### CHAPTER II

#### THE SKELETON

### A. THE EXOSKELETON

THE exoskeleton is well developed in the Crocodilia, and forms a very considerable protection to its bearer. It is both dermal and epidermal in origin.

The *epidermal skeleton* of the alligator consists of oblong horny scales, arranged in transverse rows; the long axes of the scales are parallel to that of the body. On the tail, except along the mid-dorsal line, and on the ventral side of the trunk and head these scales are very regular in outline and arrangement; on the sides of the head and trunk and on the legs they are much smaller and less regularly arranged, while along the mid-dorsal line of the tail, especially in its posterior half, they are elevated into tall keels that give the tail a large surface for swimming. The first three digits of both manus and pes are armed with horny claws, which also belong to the epidermal part of the exoskeleton.



FIG. 15. ALLIGATOR SKINS; UNDER-SURFACE AND HORN-BACK. (From Report of Commissioner of Fish and Fisheries, 1902.)



The *dermal exoskeleton* consists of bony scutes that underlie the epidermal scales of the dorsal surface of the trunk and anterior part of the tail. The overlying scales, except in very young animals, are always rubbed off, so that the bony scales are exposed. The ventral or inner surface of the scutes is flat, while the outer surface is strongly keeled and in old animals is often rough and pitted. The plates are nearly square in outline and are closely joined together in most places.

The scutes are grouped in two fairly distinct areas known as the nuchal and the dorsal shields. The former lies just back of the head, in the region of the fore legs, and consists of four larger and a number of smaller plates (Fig. 15). The latter, or dorsal shield, extends over the back in fairly regular longitudinal rows and quite regular transverse rows. At the widest part of the trunk there are six or eight of these scutes in one transverse row. They become smaller towards the tail.

The *teeth* are exoskeletal structures, partly of ectodermal, partly of dermal origin. They are conical in shape, without roots, and are replaced when lost. They will be described in connection with the skull.

Musk glands, said by Gadow to be present in all Crocodilia, are found in both sexes and are derivations of the skin. One pair, each of which may be as large as a walnut, is found on the lower side of the head, one on the inside of each half of the mandible. The other pair is inside of the lips of the cloaca.

The Histology of the Integument. To understand the structure of the integument of the Crocodilia it is well to begin with the embryo. A cross section of the epidermis of such an embryo will show the rete Malpighii as a single layer of short, cylindrical cells; over these are found more or less flattened, disk-shaped cells formed by transverse division of the underlying cells of the rete. On the outside lies the epitrichial layer which consists of a mosaic of polygonal cells, near the middle of each of which lies an oval nucleus. Between the epitrichial cells are small oval holes, not unlike the stomata in the epidermis of plant tissues. Bronn thinks these are not artifacts, but he does not suggest any explanation of their occurrence.

In the epidermis of young and half-grown animals the rete Malpighii is seen still as above noted. On these cylindrical cells are found flattened cells that gradually become very flat and lose their nuclei as they pass over into the horny layer.

The stratum corneum consists of strongly flattened cells in which the nuclei can no longer be clearly seen, though their location can usually be determined by the groups of pigment granules. On the cells of the more superficial layers of the stratum corneum are seen straight, dark lines, perhaps ridges caused by pressure of the over- or underlying polygonal cells. The individual cells of the horny

layer are usually easily isolated in the belly and neck regions where they never become very thick; but in the back the cells in this layer are very numerous and fuse with each other to form the bony plates; here the rete is the only clearly differentiated layer. Whether prickle cells are present in the epidermis of the crocodile Bronn is not certain, though he thinks they probably are.

Rathke pointed out that on the surface of certain folds of the integument, especially in the region of the jaws, are found in all Crocodilia certain small, scattered, wart-like elevations, around each of which is customarily a narrow, shallow, circular groove; they usually have a dark brown but sometimes a gray or even white color. Microscopic examination shows these warts to be of epidermal origin, consisting of bright, round cells that are closely united, without visible intercellular substance. Treatment with potassium hydroxid and then with water will show sometimes, though not always, fine granular nuclei in the cells.

In probably all members of the genus Crocodilus at least is found, on the thick swelling on the right and on the left side of the neck and trunk, a small, flat pit which has the appearance of the opening of an integumental gland. The pits are present also in the scales of the throat, under the side of the neck, sides of the body, lateral and ventral surfaces of the anterior half of the tail, and the legs. They

are near the hinder border of the scales. Only

occasionally are two pits found in one scale. These pits are found in the gavials but are absent in some, probably all, alligators. A small knob projects from the center of some of the pits. These pits are not openings of glands but have about the same structure as the pits seen in the head.

The integumental bones in the Crocodilia originate in the connective tissue of the cutis. Investigations in young animals show that these bones usually take their origin in the under and middle lavers of the cutis and generally work towards the periphery.

#### B. THE ENDOSKELETON

### I. The Vertebral Column.

The vertebral column consists of about sixty-



five vertebræ, which may be separated into the usual regions; there are nine cervical, ten dorsal, five lumbar, two sacral, and about thirty-nine caudal. It is likely that the number of caudals may be subject to frequent variation; one complete skeleton had sixty-five vertebræ in all, another had sixtyeight. A complete skeleton of the crocodile (species not known) had sixty vertebræ. A thirteen-foot skeleton at Western Reserve University had only sixty-one vertebræ, but some of the caudals were evidently missing. Two skeletons of *C. porosus* in the museum at Singapore had sixty and sixty-three vertebræ respectively. A skeleton of *Tomistoma schlegali* in the same museum had sixty vertebræ.

The Cervical Vertebræ. Since all of the cervical vertebræ bear ribs, we shall assume the distinction between them and the dorsal vertebræ to be that the ribs of the latter meet the sternum, while those of the former do not reach to the sternum. Assuming this distinction, there are, as was said above, nine cervical vertebræ.

