DISTINCTIVE SKULL CHARACTERS IN SPECIES OF THE GENUS AMBYSTOMA*

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INTRODUCTION

The skulls of amphibia in the order Caudata show interesting modifications and differ much from one another, but all agree in the following respects: (1) absence of the quadratojugals; (2) a parallel relation of the palatines or vomeropalatines with the axis of the cranium; and (3) the large size of the parasphenoid.

The separation of the frontal and parietal bones and the occurence of paired orbito-sphenoids are characteristic.

Lower types such as Necturus, Siren, Proteus, and Amphiuma, have a long, narrow type of skull which throughout life remains in much the same condition as that of a tadpole or larval salamander. Internal to the membrane bones the roof and floor of the cranial vault are formed of fibrous tissue and not of well developed cartilage. The epi-otic regions of the skull are ossified, forming large bones external to and distinct from the exoccipitals. The Stegocephalia are the only other amphibia which have these elements separately ossified. Nasals are sometimes present, sometimes absent. Teeth are usually borne on the vomers, premaxillae, pterygoids, dentaries, and angulosplenials. The suspensorium is directed forward.

Higher types of amphibia, such as the salamanders, have broad, wide skulls. In these the suspensorium is found projecting nearly at right angles to the cranium, instead of being forwardly directed. The maxillae are usually well developed, and the premaxillae are completely ankylosed together. There are no palatines. In the otic region the prootics are found distinct from the exoccipitals, and the latter are ossified continuously with the epi-otics and opisthotics.

Of the family Ambystomidae, Cope (1887) says: "The Ambystomidae are of particular interest in the Urodela as furnishing connecting links between the ordinary types of the order and those larger species which we suppose to be characteristic of former periods of the earth's history. It also furnishes us with transitional conditions

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of characters which have been regarded as indicating very diverse origin and nature." The species are mostly of large size, and probably confined to North America with the exception of a species in India.

A rather large series of characters restricts the family. The ethmoid bone is lacking. There is a fusion of vomer and palatine to form the vomero-palatine. The palatine portion is a pointed process which projects laterally from the parasphenoid. The orbito-sphenoid is separated from the prootic by a tough, membraneous wall. The internal wall of the vestibule is ossified. There are conspicuous prefrontals and pterygoids present, and the premaxillae are fully developed. Dentigerous plates are lacking on the parasphenoids.

This paper involves a comparative study of the skulls of six species in the genus Ambystoma. Distinctive characters are analyzed in terms of the factors affecting developmental mechanics. The significance of the genus and the importance of a comparative skull study are also discussed.

The entire genus numbers eleven species. The names of these, and their distribution, are listed below, after Stejneger and Barbour (1923).

Name	Range
A. annulatum Cope	Arkansas.
A. cingulatum Cope	South Carolina to north; Florida and Alabama.
A. decorticatum Cope	Coastal region of south; Alaska and British Columbia.
A. jeffersonianum Green	Canada (to Hudson Bay) and New England, south to Virginia, Illinois, and Arkansas.
A. macrodactylum Baird	Northern California, to British Columbia, Idaho, and Montana; probably to and in Iowa.
A. maculatum Shaw	Nova Scotia west to Wisconsin, southward to Georgia and Texas.
A. microstomum Cope	South Carolina to Texas; north to Ohio, Illinois, and possibly Canada.
A. opacum Gravenhorst	Massachusetts to Florida; west to Lousiana and Texas, Mississippi basin north to Arkansas, Missouri, Indiana, and Illinois.
A. paroticum Baird	Northern California, to British Columbia, Vancouver Island.
A. talpoideum Holbrook	South Atlantic and Gulf States, Louisiana to Illinois.
A. tigrinum Green	Widely distributed over almost all United States, each of the Cascade Range and Sierra Nevada, and extending ing southward over the northern portion of the Mexican plateau.

Ambystoma texanum, formerly listed as a separate species, is now considered as identical with *A. microstomum*. The names *Siredon*, *Axolotl*, *S. pisciformis* and *S. mexicanus* are still used for denoting the persistant larval condition of *A. tigrinum*.

Osteology of Ambystoma opacum

The description which follows will answer in general for any of the species as far as identification of the bony elements is concerned. It is chosen because it represents a sort of intermediate type, having neither an excessively broad brain case, nor one especially elongate.

