both deposit eggs of about the same size, which are united by a

twisted cord. Both incubate the eggs by lying in a coil about them. In their larval life the young of *Ichthyophis* possess gills and dwell in the water. Hay's embryos of *Amphiuma*, evidently near the period of hatching, had well developed gills. The young specimens I secured last February were found under rocks near the water, indicating that their transformation from aquatic to land habits had lately been accomplished. All these superficial features common to the two genera indicate affinity; but by far the stronger evidence of their affinity is based on the structure of the soft parts as well as the skeletal elements. The peculiar disposition of the fascial investment in *Amphiuma* is also seen in *Ichthyophis*. The dorsal lamina arising from the neural spines splits into two plates before reaching the lateral line, and one enters the body cavity to give rise to the transversus abdominis, which is unaffected by the inscriptiones tendineae probably on account of its late formation in the embryo. The omo-humero-maxillaris is absent in all urodels except the Coeciliidae and Amphiumidae. The lungs of *Amphiuma* are very unequal in length, a condition characteristic of the Coecilians, according to MacAlister. There is also a striking similarity in the trachea of the two families. Wiedersheim speaks thus of the Gymnophiona: "Die Luftröhre ist entsprechend den weit nach hinten gerückten Lungen für ein Amphibium von sehr bedeutender Länge und componirt sich aus zahlreichen hyalinknorpeligen Ringen, welche dorsalwärts nicht geschlossen sind, sondern hier durch Bindgewebe ersetzt werden." As I have already shown, the trachea of *Amphiuma* is comprehended in the above description of a Coecilian. The brain of the young *Amphiuma* is much more unlike the brain of the adult than the latter is unlike the brain of *Siphonops annulatus*, as figured by Wiedersheim. The distribution of the cranial nerves in the two species is almost identical.

In *Siphonops annulatus*, *Coecilia rostrata*, *Coecilia oxyura* and *Ichthyophis glutinosus* Wiedersheim has figured and described an orbital gland and peculiar tentacular apparatus of the nasal region. This apparatus consists of a canal beginning posteriorly to the eye, whence it extends forward to its external orifice

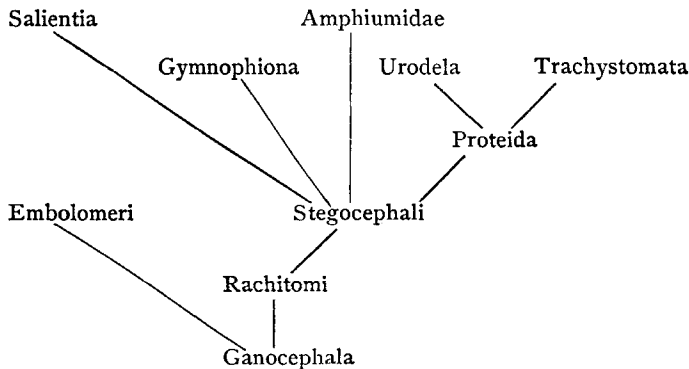
near the narial aperture, a tentacle or feeler, and a muscle by means of which the tentacle is retracted or protruded to guide the animal in its dark underground expeditions. *As I have already shown, there exists in my youngest specimen of Amphiuma the atrophied remnants of this tentacular apparatus. The columnar epithelial lining of the canal is very distinct in about one dozen transverse sections taken through the orbits. In some of the sections I have discerned what I believe to be the degenerated retractor muscle. This apparatus in Amphiuma has precisely the same relative location as in the Coecilians.* For some unexplainable reason, neither Hay nor Kingsley found this organ in the young embryo. Hay speaks of nasal glands, which, from his description, I conclude to be identical with the glands I noticed in conjunction with the olfactory cavities. The tentacular canal of *Amphiuma* cannot be mistaken for the duct of a nasal gland, as it lies too far lateralward and posterior to the nasal region. It will not answer for the duct of the orbital gland, as it is too far inferior to the orbit, although it is possible that its relation to the surrounding parts may have become somewhat distorted. However that may be, the occurrence of this degenerated structure in the young *Amphiuma* and its complete disappearance in the adult gives unmistakable evidence of the relationship of the *Coeciliidae* and *Amphiumidae*. The disappearance of the ethmoid in the latter family can be accounted for by the fact that the descending processes of the frontals have displaced the cartilage for the ethmoid so that it lies beneath the forebrain in my young specimens. The nodule of cartilage between the anterior ends of the vomeropalatines of the adult has no genealogical significance, so far as I can discover. As before stated, the dense connective tissue is being transformed into cartilage in my specimen of 68 mm. *The cause of this formation is found in the fact that the teeth of the lower jaw in biting do not meet the corresponding ones in front, but pass inside of them, pressing against the roof membrane of the mouth, thereby exciting the growth of the cartilage in the same manner as the horns originated in the Cavi-cornia and Cervidae, according to Eimer (17).* That the teeth in the adult *Amphiuma* bite anterior to the summit of the car-