With the exception of the first two, to be discussed later, these are all essentially alike and the fourth will be described as a type (Fig. 17). Its centrum is cylindrical or somewhat hourglass shaped, concave anteriorly and convex posteriorly; it is not completely fused with the neural arch but is united with it by sutures. From the anterior end of the ventral surface of the centrum projects downward and forward a small plow-shaped process,

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the hypapophysis. On each side of the centrum, near its anterior end, is a facet with which the lower branch (capitulum) of the rib articulates. The neural arch is strongly developed and is extended dorsally into a prominent neural spine and on each



FIG. 17. FIRST FOUR CERVICAL VERTEBRÆ OF A CROCODILE (C. vulgaris). (From Reynolds, partly after Von Zittel.)

- 1. pro-atlas.
- 2. lateral portion of atlas.
- 3. odontoid process.
- 4. ventral portion of atlas.
- 5. neural spine of axis.
- postzygapophysis of fourth vertebra.
- 7. tubercular portion of fourth cervical rib.
- 8. first cervical rib.
- 9. second cervical rib.
- 10. convex posterior surface of centrum of fourth vertebra.

side as a short, blunt, transverse process with which the tubercle or upper branch of the rib articulates. Posteriorly the arch is notched on each side to form the openings for the exit of the spinal nerves. Projecting dorsally and anteriorly from the arch are two short processes which bear the medially and dorsally facing prezygapophyses (Fig. 17). Just caudad to these processes are somewhat shorter processes that bear the laterally and ventrally facing postzygapophyses (Fig. 17, 6).

The atlas, as in other vertebrates, is highly specialized. It consists (Fig. 17), even in the adult animal, six feet or more in length, of four distinct portions, a ventral (4), a dorsal (1), and two lateral (2) parts. The ventral portion is relatively more massive than in most animals: its anterior surface is concave and forms the main part of the articular surface for the occipital condule of the skull. Its postero-dorsal surface articulates with the odontoid process of the axis. On its postero-lateral surfaces are the facets for articulation with the first ribs. which, unlike the other cervical ribs, have but one articular surface. Articulating dorsally with this ventral element of the atlas are the two rather heavy lateral elements which form the neural arch. Anteriorly they form the lateral parts of the articular surface for the condyle and dorsally they unite for a short distance with each other. Projecting ventrally from the posterior part of their dorsal portion are the small postzygapophyses. Ventrally and laterally they articulate with the odontoid process (Fig. 17, 3). Projecting dorsad and cephalad from the dorsal surface of these lateral elements is the dorsal element of the atlas (Fig. 17, 1), the pro-atlas, which may not be properly a part of the vertebral column at all, since it is said to be merely a membrane bone. Gadow says it is the detached neural spine of the atlas. It is 54

thin and triangular in shape, resembling in contour a large, mammalian epiglottis. It forms an arch over the space between the skull and the front of the atlas proper. Reynolds calls it the proatlas.

The Axis. The centrum differs from those following it (described above) mainly in its close articulation (not fusion) with the large odontoid process; this process not only projects into the atlas, as is usually the case, but articulates with its postero-lateral border on each side, and is distinctly visible in a lateral view of the neck (Fig. 17, 3). Like the rest of the cervical vertebræ the posterior surface of the centrum is convex. The neural arch of the atlas differs from those following mainly in having a much wider (in an antero-posterior direction) neural spine. The lateral processes and those bearing the prezygapophyses are also less strongly developed than on the following vertebræ.

The Thoracic Vertebræ. The first thoracic vertebra differs scarcely at all from the ninth cervical; and the tenth thoracic differs from the first lumbar only in bearing a short rib. Only the first three thoracic centra bear the hypapophyses noted in connection with the cervical vertebræ. The ribs of the first two thoracic vertebræ articulate with them by two processes, as in the typical cervical vertebræ; the other ribs articulate only with the transverse process. The fourth thoracic may be

described as a type of this region (Fig. 18, A). Its centrum is rather longer than in the first two thoracic and in the cervical vertebræ and has no process for articulation with the head of the rib, otherwise it is essentially the same. Like all of



FIG. 18. ANTERIOR VIEW OF A, A LATE THORACIC AND B, THE FIRST SACRAL VERTEBRA OF A YOUNG CROCODILE (C. palustris).  $\times \frac{1}{2}$ . (After Reynolds.)

1. neural spine.

- 4. sacral rib.
- 2. process bearing prezygapophysis.
- 3. facet for articulation with the capitulum of the rib.
- surface which is united with the ilium.
   concave anterior face of centrum.

the vertebræ behind it and unlike those in front it is apparently completely fused with its neural arch. The neural arch is very broad (in an anteroposterior direction) and is extended dorsally as a wide neural spine (I). The neural spines of the following thoracic and the first two or three lumbar vertebræ are increasingly broad and truncated. The transverse processes are very broad, long and thin, and in the third to eighth vertebræ they have

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two articular surfaces, an anterior and more medial one for articulation with the head of the rib (3) and a posterior and more distal one for articulation with the tubercle of the rib. These two surfaces approach each other as the vertebræ are followed caudad until, in the last two thoracic vertebræ, they form practically one surface. The processes of the pre- and postzygapophyses spring from the arch at the base of the transverse process; the former surface is directed dorsally and medially, the latter ventrally and laterally. The intervertebral foramina are smaller and more nearly circular than in the cervical region, and are more closely surrounded by bone.

The Lumbar Vertebræ. The five lumbar vertebræ are essentially like the thoracic except that the transverse processes, which, of course, bear no ribs, are both shorter and narrower. The posterolateral border of the centrum of the last of these five vertebræ has a small surface for articulation with the antero-medial border of the transverse process of the first sacral vertebra.

The Sacral Vertebræ (Fig. 18, B). These are two in number. The centrum of the first is concave in front and flat behind, instead of being convex behind, and the second is flat (instead of concave) in front, and convex behind. The neural spine and zygapophyses are as in the lumbar region. Projecting laterally from each sacral vertebra, forming a close, sutural joint with both centrum

and neural arch, is a heavy bone shaped like a truncated pyramid (4); the base of the pyramid is ankylosed with the ilium. These bones seem to be much thickened transverse processes, but since they are not completely fused with their respective vertebræ and are said to ossify separately they should probably be called sacral ribs. The two sacral vertebræ do not seem to be any more closely united than are any other two vertebræ.