The Dorsal View of the Skull

The skull (fig. 1) presents a series of smooth, graceful arcs and curves which immediately suggest a symmetry of the whole. Considering the various paired elements, this symmetry is more apparent than real. The antero-lateral part of the skull describes a partial ellipse, the anterior part of which is formed by the premaxillae (pm) meeting together in the midline and articulating with the maxillae (m) laterally and posteriorly. These bones extend the arc to about half the linear dimension of the skull, which is slightly longer than it is wide. Along the mid-dorsal plane the premaxillae also send up large, blade-like frontal processes (fpm) which are closely approximated anteriorly, but diverge slightly in the posterior direction. Laterally they overlap the nasals (n), and posteriorly the frontals (f). It is a general rule that the anterior bone overlaps the element posterior to it. The maxillae, near their junction with the premaxillae, send up an ascending ramus (ar) which articulates with the prefrontals (pf) laterally. The nasolacrimal duct bears a relation to it medially and posteriorly (nld). The external nares (nc), oval in shape, are immediately back of the premaxillae and originally are covered by membrane and a nasal roof cartilage. A small bony element, the septomaxillary (sm) is found in the nasal capsule near the ramus of the maxilla. It is irregular in shape and bent upon itself medially, where it faces the naso-lacrimal duct. A foramen is usually evident in the bone. Primarily it serves for the origin of the muscle dilator naris accessorius. In the Urodela it is found to be an ossification of the cartilage in the posterior wall of the nasal cavity. The work of Lepage (1928) indicates "a chondral origin for the septum." Gaupp considered the homology of the bone in anurans, urodeles, and sauropsida as settled.

The nasals (n) are thin plates of bone, irregular in contour but approximating a wedge. Each bone presents a straight margin toward the nasal process of the premaxilla; a slightly concave margin toward the external nares; and a somewhat convex lateral border which articulates with the prefrontal and is extended posteriorly to articulate with the frontal.

It has already been indicated that the maxilla forms the lateral boundary of a partial ellipse, with the result that the posterior limit becomes far removed from any direct bony attachment with the skull. Its ramus describes an arc directed medialward and slightly posterior and this is continued by the prefrontal in such a way that these bones diverge from one another, leaving an interspace in which part of the vomero-palatine is displayed beneath (v, pa).

The prefrontals are large, irregular, six-sided bones. They are partially overlapped by the ascending ramus of the maxilla. The free lateral margin contributes to the orbit in front, and medially as well, where it helps to form the brain case. Its posterior limit usually indicates the narrowest portion of the brain case. Medially the bone presents two sides, the anterior overlapped by the nasal, whereas the posterior overlaps the frontal. Anteriorly, a small, slightly concave margin borders the external nares. This wedge of bone was evidently overlooked by Parker (1876) who speaks of an "articulation of the ramus of the maxilla with the nasal" at this exact point. The bone is extended under the ramus of the maxilla for some little distance.

The frontal (f) is an irregular, long, flat bone with five distinguishable sides and pointed anterior and posterior extremities. Anteriorly, the bone is overlapped for some distance by the nasal and frontal processes of the premaxilla and extends under these almost to the external nares. Medially, the articulation of the two frontals is serrated. Posteriorly the articular faces are found ventral on the bone because of the overlapping of the frontals on the parietals. Laterally, the bone is partially covered by the prefrontal. The frontal bones dip slightly toward the median suture, and are closely approximated except near the posterior end, where they become narrow and irregular. One side extends to the mid-dorsal line, while the other runs forward and laterally to the posterior tip of the prefrontal, where it contributes slightly to the medial side of the skull.

The parietal (p), although not as long as the frontal, is more broad and irregular, and were it not for a pointed process arising anteriorly and laterally, the shape would be roughly rectangular. The two bones form a gentle parietal crest along the median line. Posteriorly and laterally the bone displays more character because of its relation to the otic and occipital regions. Four borders can be distinctly recognized. Medially and anteriorly respectively, the facets for the opposite parietal and frontal bones are found. Posteriorly, the bone is modeled well over the endocranium, and correlated growth is suggested here, as well as the presence of the anterior and posterior semicircular canals. Here the bone presents an angle as it descends posteriorly (ap), to end in a lobulated margin which overlaps the fore part of the occipital roof.

The occipito-auditory region is well ossified (a). There is a well defined prootic (pr) which is distinct from the exoccipital and is visible dorsally as a protuberance near the parietal angle. Medial and posterior, the articulation is with the parietal which partially overlaps it in this area. Laterally and posteriorly it articulates with the squamosal. The opisthotics and epiotics are co-ossified with the exoccipitals, and all sutural landmarks are obliterated. A rather broad tract of cartilage still separates the two sides of the occipital segment. The otic capsules display considerable character and suggest the canals of the labyrinth. The capsules are in part overlapped by the parietals and squamosals. The condyles are massive, with a convex posterior surface and sharp, lateral angle. The foramen magnum appears crescent-shaped in dorsal view (fm).

The squamosal (s) is found posteriorly and laterally on the skull where it overlaps the otic capsule and articulates with the prootic. The bone is a dense, strong plate, knobbed and transversely ridged above and below; spiked in front and lobate behind. Dorsally it is smooth and superiorly a pronounced groove suggests muscle attachment, as does a small, sharply pointed process immediately posterior to it. The quadrate (q) articulates with the distal ventral surface. This bone, and the pterygoid are partially visible in dorsal view.

Generally, the bones on the dorsum of the skull of Ambystoma opacum are characterized by their smoothness. The contours are gentle and sweeping, and one gets the impression of a clean-cut skull.

Lateral Relations of the Cranial Vault

The lateral walls of the cranium immediately in front of the otic region are unossified for a distance between the exit of cranial nerves II and V (figs. 2, 3, 4). This portion is covered by membrane. Anterior to this, however, are found the ossified, paired orbito-sphenoids, covering a distance from the exit of the second nerve (which forms a partial foramen in the bone) to a short distance behind the internal nares or nostrils (in). Laterally, the bone is slightly convex, whereas the medial surface is concave. It articulates above with the parietal and prefrontal; below with the parasphenoid and the vomero-palatine.