tilage, is explained by the anatomy of the young, in which the lower jaw is relatively shorter than in the adult. A similar abbreviation of the lower jaw is exhibited by the majority of the *Gymnophiona*, as shown by Wiedersheim (Taf. V, Figs. 58 and 59).

The vertebrae of *Amphiuma* are highly specialized, having definite processes for the attachments of its complexly constructed trunk musculature. As Cope has already suggested, the prominent anterior hypapophyses are peculiar to the *Coeccilians* and *Amphiuma*. Thus far I have pointed out the features in these two families which give evidence of genealogical affinity. The proof of relationship furnished is to my mind conclusive ; but the gravest question — what that relationship is — remains to be answered. If Huxley's dictum, "It is more important that similarities should not be neglected than that differences should be overlooked" were maintainable, near affinity of these two families must be admitted. Before such affinity can be asserted, important contrasts in skull structure must be explained. Thus Kingsley says : "The presence of an ethmoid in the *Gymnophioma* (and its absence from *Amphiuma* and other Urodeles), the existence of a turbinal, the absence of a parasphenoid, and the presence of a basisphenoid are all points of importance." Another striking contrast is seen in the structure of the orbit which is only partially encircled by the bony elements in *Amphiuma*, there being no jugal or quadrato-jugal bone present. Gervais gives a concise description of the coecilian orbit : "Cependant l'orbite des Cécilies n'est percée ni dans le maxillaire seul ni dans le corps de l'os jugal ; c'est ce que l'on voit très-bien sur la tête d'un jeune animal de ce genre ; et avec quelque attention, surtout en se servant d'une loupe, on retrouve même chez l'adulte des traces de la suture des deux os entre lesquels l'œil est ici placé, et qui concourent, comme chez beaucoup d'autres animaux, à former un cercle orbitaire." These differences in skull structure make it patent that *Amphiuma* cannot be the connecting link between the leg-bearing Urodeles and the Coecilians, as Cope has asserted. The elongated cranium, the double series of teeth, the tentacular apparatus, the degenerated optic sense, the manner of



fructification and incubation of the eggs, the habits of the young, the degenerate limbs, the unusual disposition of the transversalis-abdominis, the inequality of the length of the lungs, the anterior hypapophyses and the amphicoelous vertebrae, all of which these two families possess in common, point to a common parent form of the *Cocciliidae* and *Amphiumidae*. The numerous differences in the skull structure of the two families make it manifest that the common ancestor is a form far back in Geologic time ; a fact which tends to verify Wiedersheim's statement that the origin of the *Cocciliidae* is to be sought in the Stegocephalans of the Carboniferous. The well-developed columella auris of *Amphiuma* is very probably a character retained from the *Ganocephala* and *Rachitomi*. In the light of present paleontological and embryological knowledge any detailed phylogeny of Amphibia must be very uncertain. However, the facts at hand seem to me of such significance as to warrant the following table : —



Although *Amphiuma* is considered a degenerate form, yet certain parts of its structure are highly specialized. The general shape of the cranium presents a marked contrast in comparison with other Amphibian skulls. The great length of the face and the pointed snout are of no phylogenetic significance, as they have been developed by the habits of the animal. The vertebrae with their numerous processes cannot be accounted for on any other ground than that of adaptation to the mode of life which rendered it necessary that a complex trunk