The Caudal Vertebræ (Fig. 16, C). These are characterized by the entire absence of ribs, and by the presence on all but the first and the last four or five of V-shaped chevron bones. The first ten or twelve of these chevron bones articulate chiefly with the postero-ventral ends of the centra. but they also articulate with the antero-ventral ends of the vertebra behind themselves; and as they are followed caudad they seem to lie directly below the intervertebral regions and to articulate equally with the vertebræ before and behind. The chevron bones gradually diminish in size from before back. The neural processes of the first four or five caudals are broad, like those of the more anterior regions, but caudad to this point they become narrower and more pointed, though they retain the same height until about the last ten or twelve vertebræ. Towards the tip of the tail the dorsal spines diminish in height and finally disappear. The transverse processes of the first five

or six of the caudals are long and narrow. They gradually diminish in length until the eighteenth caudal, back of which they are no longer to be seen. The zygapophyses are mostly about the same as in the more anterior vertebræ, but towards the posterior end of the tail the postzygapophyses come to lie between rather than above the prezygapophyses. The neural canal diminishes, of course, in size towards the tip of the tail until it is no longer present, the last five or six vertebræ consisting only of the centra.

### II. The Skull.

The skull of the alligator is very massive and has several peculiarities. I. The bones of the dorsal surface are rough and pitted, especially in old animals. 2. The jaws are enormously large in proportion to the brain cavity, and are armed with many large teeth. 3. The mandibular articulation is some distance caudad to the occipital condyle. 4. The interorbital septum is mainly cartilaginous. 5. There is a complicated system of Eustachian passages connecting with the back of the mouth by a single opening. 6. The posterior nares are placed very far back and the palate is correspondingly long.

The skull as a whole may be divided into three regions: the cranium, the lower jaw, and the hyoid; these will be described in the order given.

The Cranium. As a matter of convenience the

bones will be described as seen from the different aspects—dorsal, ventral, lateral, posterior, and in sagittal section—without particular regard to their grouping into segments or regions.

The Dorsal Aspect (Fig. 19). At the extreme posterior end of the median line lies the *parietal* (23), double in the embryo but a single bone in the adult. It forms a part of the roof of the cranial cavity and articulates anteriorly with the frontal, laterally with the postfrontals, squamosals, and, according to Reynolds, with alisphenoids, pro-otics and epiotics, and ventrally with the supraoccipital. It forms the median boundary of each of the two *supratemporal fossæ* (sf).

On each side of the parietal and forming the posterior corners of the rectangular postero-dorsal region of the skull are the *squamosals* (7). Each squamosal articulates medially with the parietal, anteriorly with the postfrontal, and ventrally with the quadrate and exoccipital. It forms part of the posterior and lateral boundaries of the supratemporal fossa and a part of the roof of the external auditory meatus.

Articulating with the anterior border of the squamosals and forming the anterior corners of the rectangular region mentioned above are the *postfrontals* (6). The postfrontal articulates medially with the parietal and frontal, and ventrally with the alisphenoid and a small part of the quadrate. It sends, in a ventro-lateral direc-

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tion, a thick process that unites with a similar process from the jugal to form the *postorbital bar* (pb) which lies between the orbit (o) and the temporal fossa (tf). The postfrontal forms the anterolateral boundary of the supratemporal fossa.

Articulating posteriorly and laterally with the parietal and the postfrontals, and forming the highest point of the skull, is the single *frontal* bone (24), which, like the parietal, is paired in the embryo. It is a heavy bone whose dorsal surface is flattened posteriorly, deeply concave in the middle region, and drawn out into a long projection anteriorly. It forms part of the roof of the cranial cavity and articulates ventro-laterally with the alisphenoid and anteriorly with the prefrontals and nasals. It forms a part of the median boundary of the orbit.

The *prefrontal* (4) is an elongated bone in the latero-median border of the orbit. Medially and anteriorly it articulates with the frontal and nasal, laterally with the maxillary and lachrymal, and ventrally, by a heavy process, with the pterygoid.

The *nasal* (25) is a long narrow bone forming the greater part of the roof of the nasal passage. Along the median line of the skull it articulates with its fellow; posteriorly with the frontal; laterally with the prefrontal and maxillary; and anteriorly with the premaxilla. In the crocodile, caiman, and gavial it also articulates with the lachrymal. In the alligator the anterior ends of the



FIG. 19. DORSAL VIEW OF THE SKULL OF THE ALLIGATOR (A. Mississippiensis).

- 1. premaxilla.
- 2. maxilla.
- 3. lachrymal.
- 4. prefrontal.
- 5. jugal.
- 6. postfrontal.
- 7. squamosal.
- 8. quadrate.

- 12. quadratojugal.
- 23. parietal.
- 24. frontal.
- nasal. an, anterior nares;
  o, orbit; pb, postorbital bar; sf, supratemporal fossa; tf, lateral temporal fossa.



two nasals form a narrow rod of bone that extends across the anterior nares, and, meeting a projection from the premaxillaries, divides the opening into right and left halves. In the crocodile the nasals project only a very little way into the nares; in the caiman (according to Reynolds) they do not extend into the nares at all, and in the gavial, whose much elongated snout is mainly due to the great length of the maxillaries, the nasals do not extend more than a third of the distance from the prefrontals to the anterior nares.

The maxilla (2) is a large bone that forms a large part of the upper jaw and that holds most of the teeth of that jaw. On the ventral side, as will be described later, it articulates with its fellow in the middle line, with the premaxilla, with the palatine, and with the transpalatine. Dorsally it articulates with the premaxilla in front; with the nasal and prefrontal on the medial side; and with the lachrymal and jugal behind.

The *premaxilla* (I) forms, with its fellow, the extreme tip of the upper jaw. Each bone forms the anterior and lateral borders of its half of the anterior nares. It articulates medially with its fellow and posteriorly with the nasal and maxilla. Ventrally, as will be noted later, it bears five teeth and articulates with its fellow medially and with the maxilla posteriorly. Between the premaxillæ on the ventral side is the large anterior palatine foramen.