The prootic (pr) articulates above and below with the pterygoid.

Ventral View of the Skull

In ventral view (fig. 2) the premaxillae and maxillae display a concave surface which ends in a thickened margin for the close-set teeth (t). The teeth are conical and show a bulb-shaped enlargement on the distal ends. Dorsally, the palatal portions of the bones are not well developed, and overlap the large vomero-palatines. This is true except in the median plane, where the removal of the internasal cartilage (fs) from between the vomero-palatines of the two sides exposes the frontal processes of the premaxillae.

The large vomero-palatines (v) extend backward on the cranium for about a third of its length and present a concave border medially. The teeth-bearing palatine portions (pa) extend laterally as pointed processes. Anterior to them, the lateral borders are notched to inclose the internal nostrils (in). The deficient side of the foramen is in each case filled in by a ligament. From here the lateral borders are continued forward and outward to the maxillae. Medially and posteriorly for about one fourth of the length of the bones, an interspace discloses the most anterior extension of the parasphenoid (e). The tooth-bearing portion discloses the suture of the bones of the two sides. All teeth point posteriorly and are ankylosed. The vomero-palatines, in the region of the mesial border of the suspended (free) portions of the bone, send out a wedge-shaped slip which articulates with the lateral border of the parasphenoid and above with the tubercle-like anterior extremity of the orbito-sphenoid (seen to better advantage in Fig. 8, pvp).

The parasphenoid is a large, unpaired, thick bone, forming practically the entire ventral floor of the cranium and extending from the level of the internal nares anteriorly to the foramen magnum (fm) posteriorly. Its six sides are fairly symmetrical. In the mid-line it displays a prominent ridge, on each side of which the bone is appreciably depressed. Anteriorly, the sides converge under the vomero-palatines to a blunt point. About one fifth of the parasphenoid is overlapped by the vomero-palatines. The anterior half articulates with the orbito-sphenoid dorsally. Posteriorly, the unossified basi-occipital and basi-sphenoid regions are covered and the lateral extensions of the bone come into relation with the bulging, bony floor of the otic capsule. Here a slit-like indentation of the bone is obvious. It transmits a large branch of the seventh nerve (VII). Dorsally, it articulates with the prootic.

As indicated, the primordial basi-cranial axis is covered by the parasphenoid. Laterally and posteriorly, however, the condyles of the exoccipitals and the floor of the optic capsule (vestibule) are prominent. The foramen for cranial nerve IX is lateral and anterior to the condyles. Because of the bulbous nature of the floor of the ear capsule, the term "bulla" is not inappropriate. The small stapes consists of a disc-like piece of bone, the operculum, with a short columella. More directly posterior and lateral, the bulla is stoppered with a partially ossified disc of cartilage. The ear capsule itself is directed backward, downward, and lateralward. It occupies practically the entire postero-lateral part of the vault from the occipital condyles to the ventral pterygoid articulation.

The pterygoid is roughly triangular in outline. From ventral view its surface is dominantly convex. The contours suggest smooth-flowing lines. The apex of the bone is directed outward and forward; its base, backward and inward. The posterior portion is spatulate. The anterior, inferior portion is rounded and thick and the anterior border considered entire, is rounded. The articulations are as follows: anteriorly and medially with facets on the prootic; posteriorly and inferiorly, with the quadrate.

The quadrate, which is dorsal to the pterygoid and intermediate between it and the squamosal, is for the most part ossified. The knobbed condyles are readily distinguishable. Posteriorly, the element shows a bulb-shaped enlargement which functions as an attachment of the hyoid, while ventrally and laterally is a saddle shaped articulation for the articulare of the lower jaw. The remainder of the bone might be described as a splint, in relation ventrally and laterally with the squamosal.

Lower Jaw

The mandible or lower jaw has three closely articulated elements which are duplicated on each side. The dentaries meet in an anterior symphysis and form about two thirds of the arc of the jaws, and the angulare which is medially articulated to the dentary by a long, forward projecting process, incloses the partially calcified articulare. The dentary bears the teeth, which are closely set and knobbed. Parker mentions a tooth-bearing splenial, but I have been unable to identify such a bone in this species.

The Articulation of the Lower Jaw with the Quadrate

Two ligaments are associated with this joint, (1) a ligamentous round band connecting the posterior tip of the maxilla with the anterior tip of the pterygoid, and (2) a ligament which binds down the proximal end of the ossified portion of the hyoid with the articular cartilage of the quadrate. This added articular cartilage is found posterior-superior to the quadrate condyle and extends somewhat laterally. Anteriorly, it borders the squamosal. It would seem that because of the attachment of the hyoid in this position, some support would be given the articulation of the lower jaw with the quadrate posterior and medially.

The articular portion of the lower jaw is roughly cone-shaped (a broad cone with the apex above). The superior and anterior portions of this ascending ramus of the lower jaw is in relation medially with the pterygoid, and anteriorly with a ligament which binds the anterior tip of the pterygoid and the posterior tip of the maxilla at this point.