musculature should exist, and the required processes for the many attachments. The conical arrangement of fibres in the dorsal muscle reveals a condition quite the opposite of degeneration. The fact that similar muscular cones are found in the alligator (13) and *Sphaenodon* does not imply that these three forms are in any way related. The existence of an unusually long and strong temporo-cervical tendon in *Amphiuma* and *Desmognathus* does not furnish sufficient evidence that they are closely allied, as Cope has tabulated them. These are merely cases of parallelism, as is plainly shown when we take into consideration the marked contrast of the more important structural elements of the two families. Scott (19) has demonstrated this condition of parallelism in numerous mammalian families. "The prismatic, cement-covered molar has been independently developed in many forms: *e.g.*, several of the ruminants, certain pigs, the horses, one of the rhinoceroses (*Elasmotherium*), the elephants, many rodents, *etc.* The selenodont molar pattern has been several times independently evolved; (1) in the true ruminants; (2) in the camels; (3) in the oreodonts. The spout-shaped odontoid process of the axis has arisen in the true ruminants, the horses, the camels, and, to a certain degree, in the later oreodonts, such as *Merychys*." Gegenbaur (20) [p. 669, Fig. 232] has described and figured incorrectly the muscular arrangement in the tail of the fish. The wall of the cone is incomplete adjacent to the spinal column, in all the fish which I have examined. This tendency toward conical arrangement of fibres in the tail of the fish has been evolved by the same mechanical principles that obtain in *Amphiuma*. Thus it may be noticed that in many respects *Amphiuma* is not a degenerate form, but on the contrary possesses highly developed structures; and were it not for the fact that the brain exhibits such primitive characters [Osborn (8), p. 178], I would consider this type the result of progressive rather than retrogressive evolution.

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## EXPLANATIONS OF PLATES XXXIII AND XXIV.

FIG. 1. Dorsal aspect of *Amphiuma*'s skull, X 2. *P*, premaxillary; *n*, nasal; *m*, maxillary; *f*, frontal; *pi*, parietal; *pf*, prefrontal; *q*, quadrate.

FIG. 2. *p*, premaxillary; *m*, maxillary; *pd*, parasphenoid; *pt*, pterygoid; *q*, quadrate; *st*, stapes; *a*, exit for ninth and tenth nerves.

FIG. 3. Lateral view of premaxillary with nasal, maxillary, prefrontal, and portion of frontal removed, X 2. *a*, brain cavity; *g*, frontal bone; *h*, canal for exit of olfactory nerve; *i*, nasal septum of premaxillary; *b*, a break in the septum.

FIG. 4. Dorsal muscles of head. *f*, pterygo-maxillaris; *h*, masseter; *i*, cervico-parietalis; *d*, *e*, temporo-cervical tendons; *a*, frontal bone; *g*, proötic.

FIG. 5. Muscles on dorsal aspect of posterior limb. *c*, femur; *a*, rectus femoris; *e*, ilio-peroneal.

FIG. 6. Muscles on ventral aspect of posterior limb. *c*, adductor magnus; *e*, gracilis; *a*, inscriptiones tendineae.

FIG. 7. Great adductor muscle of posterior limb. *d*, femur; *h*, tibia; *a*, cartilaginous plate; *e*, trochanter; *g*, pectineus; *b*, ossified disc; *c*, pubo-tibialis.

FIG. 8. Transverse section of adult at the fortieth vertebra. *a*, left side; *i*, transversalis-abdominis; *h*, obliquus internus; *g*, obliquus externus; *k*, fascia; *e*, fascia split from external envelope.

FIG. 9. Incision through right body wall and both walls reflected. *l*, lateral fascia line; *c*, muscular cones.

FIG. 10. The three rows of cones seen when the skin and fascia are removed from right side of *Amphiuma*. *b*, triangular rod of fat lying above the vertebrae; *c*, tendinous cord connecting apices of cones; *a*, fascia of cone reflected to form an inscriptio tendinea.

FIG. 11. Vent of the female longitudinally split open. *c*, capillary tubes; *b*, folds of membrane; *a*, entrance to the oviduct; *d*, lip of vent.

FIG. 12. Young *Amphiuma*, 78 mm.  $\times 1\frac{1}{2}$ . *a*, gill opening.

FIG. 13. Hyoid apparatus of adult. *e*, epibranchialis; *b*, cerato-branchial; *c*, basibranchial; *d*, basihyal.

FIG. 14. Brain of young *Amphiuma* seventy-two millimetres long. *a*, *b*, prosencephalon; *c*, mesencephalon; *d*, metencephalon; *e*, spinal chord.

FIG. 15. Transverse section of the optic region of young *Amphiuma* sixty-eight millimetres long. *d*, eye; *r*, retina; *o*, orbitosphenoid; *p*, parasphenoid; *f*, atrophied tentacular canal; *e*, degenerated gland; *a*, brain; *m*, ramus; *n*, Meckel's cartilage; *h*, *i*, *k*, hyoid apparatus.