The *lachrymal* (3) is a fairly large bone that forms the anterior border of the orbit. It is bounded laterally by the jugal, anteriorly by the maxilla, and medially by the prefrontals. Its posteromedial border is pierced by a large lachrymal foramen that extends lengthwise through the bone and opens, at its anterior end, into the nasal chamber.

The *supraorbital*, missing in the skull figured, is a small bone lying in the eyelid close to the junction of the frontal and prefrontal. Being unattached it is usually absent from prepared skulls.

The jugal or malar (5) is an elongated bone that forms a part of the lateral border of the head, on the one hand, and most of the lateral border of the orbit on the other. Anteriorly it articulates with the maxilla; medially with the lachrymal and prefrontal; posteriorly with the quadratojugal, and ventrally with the transpalatine. With the transpalatine it sends, in a dorso-medial direction, a process that meets the process, described above in connection with the postfrontal, to form the postorbital bar.

The *quadratojugal* (12) is a small bone, wedged in between the jugal in front and the quadrate behind.

The *quadrate* (8) is more irregular and has more complicated articulations than almost any bone in the skull. Its posterior end, which forms the articular surface for the lower jaw, is elongated laterally and slightly concave. Anteriorly the





FIG. 20. VENTRAL VIEW OF THE SKULL OF THE ALLIGATOR (A. Mississippiensis).

- 2. maxilla.
- 5. jugal.
- 8. quadrate.
- 9. palatine.
- 10. pterygoid.
- 11. transpalatine.
- 12. quadratojugal.
- 14. basioccipital. a, anterior palatine vacuity; eu, opening of the median Eustachian canal; pn, posterior nares; pv, posterior palatine vacuity.

quadrate articulates with the quadratojugal; medially with the basisphenoid and exoccipital; dorsally with the exoccipital, squamosal, postfrontal, and, possibly, with the pro-otic; ventrally with the pterygoid, alisphenoid, and probably with some of the otic bones. Its dorsal side forms most of the floor of the external auditory meatus which will be described later. While the basioccipital may be seen from the dorsal side, it is not really one of the dorsal bones of the skull and will be described later; the same is true of the pterygoids and palatines which may be seen through the empty orbits.

The Ventral Aspect (Fig. 20). The larger part of this side of the skull is made up of four pairs of bones: the premaxillæ, the maxillæ, the palatines, and the pterygoids, lying, from anterior to posterior, in the order named.

The *premaxilla* (1), as described in the dorsal view of the skull, is a triangular bone which, with its fellow, forms the anterior end of the snout. Each premaxilla bears five teeth, not only in the alligator but in the crocodile, the caiman, and in the gavial. Of these teeth the fourth from the front is the largest; the first two are small, and the third and fifth are of intermediate size. This arrangement as to size is also true, apparently, in the other groups of Crocodilia. The ventral surface of the premaxilla, which is more or less flat and horizontal, is pierced by a number of small foramina, in a row parallel to the curved outer margin of the bone. Between these foramina and the base of the teeth are four rounded depressions to receive the points of the first four teeth in the lower jaw; of these depressions the first and fourth are the deepest. The first pit often becomes so deep as to perforate the bone; this is true also with the crocodile and, according to Reynolds, with the caiman, but is not true of the gavial, whose interlocking teeth project outside of the jaws. It will be remembered that one of the chief distinctions, given early in this work, between the crocodile and the alligator is that in the former the fourth tooth in the lower jaw fits into a notch and not into a pit in the upper jaw.

The maxilla (2), which with its fellow forms most of the hard palate, has also been mentioned in connection with the dorsal aspect. Each maxilla is notched, posteriorly, to form the anterior border of the posterior palatine vacuity, and together they are notched to receive the rectangular anterior ends of the palatines. The postero-lateral extremity of the maxilla articulates with the transpalatine. Along the outer border of the bone are the teeth, of which there are fifteen or sixteen in the alligator, about the same number (perhaps one or two less) in the caiman and crocodile, and about twenty-four in the gavial. The first or anterior eight or ten teeth have individual sockets, the rest are placed in a groove. In the crocodile none of the teeth have individual sockets, and in the gavial

they all have sockets. The premaxillary and more anterior of the maxillary teeth are slightly recurved and are sharper than the posterior maxillaries which besides being blunt have a constriction above the surface of the socket.

The crocodilian tooth consists of three layers (Fig. 20 A).

The enamel (e) forms a fairly thick layer over the crown of the tooth; it exhibits a very clear striated structure, the striations being apparently due to stratification.

Some of the tubules of the dentine (d) continue into the enamel, where they may be distinguished by their remarkable fineness and their straight course.

The cement (c) covers the root of the tooth that projects into the alveolus of the jawbone; it is much more strongly developed than in the lizards and contains a very large number of bone corpuscles which are distinguished from the bone corpuscles proper by their greater circumference.

The fairly large pulp cavity (p) has, like the tooth itself, a conical form.

Parallel to the teeth is a row of small foramina, a continuation of those noted in the premaxilla; some or all of these foramina open into a longitudinal sinus along the alveolar border of the maxilla; this sinus opens posteriorly by one or more large apertures into the posterior palatine vacuity.

The *palatines* (9) form a broad bar of bone from <sup>5</sup>

the pterygoids behind to the maxillæ in front. They are united with each other by a straight median suture and form a considerable part of the floor as well as a part of the side walls and roof of the nasal passage. They form most of the median boundaries of the posterior palatine vacuities (pv). Dorsally they articulate with the pterygoids, prefrontals, and vomers.

The *ptervgoids* (10) are the very irregular bones that project ventrad and caudad from beneath the orbits. Their suture is continuous, caudad, with that between the palatines and at the posterior end of this suture is the posterior opening of the nasal chamber, the posterior nares (pn). This opening is divided by a vertical, longitudinal, bony septum, and the part of the chamber into which it immediately opens, which lies in the pterygoids, is divided by a number of transverse, vertical septa. Posterior and dorsal to the posterior nares the pterygoids are fused. Anteriorly the pterygoids articulate with the palatines: dorsally with the quadrates, basisphenoid, alisphenoids, and prefrontals, and dorso-laterally with the transpalatines. The lateral vertical border of the pterygoid is roughened and is, according to Reynolds, covered, during life, with a pad of cartilage against which the medial side of the mandible plays.