The posterior and inferior part of the ramus is convex and is received into an intercondylar groove on the inferior surface of the quadrate condyle.

The cartilage bones and dermal bones of the skull may be summarized as follows:

Chondral bones	*Dermal bones*	
prootic	parietal	vomero-palatine
fused epi-otic, opisthotic and ex-occipitals	frontal	pterygoid
orbito-sphenoid	nasal	premaxilla
quadrate—partly ossified	pre-frontal	maxilla
articulare—partly ossified	squamosal	dentary
stapes	parasphenoid	angulare
septo-maxillary, status still questioned.		

Cranial Nerve Foramina

The following consideration of cranial nerve exits is a summary of the findings of Gaupp, Coghill, Drüner, Herrick, and others. Some of these are specific as applied to the Ambystomidae; others are general for the urodeles. One would naturally expect to find slight differences in the relative position of these foramina in the various species in the genus Ambystoma and in individuals of the same species. Many such instances are already recorded. The following is offered as a general treatment of the nerve exits in a type Ambystoma skull.

I. The olfactory nerve perforates the cartilaginous trabeculae on each side. In some urodeles (according to Gaupp) the nerve is incased in the frontal bone.

II. The optic nerve . . . . has its foramen in the lateral wall of the cranial vault in relation with the posterior border of the orbito-sphenoid. In fact, in most species studied, a partial foramen is found here in the bone itself (see ventral view of the skulls).

III. The oculo-motor nerve leaves the lateral wall of the skull via the membrane connecting the orbito-sphenoid to the prootic. It lies posterior to the optic foramen and usually at the same level.

IV. The trochlear nerve exit is found high up in the lateral wall in relation to the optic and oculomotor foramina which are ventral to it. There are evidently two possibilities—one may be an exit on the dorsal-posterior part of the parietal bone itself, as in *Ambystoma tigrinum,* or it may take its exit through the suture between the parietal and orbitosphenoid, as Gaupp's work indicates. The foramen is quite small, but discernible to the naked eye.

V. The trigeminal nerve leaves the cranium through the foramen prooticum at the boundry of the lateral wall and the otic region, mesial and anterior to the prootic.

VI. In salamanders the exit of the abducens nerve is typically in the forepart of the basal plate, medial to the foramen of the facial nerve, but in the larval *A. tigrinum,* it leaves with the trigeminal through the foramen prooticum.

VII. The relations of the exit of the facial nerve in the larvae of *A. tigrinum* may be considered as fairly typical. In this species it leaves the skull by a separate foramen which is found on the boundry of the basal plate near the ear capsule, and just posterior to the suspensorium.

VIII. The acoustic nerve passes through the medial otic wall.

IX.; X. The glossopharyngeous and vagus nerves both leave the cranium by way of the jugular foramen, which is found anterior and lateral to the occipital condyles.

Comparative Osteology of the Skulls

The skulls vary in size, that of *A. tigrinum* being the largest and that of *A. macrodactylum* being the smallest. Actual dimensions of the skulls used are appended in a separate table.

A comparison disclosed some interesting and rather extensive differences. The most obvious ones so modify important regions of the skull as to make them diagnostic.

Some of these involve the shape of the brain case. Examination of the figures discloses three general types. *Ambystoma talpoideum* (figs. 7, 8) has the broadest brain case, whereas *A. microstomum* (figs. 9, 10) has relatively the most elongate type. In the latter, the sides are straight and practically parallel, whereas in *A. talpoideum* the dorso-lateral margins are irregular. *Ambystoma opacum* (figs. 1, 2) represents an intermediate type of skull, its concave lateral margins effecting a gradual expansion of the cranium in front and behind. The skull of *A. maculatum* is similar in this regard, whereas *A. macrodactylum* closely approximates the elongate type of *A. microstomum*. The skulls of *A. tigrinum* and *A. talpoideum* represent departures which are even distinctive for the brain case, the lateral contour in the former and the extreme width in the latter being sufficient to isolate them from other species.

The anterior arc formed by the premaxillae and maxillae seems to change in the separate species, being circular in *A. tigrinum* and elliptical in *A. opacum*. The arcs in *A. talpoideum* and *A. microstomum* are more angular, and in the last, a more pointed fore-part of the skull is evident. Since this arc reflects its counterpart, the mandible below, and possibly other mechanical factors suggested by the suspensorium, measurement of any phase of this arc might prove useful. Lines could be drawn from the symphysis of the premaxillae to the posterior tip of the maxillae and along the mid-dorsal line, respectively. The angle between the two would be a measure of the trend of the maxillae posteriorly. Another noticeable feature of this anterior arc is that it extends posteriorly for varying distances in the separate species. This extension differs from less than one-half to almost two-thirds the linear dimension of the skull.

A reference to the ventral views of the skulls shows that the vomero-palatines are deficient in bone near the mid-line, and display medial borders which are variable for the species. These outline a fossa (fs) (when the internasal cartilage has been removed) which is distinctive in each case.