The *transpalatine* (11) is a T-shaped bone articulating ventrally with the pterygoid and dorsally with the maxilla, the jugal, and the postfrontal.



FIG. 20A. LONGITUDINAL SECTION OF THE JAW AND TOOTH OF A CROCODILE. (After Bronn.)

c, cement; d, dentine; e, enamel; p, pulp, of functional tooth; c', cement; d', dentine; e', enamel, of rudimentary tooth; e'', epidermis; k, bone of jaw.



The *basioccipital* (14) is seen projecting caudad as the single occipital condyle; it will be described in connection with the posterior aspect of the skull.

The jugal (5), quadratojugal (12), and quadrate (8) may all be seen from this view. The first two have been sufficiently described in connection with the dorsal aspect; the last will be further described in connection with the lateral aspect.

Just caudad to the posterior nares is a small opening, the unpaired Eustachian canal (eu).

The Lateral Aspect (Fig. 21). As will be seen by the figure, practically all of the bones visible in this view have already been described, except those of the mandible, which will be described separately. At the base of the skull are, however, two bones. the basi- and alisphenoid, that have not been described and that show as well in this as in any other view. The basisphenoid (just below v and hidden by the pterygoid) was mentioned in connection with the quadrate, with whose posterior margin it articulates. It is an unpaired bone of very irregular shape. Anteriorly it is flattened out to form the rostrum, a rectangular process that forms the posterior part of the interorbital septum; in fact it is the only part of the septum present in a prepared skull, since the rest is cartilaginous. Dorso-laterally the basisphenoid articulates with the alisphenoid; posteriorly with the basioccipital; ventrally with the pterygoid; and posteriorly with the exoccipital and basioccipital. On the dorsal

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surface of the basisphenoid is the pituitary fossa, not seen, of course, in this view of the skull.

The alisphenoids (crossed by the dotted line from V) are a pair of very irregular bones that form most of the antero-lateral walls of the brain case. They articulate dorsally with the parietal, frontal, and postfrontal: ventrally with the basisphenoid and pterygoid; and posteriorly with the quadrate and some of the otic bones not visible in this view. Between it and the quadrate, plainly visible in this view, is a large opening, the foramen ovale (V), through which, according to Revnolds, the trigeminal nerve passes. In the middle line, directly under the frontal bone, is an opening between the anterior wings of the two alisphenoids, for the exit of the optic nerves. Ventrad and caudad to this opening, and sometimes continuous with it, is another large foramen, just dorsad to the rostrum, for the exit, according to Reynolds, of the oculomotor and abducens nerves. Projecting caudad is seen the rounded condylar part of the basioccipital (14) to be described later, and dorsocephalad to this is a part of the exoccipital (13) in which four foramina may be seen; of the dorsal three the one nearest the condyle and foramen magnum is for the exit (Reynolds) of the hypoglossal nerve (XII); slightly dorso-cephalad to this is one for the vagus nerve (X); between these two is a very small one for a vein; the largest and ventrally located foramen is for the entrance of the



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internal carotid (15). Another large foramen in the exoccipital bone will be seen and described in connection with the posterior view of the skull. Dorsal to the quadrate and largely bounded by it is the wide *external auditory meatus* (16), which leads into the tympanic cavity. This cavity is complicated by a number of canals that lead from it in various directions. Overhanging the cavity and meatus is the squamosal bone, described in connection with the dorsal aspect of the skull.

The Posterior Aspect (Fig. 22). Most of the bones seen in this view have already been described. The *pterygoids* (10) form the two prominent, ventrolateral projections, while dorsal to these is the large process formed by the quadrate (8) and quadratojugal (12). The dorsal margin is formed by the edges of the parietal (23) and the squamosals (7). Immediately below the parietal is the supraoccipital (26); it is a small, triangular bone, articulating above with the parietal and squamosals, below with the exoccipitals, and anteriorly with the epiotic. It takes no part in the formation of the foramen magnum.

The *exoccipitals* (13) form the entire boundary of the foramen magnum except the narrow ventral portion formed by the basioccipital. Each exoccipital is a wing-shaped bone, articulating dorsally with the squamosal and supraoccipital, ventrally with the quadrate, basioccipital, and basisphenoid, and anteriorly with the opisthotic. It is pierced by



- FIG. 22. POSTERIOR VIEW OF THE SKULL OF A. MISSISSIPPIENSIS.
- squamosal. ż
  - quadrate. ź
    - 10.
- transpalatine. pterygoid. . I I.
- quadratojugal. 12.
  - exoccipital. 13.
    - basioccipital. 14.

- 15. foramen for carotid artery.
- supraoccipital. parietal. 23. 26.
- foramen for 7th nerve and certain bloodvessels. bs, position of basisphenoid. VII.

- FIG. 24. DORSAL VIEW OF LOWER JAW OF ALLIGATOR (A Mississippiensis).
- 18. dentary. 19. splenial.
  - 21. supraangular.
- 22. articular. 23. coronoid.

, cetustion .rs and an art function of a structure for any . ar character 


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five foramina, four of which were described in connection with the lateral view. Some distance laterad and somewhat dorsad to the pair already described is the fifth and largest foramen (VII); it really lies between the exoccipital and quadrate, but the former bone forms almost its entire boundary; through it, according to Reynolds, pass the seventh nerve and certain blood-vessels.

The *basioccipital* (14) which, as has been said, forms a small part of the ventral wall of the foramen magnum, consists of a heavy dorsal portion, the ventrally curved condyle, and of a broader, irregular ventral portion, between which and the basisphenoid is the single opening of the Eustachian canals (eu). Dorsally and laterally the basioccipital articulates with the exoccipitals; ventrally, laterally, and anteriorly with the basisphenoid which was described in the lateral view.

The Sagittal Section (Fig. 23). The only bones shown in this figure (besides those of the mandible, to be described later) that have not already been described are the vomers and those of the auditory capsules.

The *vomers* (15) are delicate bones articulating with the maxillæ, the palatines, the pterygoids, and with each other. They form a part of the septum and roof of the nasal passage.

The mesethmoid is not ossified.

Reynolds describes the bones of the auditory capsules as follows:

"Three bones, the epiotic, opisthotic, and prootic, together form the auditory or *periotic* capsule of each side. They are wedged in between the lateral portions of the occipital and parietal segments and complete the cranial wall in this region. Their relations to the surrounding structures are very complicated, and many points can be made out only in sections of the skull passing right through the periotic capsule. The relative position of the three bones is, however, well seen in a median longitudinal section. The *obisthotic* early becomes united with the exoccipital, while the epiotic similarly becomes united with the supraoccipital. the pro-otic (Fig. 23, 7)—seen in longitudinal section to be pierced by the prominent trigeminal foramen-alone remaining distinct throughout life. The three bones together surround the essential organ of hearing which communicates laterally with the deep tympanic cavity by the fenestra malis

"The tympanic cavity, leading to the exterior by the external auditory meatus (Fig. 21, 16), is well seen in a side view of the skull; it is bounded on its inner side by the periotic bones, posteriorly in part by the exoccipital, and elsewhere mainly by the quadrate. A large number of canals and passages open into it. On its inner side opening ventro-anteriorly is the *fenestra ovalis*, opening ventro-posteriorly the *internal auditory meatus* (Fig. 23, VIII), while dorsally there is a wide open-

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ing which forms a communication through the roof of the brain case with the tympanic cavity of the other side. On its posterior wall is the prominent foramen through which the facial nerve passes on its way to its final exit from the skull through the exoccipital: this foramen is bounded by the quadrate, squamosal, and exoccipital. The opening of the fenestra ovalis is in the fresh skull occupied by the expanded end of the auditory ossicle, the columella, whose outer end articulates by a concave facet with a trifid extracolumellar cartilage which reaches the tympanic membrane. The lower process of this extracolumella passes into a cartilaginous rod which lies in a canal in the quadrateand is during life continuous with Meckel's cartilage within the articular bone of the mandible.

"The columella and extracolumella are together homologous with the chain of mammalian auditory ossicles."

The Lower Jaw (Figs. 21, 23, and 24). The mandible consists of two similar rami, rather closely united at the anterior-median symphysis with each other. Each ramus consists of six bones.

The *dentary* (Figs. 23 and 24, 18; Fig. 21, 20) is a long bone that unites at the symphysis with its fellow to form the point of the jaw. It bears, along its dorsal edge, about twenty teeth; all but the posterior four or five of these teeth are in individual sockets; this may vary somewhat with age. The outer surface of the dentary, especially towards the symphysis, is covered with numerous, small, deep pits, while along its inner side, parallel to the row of teeth, is a row of somewhat larger pits like those noted in the maxilla and premaxilla. Articulating with the mesial side of the dentary along the greater part of its length is a flat bone, the *splenial* (Figs. 23 and 24, 19); between these two bones is a long cavity that makes the ramus hollow almost to the symphysis. A large foramen, not shown in any of the figures, leads through the splenial into this cavity.

Articulating with the caudal end of the splenial and forming the anterior border, as seen from the mesial side, of the large *external mandibular foramen* (Fig. 23, 27) is a small bone, the *coronoid* (Figs. 23 and 24, 23, Fig. 21, 21); it articulates with the splenial anteriorly, with the supra-angular dorsocaudally, and with the angular ventrally.

The *supra-angular* (Figs. 23 and 24, 21, Fig. 21, 18) is an elongated bone that forms the dorsal border of the external mandibular foramen; it also forms the lateral edge of the articular surface for the quadrate. It articulates anteriorly with the splenial, the dentary, and the coronoid; and posteriorly with the angular and articular.

The *articular* (Figs. 23 and 24, 22, Fig. 21, 19), which is scarcely visible in a lateral view, forms most of the surface for articulation with the quadrate, and sends back the large process so characteristic of the crocodilian skull. On the dorsal side 76

of this process is a concavity that looks like another articular surface. Laterally the articular articulates with the supra-angular; ventrally and posteriorly with the angular.

The angular (Fig. 23, 20, Fig. 21, 22) forms the ventro-posterior border of the jaw and of the external mandibular foramen. Its narrow, posterior end forms a part of the prominent process mentioned in connection with the articular. Between it and the posterior edge of the splenial is the *internal mandibular foramen*, which is much smaller than the external (Fig. 23, 28). Anteriorly the angular articulates with the dentary, coronoid, and splenial; dorsally with the supra-angular and the articular.

*The Hyoid* (Fig. 25). The hyoid being mainly of cartilage is usually not seen in prepared skeletons. It is thus described by Reynolds:

"The hyoid of the Crocodile consists of a wide flattened plate of cartilage, the *basilingual plate* or *body of the hyoid*, and a pair of *cornua*.

"The *basilingual plate* (Fig. 25, 1) is rounded anteriorly and marked by a deep notch posteriorly. The *cornua* (Fig. 25, 3), which are attached at a pair of notches near the middle of the outer border of the basilingual plate, are partly ossified, but their expanded ends are formed of cartilage. They pass at first backwards and then upwards and inwards. They are homologous with part of the first branchial arches of Selachians."

III The Ribs and Sternum

The Cervical Ribs. As noted above, all of the cervical vertebræ possess ribs. The first rib.



FIG. 25. HYOIDS OF AN ALLIGATOR (Caiman latirostris) (TO THE LEFT) AND OF A GREEN TURTLE (Chelone midas) (TO THE RIGHT).  $\times \frac{5}{8}$ . (Brit. Mus.) (After Reynolds.)

The cartilaginous portions are dotted.

- 1. basilingual plate or body of 3. first branchial arch (anterior the hyoid. cornu).
- 2. hyoid arch.