The internal nares, found as partial foramina in the vomero-palatines, vary in completeness and shape.

Perhaps the last of the very obvious features of the skulls is the relative extent of the bones comprising the roof of the cranial vault. The frontal processes of the premaxillae, the prefrontals, and the frontals figure most strongly here. Certainly their relation to landmarks such as the prootics, anterior tips of the pterygoids, posterior limits of the maxillae, etc., change in the different species. The extent of variation of this character in individuals of the *same species* has not been determined. For another comparison, their extent could be referred directly to the linear dimension of the skull in each case.

Summary

The *Ambystoma talpoideum* skull is distinctive not only because of its broad brain case but also because this broadness is reflected in the wide character of the separate bone pairs which all contribute to the general effect of massiveness. Bony markings are accentuated.

Although *A. opacum* and *A. maculatum* resemble each other in brain case outline (of the intermediate type) and by a general smoothness in borders and surfaces, a more minute study yields several differences. The *A. opacum* skull is more flattened anteriorly from above downward, whereas in this species, the prefrontal is six-sided, it is practically crescent-shaped in *A. maculatum*. The transverse diameter of the cranial vault is appreciably greater in the latter species (relatively speaking) and the pterygoid bone presents a more straight mesial border, in contrast to the convexity found in *A. opacum*. Especially because of the differences noted above, a space bounded anteriorly and laterally by the maxilla, medially by the prefrontal and parietal, and posteriorly by the parietal and pterygoid, is changed in contour and presents a key to the analysis of differences which are at first imperceptible in a comparison of very similar skulls such as the above. This space changes radically when species such as *A. opacum* and *A. tigrinum* are compared.

Mention has been made of the fact that *A. microstomum* and *A. macrodactylum* possess the elongate type of brain case, showing a proportionately smaller transverse diameter. Segregation depends on a series of minor characters, the constancy of which can be determined only after a more adequate number of skulls has been studied. The disposition of the parietal bone over the occipito-auditory region is different in the two species. In *A. microstomum*, the bone more closely approximates the squamosal and the prootic, whereas in *A. macrodactylum* no portion of the bone is contiguous with the squamosal, and the prootics are much more visible dorsally. A definite parietal angle is evident only in *A. microstomum*. In general, there seems to be greater conformity of the parietal and parasphenoid bones with the occipito-auditory mass in *A. microstomum*. There seems to be a more forward inclination of the suspensorium in *A. macrodactylum*.

Ambystoma tigrinum is not directly comparable to any of the other five species. This is not due primarily to the size of the skull, but to a variety of differences which not only involve many particular bones, but also gross contours as well. The more apparent differences are:

1. The almost circular arc described by the premaxillae and maxillae.

2. The straight lateral border of the prefrontal, and the sharp angle it effects with the parietal. (In some species the relation posteriorly is with the frontal.)

3. A distinctive, hook-shaped process on the pterygoid.

4. A foramen dorsally on the parietal, for the exit of nerve IV.

5. The very triangular dorsal contour of the foramen magnum.

This species has such a wide distribution that possibly the description here covers a geographical type only. *A. tigrinum* also represents a dimorphic species, and this further complicates a study of its morphology. Despite all this, it is comparatively easy to segregate the species from the others in the genus because of the variety of differences the skull displays. It is expected that those which involve gross skull contours will be fairly constant in the separate individuals.

SKULL DIMENSIONS

Name	Greatest length of skull *Millimeters*	Smallest transverse diameter of brain case *Millimeters*
Ambystoma opacum	11	3½
Ambystoma tigrinum	17	5⅔
Ambystoma microstomum	8	3
Ambystoma talpoideum	10¾	4
Ambystoma maculatum	13	4½
Ambystoma macrodactylum	9½	3

Factors Affecting the Form of the Skulls

The adult cranium in amphibia, as in all higher vertebrates, is acquired by the addition of cartilage and dermal bones. The former (Wilder, 1923) "appear as centers of ossification within the cartilage of the primordial cranium itself, developing at those spots where either the strain of some other movable joint or that of some other mechanical force causes stress. Examples of these are the quadrate-articulare and skull-vertebral column articulations. In other words, their origin seems to be due to physiological reasons. Sometimes a cartilage bone serves to protect particularly delicate parts, as the prootic, which helps to form a cap about the otic capsule, and the orbito-sphenoid, which protects the exit of the optic nerve from the cranium." The dermal (skin) bones have no close relation to the primordial cranium but are closely applied, especially posteriorly, where the parietals and parasphenoid are seen to take the shape of the otic region. Because the brain is contiguous with the vault here, one can conclude that it partially ordered the shape of the brain case in this region.

Perhaps the greatest single factor tending to modify the skull in all phases of development, is the musculature. Its coincident development with bone, and the formation of joints which permit the movements effected by it, suggest stresses which operate in the formation of the skull. Miner (1929) points out that "we know from the physiological processes involved in bone formation that the vertebrate skeleton is deposited in the interstices of the connective tissue network which also incloses the contractile cells. It is obvious that these skeletal deposits cannot exist where they would interfere with muscle action, and conversely they would occur in most highly developed condition where they would assist and strengthen that action. The areas of lost motion between opposing muscle groups would best answer that purpose, and it is in such intermuscular, fibrous regions of connective tissue that the fundamental internal bony or cartilaginous skeleton is found." A reference to the skulls illustrates that the more gross differences are found in the anterior and posterior regions, and that these are most directly involved in muscle and joint mechanics.