- 4. second branchial arch (pos
  - terior cornu).

attached to the atlas, consists of a single, long blade projecting backward at an acute angle (Fig. 17, 8) as far as the middle of the fourth vertebra. As described above it articulates with the atlas at but one place. All of the other cervical ribs have two articular surfaces, a tuberculum and a capitulum,

with a well-marked vertebrarterial canal between them. The ventral surface or capitulum articulates with a short process on the centrum; the dorsal surface or tuberculum (7) articulates with the transverse process. The third to seventh ribs are somewhat T-shaped, the stem of the T being the tubercle and head, while the cross arm of the T extends parallel to the axis of the neck (Fig. 17, 7). In the eighth rib the posterior arm of the T is elongated and projects out at a wide angle from the body; and in the ninth or last cervical rib this arm extends laterally as far as the vertebral portion of the thoracic ribs and has a cartilaginous tip.

The Thoracic Ribs (Figs. 16 and 26). These are ten in number, the first eight pairs being connected with the sternum. The fourth may be taken as typical. It consists of a bony vertebral portion and partially ossified intermediate and sternal portions. The vertebral portion articulates with its corresponding transverse process by two surfaces, as described in connection with the thoracic vertebræ. In the first and second ribs only the tuberculum articulates with the transverse process. the head having a separate articular surface on the side of the centrum, as in the typical cervical rib. In the last thoracic rib the head and tubercle are not distinguishable from each other. Near the distal end of all the vertebral portions except the first and the last two ribs is a caudally projecting. partially ossified, uncinate process. The inter-



FIG. 26. STERNUM AND ASSOCIATED MEMBRANE BONES OF A CRO-CODILE (C. palustris). ×13. (Brit. Mus.) (After Reynolds.)

The last pair of abdominal ribs which are united with the epipubes by a plate of cartilage have been omitted.

1. interclavicle.

. . . . . . . .

2. sternum.

- 4. abdominal splint rib.
- 5. xiphisternal horn.

3. sternal rib.

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mediate portion is present in all but the tenth rib, and wherever present, except in the ninth rib, it articulates distally with the sternal portion. The sternal portions extend medio-cephalad in a direction at right angles to the intermediate portion; the first two articulate with the sternum, the next six with the xiphisternal horns, and the ninth and tenth are missing.

The Abdominal Ribs (Fig. 26, 4). While these ribs are membrane bones and are not homologous with the other ribs, they may as well be mentioned at this time. They consist of about seven V-shaped sets of slender bones, the point of each V being directed cephalad. Each V is made up of from two or five slender bones, the number and arrangement being subject to considerable variation. The last V of the series (not well shown in the figure) is considerably larger than the rest and is made up of four curved bones that extend around the anterior ends of the pubic bones and are united to them by a broad tough membrane. The first or most anterior V is united by a narrow membrane (not shown in the figure) with the membrane that extends between the xiphisternal horns. All of the V's are more or less connected with each other by fibrous membranes. Since these ribs lie superficial to the recti muscles of the ventral body wall they are sometimes missing in carelessly prepared skeletons.

The Sternum (Fig. 26). The sternum consists of

the cartilaginous sternum proper (2), the xiphisternal horns (5), and the bony episternum or interclavicle (1). The latter is an elongated. flattened bone of somewhat spatulate outline. lving in the midventral line: it projects forwards to about the sixth cervical vertebra, while the anterior edge of the sternum is below the eighth cervical. Lying dorsal and lateral to the episternum is the flat. almost membranous sternum, to the posterior border of which the first two thoracic ribs are attached. The xiphisternum consists of two long, slender rods of cartilage: the anterior ends of these rods are in contact with each other and with the posterior border of the sternum: from this point they gradually diverge from each other as they extend caudad. A membrane extends between the horns as far back as the attachment of the last thoracic ribs.

#### IV. The Appendicular Skeleton.

The Pectoral Girdle and Anterior Limb. The pectoral girdle (Fig. 27) is of a very simple type, consisting, unless the episternum (interclavicle) be counted, of but two bones, the *scapula* (*s*) and *coracoid* (*c*). The former consists of an upper, flat, paddle-shaped portion and a thicker lower portion which articulates anteriorly with the coracoid, and posteriorly forms about half of the notch-like glenoid cavity. The dorsal edge of the flattened portion is continued as a small, cartilaginous supra-

scapula. The coracoid is a flattened bone, wide at either end and narrow in the middle, so that in a dorsal view it is shaped like an hourglass. It is decidedly curved, with the convex side down.



FIG. 27. PECTORAL GIRDLE AND ANTERIOR LIMB.

c, coracoid; ce, centrale; cl, claw; e, episternum; h, humerus; m, metacarpals; p, pisiform; r, radius; r', radiale; s, scapula; u, ulna; u', ulnare.

Its outer edge articulates with the scapula and is thickened to form the anterior border of the glenoid cavity. Its median end is attached to the sternum Near its scapular articulation there is a well-marked foramen that passes entirely through the bone. The episternum (e) or interclavicle was described in connection with the sternum and ribs.

There is no clavicle nor other coracoid elements. The *anterior limb* consists of the usual parts, the upper arm, forearm, and manus. The *humerus* (Fig. 27, h) is rather thick in proportion to its length; it has an elongated articular surface at its proximal end for articulation with the glenoid

cavity, and a larger, somewhat bilobed surface for articulation with the radius and ulna. On its ventral side, near the proximal end, is a very prominent protuberance, the deltoid ridge. The ulna (u) is slightly heavier and longer than the radius and forms the greater part of the elbow joint and about half of the wrist joint. Its proximal end is considerably larger than the distal, but has no olecranon process. Its distal end articulates with the ulnare and pisiform. The ulna as a whole is slightly curved, while the radius is quite straight.

The radius (r) consists of a cylindrical shaft with enlargements of about equal size at the ends. The proximal end articulates with the side of the ulna and with the humerus; the distal end with the radiale.

The carpus consists of a proximal row of three distinct bones and a distal row of smaller and less fully ossified elements. Of the proximal row the radiale (r') is much the largest bone. It is hourglass shaped, with the proximal end somewhat larger than the distal. Proximally it articulates mainly with the radius but also slightly with the ulna and ulnare. Distally it articulates with the centrale. The *ulnare* (u'), the second bone in size in the wrist, has about the same shape as the radiale but is much smaller. Proximally it articulates with the pisiform, radiale, and, apparently, with the ulna; distally it is in contact with the fused carpalia elements. The *pisiform* (p) is a small,

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irregular bone, articulating with the ulna and the ulnare; it is apparently connected by a long ligament with the fifth metacarpal but does not actually articulate with it. The *centrale* (*ce*) is a flattened, partially ossified element between the radiale and the first and second metacarpals. The distal carpal bones are represented by two irregular, partially ossified elements between the ulnare and the third, fourth, and fifth metacarpals.

The manus proper consists of five digits. The *metacarpals* (m) are of about the same shape, but vary in length and thickness; each consists of a cylindrical shaft with a slight enlargement at each end. The first digit or pollex has two phalanges, the second has three, the third has four, the fourth has four, and the fifth has three. The terminal phalanx of each of the first four digits is pointed, has a pair of lateral grooves, and is encased in a large, horny *claw* (cl).

The Pelvic Girdle and Posterior Limb. The pelvic girdle is described differently by Wiedersheim and Reynolds; the bone called by the former the pubis, the latter calls the epipubis. The bone called by Wiedersheim the pubis takes no part in the formation of the acetabulum; the pubis of Reynolds helps form the acetabulum but is a very small, unossified structure. Gadow also calls the lower bone the epipubis. I shall follow Reynolds's interpretation.

The ilium (Fig. 28, 1) is a heavy bone with

a dorso-laterally projecting crest; medially it is firmly united to the sacral ribs (Fig. 18, 5) while its outer side forms the upper and greater part of the



FIG. 28. PELVIS AND SACRUM OF AN ALLIGATOR (Caiman latirostris). × 1/2. (Brit. Mus.) (After Reynolds.)

- 1. ilium.
- 2. ischium.
- 3. true pubis.
- 4. epipubis (so-called pubis).
- 5. acetabular foramen.

- neural spines of sacral vertebrae.
- 7. symphysis ischii.
- 8. process bearing prezygapo-) physis.

acetabulum. Its outer and lower border has two surfaces, the larger and more posterior articulating with the ischium, the other with the cartilaginous publis.

The *ischium* (2) is a slightly arched bone, its ventral end a flattened blade articulating with its fellow, its dorsal end enlarged and thickened to articulate with the ilium, pubis, and epipubis. This dorsal end, which forms the ventral side of the acetabulum, is divided into two distinct articular surfaces by a deep, rounded notch; the posterior and larger surface articulates with the ilium, the anterior surface about equally with the pubis and epipubis.

The *pubis* (3), which is much the smallest element of the pelvis, is a small mass of cartilage lying between the ilium above and the ischium below. It forms a small part of the anterior wall of the acetabulum.

The *epipubis* (4) is a slightly arched bone, somewhat enlarged at its proximal end where it unites with the ischium, and flattened out into a fanshaped extremity, where it is united with its fellow and with the last pair of abdominal ribs by the broad, thin sheet of cartilage or fibrous tissue noted in connection with the abdominal ribs. As mentioned above, it is called by Wiedersheim and others the pubis. Near the center of the acetabulum there is a small foramen.

The *posterior limb* (Fig. 29) consists of the usual divisions—thigh, shin, and foot. The *femur* (f) is a bone of the same general outline as the humerus, though slightly longer and heavier. The head, for articulation with the acetabulum, is rather hemielliptical than hemispherical in shape, the long axis of the ellipse being vertical. The distal enlargement is of at least as great, if not greater, bulk than the proximal and shows some indication

of a division into two articular surfaces. The ventral side of the femur near the proximal end shows a fairly distinct trochantal ridge.

The shin or crus is made up of two well-developed bones, the *tibia* (t) and *fibula* (fb), the former being somewhat longer and considerably thicker than the latter.

The tibia consists of a cylindrical shaft with enlargements of about equal size at the ends. The proximal end forms most of the knee joint, the distal end articulates with a tarsal element said by Reynolds to represent the fused astragalus and centrale, by Wiedersheim called the astragalus, and said to represent the united tibiale, intermedium, and centrale (tb,



FIG. 29. POSTERIOR LIMB.
ca, calcaneum or fibulare; cl, claw;
f, femur; fb, fibula; l, tibia;
i3, ti-5, tarsalia; tb, tb<sup>1</sup>, tibialecentrale; IV, V, 4th and 5th metatarsals.

tb'). The fibula articulates by a small enlargement at its proximal end with the femur, and by an enlargement of about equal size, at its distal end, with the fibulare or calcaneum (ca), and with a small facet on the above-mentioned tibiale-centrale element.

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The tarsus is much modified and consists of four elements, in two rows: those of the proximal row are much larger than the two distal elements. Articulating with both tibia and fibula, as mentioned above, and with the first metatarsal and one of the distal tarsalia, is the large and irregular tibiale-centrale element of Revnolds (tb. tb'). In the tarsus here shown it consists of two elements. Post-axial in position is the *calcaneum* or *fibulare* (ca), articulating with the preceding tarsal element. with the fibula, with the rudimentary fifth metatarsal, and with the distal tarsal element said by Revnolds to represent the fourth and fifth tarsalia. The calcaneum is extended caudad into a prominent knob quite like the heel of the higher mammals

The two distal tarsal bones are small; one is said by Reynolds to represent the first three *tarsalia*  $(t^3)$ , the other  $(t^{4-s})$  the fourth and fifth. Wiedersheim says one of these bones represents the first three tarsalia, the other the fourth. In the tarsus here shown these two elements are fused.

The foot has five digits, though the fifth is small and consists merely of a small, distally pointed metatarsal bone. According to Wiedersheim this fifth metatarsal is fused with the fifth tarsalia. The metatarsals of the first four digits are long and progressively more slender from the first to the fourth; each is distinctly enlarged at the ends. The first digit or hallux has two phalanges, the

second has three, the third has four, and the fourth has four. According to Reynolds, the fourth toe has five phalanges; the figure here shown, which was drawn from nature, has only four on the fourth toe; the latter is the number given by Bronn for the crocodiles. The terminal phalanges of the first three digits are large and pointed, with the same lateral grooves noted in connection with the fore foot; each is sheathed in a horny claw. The four fully developed digits of the pes are nearly twice as long as the corresponding digits of the manus, but they are not proportionately thicker.