Another apparent feature of these skulls is the varying degree in which the bones approximate each other. This applies to paired bones as well as regions. The bones articulate with each other in two general planes, the longitudinal and the transverse. The greatest number of sutures are found in the longitudinal plane, whereas the transverse plane is characterized by two fused regions, the auditory-occipital and the vomero-palatine. It is to be remembered that the first parts of the skull to chondrify are the occipital and sphenoidal. This linear growth would favor fusion in the transverse plane, especially anteriorly and posteriorly, where the stresses due to developmental mechanics is most felt. The dorsal-posterior inclination of the vomero-palatine favors its fusion. This inclination varies in the separate species and might be a factor in explaining the condition of the internal nares and the space outlined by the mesial border of the bones. The constancy of the above characters has not been exactly determined.

It seems probable that the brain is secondary to the musculature as a factor in moulding the shape of the skull, due primarily to the general lack of proximity of brain to vault.

The cranial nerves, in their exit from the vault, create foramina that are sometimes distinctive. Blood vessels usually accompany the nerves.

The skeleton in general must reflect the degree of physiologic activity of a series of body systems and in particular the muscular. The impresses of these systems also suggest the sequence of their development. These stresses, further, have attained their status through definitely external stimuli, i. e., air, water, heat, moisture, cold, topography, local habitat, etc. The status of a particular system might be considered as the end result of chemical processes instituted by genes which can themselves be affected so as to alter these chemical reactions. Similarities between skulls such as that of *A. macrodactylum* and *A. microstomum,* and that of *A. opacum* and *A. maculatum* cannot be explained on the basis of geographical distribution. In the case of *A. tigrinum,* which is essentially dimorphic, and is distributed over almost all United States and the northern portion of the Mexican plateau, it is more reasonable to expect to find geographical types. The fact that in some localities the larval form is retained throughout life (Axolotl) points toward metamorphosis as a big causal factor in variations within this species.

In a comparative study of species in the genus, apparent differences involving *A. tigrinum* must be considered with caution. Specific characters and even generic characters apparently vary in this species. Cope (1887) explained individual variations on the basis of "variations in time and degree of metamorphosis, resulting in the partial retention of some larval characters." He rather considered metamorphosis as instituted and controlled at will by external factors, such as temperature, etc., with the result that he stressed geographical types to the extreme. Powers, in an extensive paper dealing with variations and its causes in this species, explains that some of Cope's most important geographical types were collected within a radius of six miles! This point is raised to emphasize the very plastic nature of *A. tigrinum.* Extensive experimental evidence produced by Powers (1907) shows that "the variations of *A. tigrinum* are primarily acquired variations of the larvae, that is, the direct or indirect result of environment during the larval lifetime. Some of the factors listed in the order of importance are (1) nutrition, (2) functional variations, use and disuse in varying degrees effecting changes." Powers concludes that "specific characters, in species which vary as *Ambystoma tigrinum* varies, are after all, strongly determined by environmental conditions. Congenital tendencies in such species are not definitely specific but only indefinitely specific." It was pointed out earlier that in this species they are not always definitely generic.

The problem in the genus *Ambystoma* seems to be to trace and properly classify ontogenetic forms such as result from the *A. tigrinum* species and to consider the phylogenetic significance of the others. Most of the variations pointed out by Powers are external and involve skin folds, muscle masses, fatty depositions, size of glands, etc., all of which are readily changed by such a factor as nutrition. Too little stress has been laid on comparative osteology in this genus, and particularly in this species.

Conclusion

The exact structure of the skull of salamanders is being used more and more to demonstrate genetic relationships. However, Noble (1921) points out that "fusion and losses of bones have occurred independently in many different genera and these are not always indicative of genetic relations." This fact was particularly recognized by other workers such as Cope, Fowler and Dunn. The question of whether a bone has fused with another or dropped out involves the problem of homology. It is stated on good authority that even in the single order Caudata, the cranial elements cannot be homologized with certainty, as contacts do not always determine homology. According to Noble (1921) "we cannot be certain of the homology of the anterior cranial elements of Rhyacotriton until the skull structure of the different short-toed species grouped under the genus *Ambystoma* have been investigated. After the crania of the species in the various genera of urodeles have been worked out, we will be in a position to compare the crania of closely related forms."

It is true that the old criteria of species determination are less effective as a result of recent advances in the fields of plant and animal cytology, physiology, and other correlated fields. This indefiniteness regarding the question of what constitutes a species is a good sign, as it is indicative of a more careful survey by scientists, of the interrelations of body systems and the interdependence of the various branches of biology. Skeletal studies are helpful because this system is especially susceptible to the impress of the other parts of the organism, especially the muscular, and this impress is open to direct observation.

BIBLIOGRAPHY

Cope, E. D., Batrachia of North America, U. S. Nat. Mus. Bull. No. 34, 1887.

Lepage, Enid, The septomaxillary in the Urodele amphibia, Journ. of Morphology, vol. 45, 1928.

Miner, R. W., The pectoral limbs of Eryops and other primitive tetrapods, Bull. Am. Mus. Nat. Hist. vol. 51, 1925.

Parker, W. K., On the structure and development of the skull in the urodelous amphibia, Phil. Trans. Royal Soc. part 2, 1877.

Powers, J. H., Morphological variations and its causes in Ambystoma tigrinum, Univ. Stud. Nebr. vol. 7, 1907.

Stejneger and Barbour, Check list of North American amphibians and reptiles, second edition, 1923.

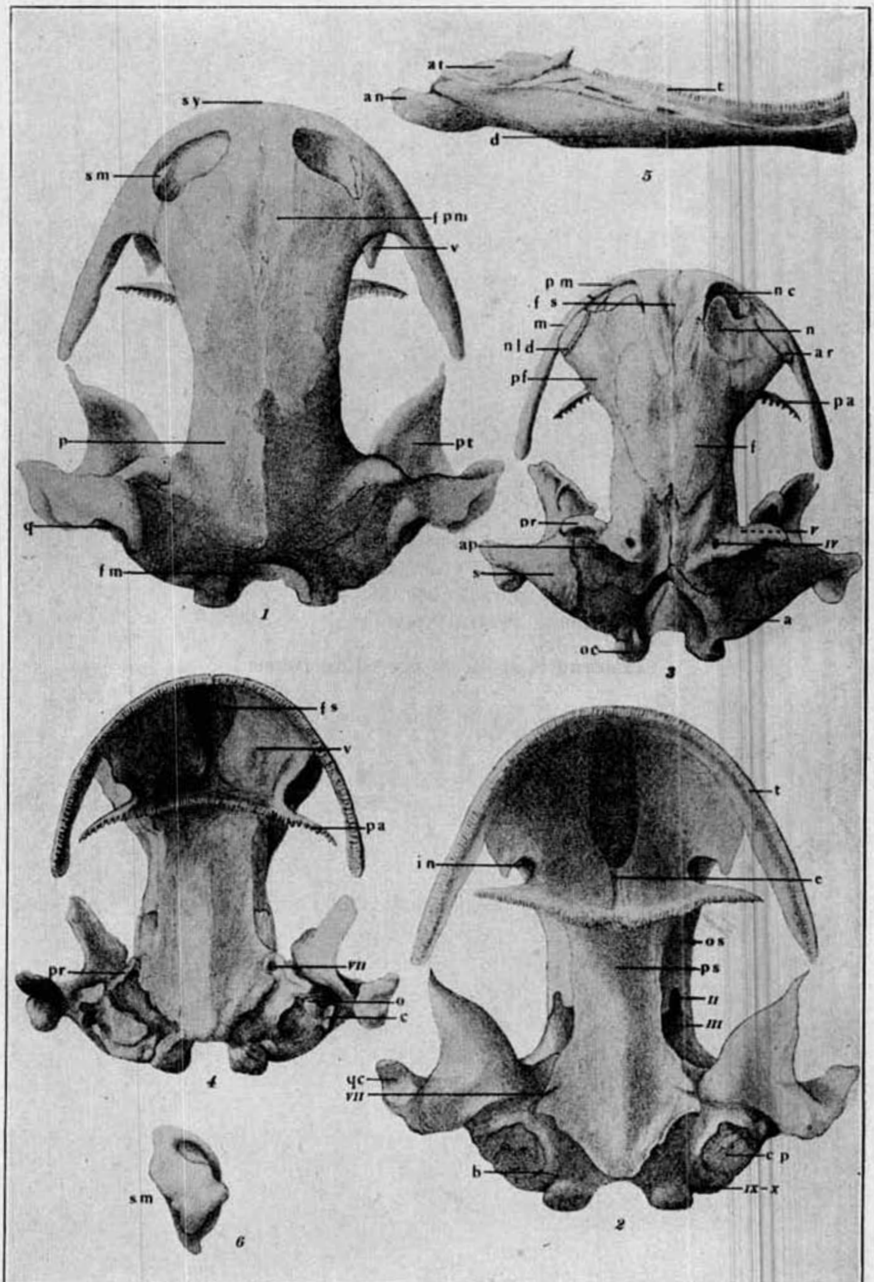
Wilder, H. H., The history of the human body, 1923.

EXPLANATION OF FIGURES

1. Skull of *Ambystoma opacum*, dorsal view, x8.
2. Skull of *Ambystoma opacum*, ventral view, x8.
3. Skull of *Ambystoma tigrinum*, dorsal view, x4.
4. Skull of *Ambystoma tigrinum*, ventral view, x4.
5. Lateral view of lower jaw of *Ambystoma tigrinum*, semi-diagrammatic, x8.
6. The septomaxillary of *A. tigrinum*, dorsal view, x8.

LEGEND

a, fused auditory-occipital region
an, angulare
ap, angle of parietal
ar, ascending ramus of maxilla
at, articulare
b, bulla of auditory capsule
c, columella of stapes
cp, cartilaginous plug
e, extension of parasphenoid under vomero-palatine
f, frontal bone
fm, foramen magnum
fpm, frontal process of premaxilla
fs, fossa indicating former position of internasal cartilage
in, internal nares
m, maxilla
n, nasal
nc, nasal cavaity
nld, superficial course of naso-lacrimal duct in prefrontal bone
o, operculm (of stapes)
oc, occipital condyles
os, orbito-sphenoid
p, parietal
pa, palatine portion of vomero-palatine
pf, prefrontal
pm, premaxilla
pr, prootic
ps, parasphenoid
pvp, posterior process of vomero-palatine
q, quadrate
qc, quadrate condyles
s, squamosal
sm, septomaxillary
sy, symphysis of premaxillae
t, teeth
v, vomero-palatine (fused vomer and palatine bones)
II, exit of optic nerve
III, exit of oculo-motor nerve
IV, exit of trochlear nerve
V, the dotted line indicates an anterior and mesial position of the exit of the trigeminal nerve
VII, partial exit of facial nerve.
IX, X, exit of the glossopharyngeal and vagus nerves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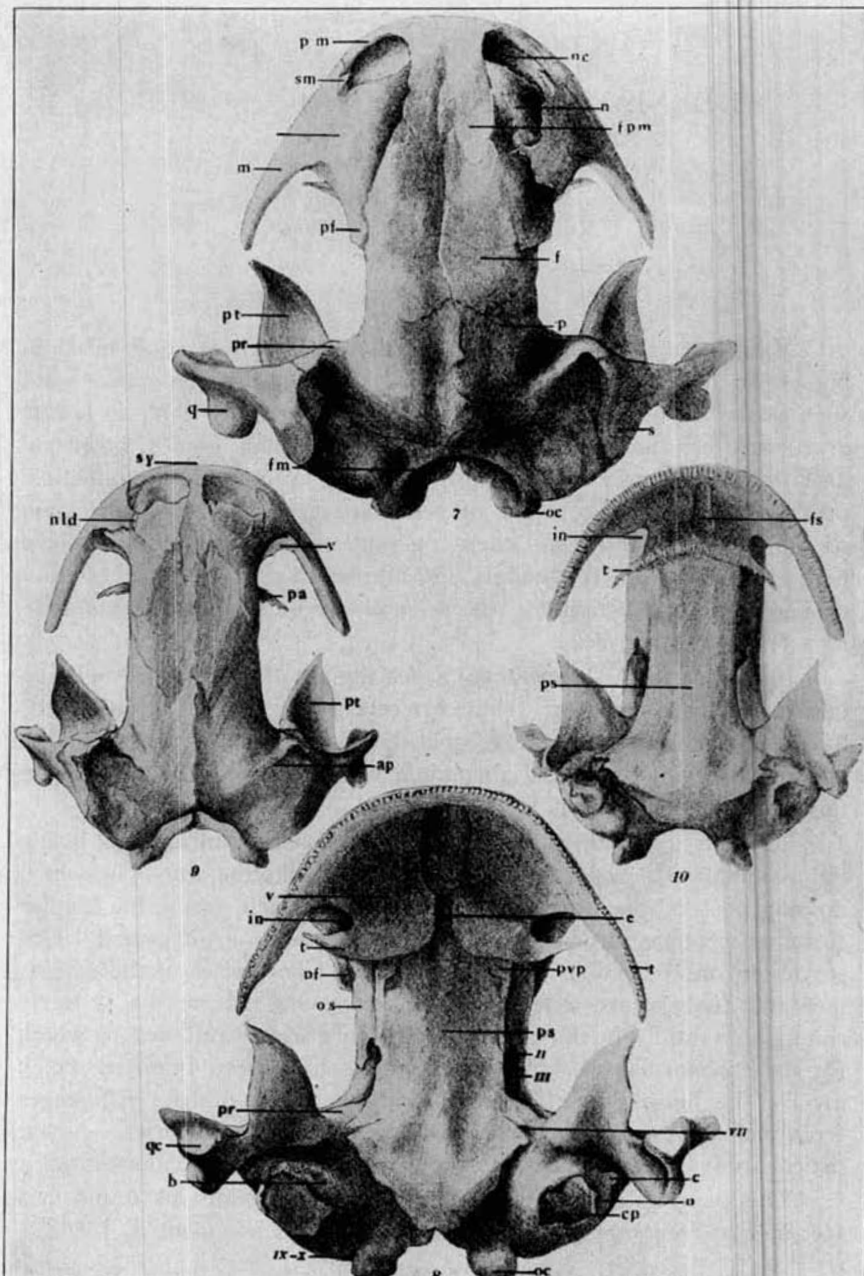
Figs. 1-6

EXPLANATION OF FIGURES

7. *Ambystoma talpoideum*, dorsal view, x8.
8. *Ambystoma talpoideum*, ventral view, x8.
9. *Ambystoma microstomum*, dorsal view, x8.
10. *Ambystoma microstomum*, ventral view, x8.

(Legend is given on preceding page.)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FIGS. 7-10