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THE STRUCTURE AND RELATIONSHIPS OF DIPLOCAULUS

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THE STRUCTURE AND RELATIONSHIPS OF DIPLOCAULUS

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I. INTRODUCTION AND HISTORICAL REVIEW

The curious amphibians known under the name of *Diplocaulus* have been the subject of study and speculation by a considerable number of investigators. But of the fifteen or more papers that have been published, only a few contribute much information. Moreover, papers that have appeared recently contain errors, leaving the subject of the structure and relationships of the group in an unsatisfactory condition, such that only a careful study of an abundance of material will suffice to clear up these points.

Professor Williston has placed at my disposal for this study the *Diplocaulus* material of the University of Chicago collection, which is without doubt the best and largest collection of this group in existence. A careful study of this material has enabled me to determine beyond reasonable doubt the structure of the skull and lower jaw and has added materially to our knowledge of the rest of the skeleton. All of the statements made herein have been determined from several specimens unless otherwise specifically stated. My thanks and acknowledgments are due to Professor Williston for careful criticisms which have uncovered many errors in the preparation of this paper.

The materials studied consist of about ten fairly complete skeletons; at least ten additional skulls in fairly good condition, many of them unusually perfect; and additional material, either not removed from the matrix or fragmentary, amounting to perhaps forty additional specimens. Much of this fragmentary material is unusually perfect for morphological study. This excellent collection of material permits the careful determination of every point in at least four or five specimens unless otherwise stated.

The following brief review of literature takes into consideration only the more important papers on *Diplocaulus*. The papers are likewise considered in the body of this account, in connection with the topics they treat.

We are indebted to Cope for our first knowledge of this group of amphibians. He first described and named three of the species, *D. salamandroides* (1877), from the Permian of Illinois; *D. magnicornis* (1882), from Texas; and *D. limbatus* (1896), also from Texas. He gave us our first important knowledge of their anatomy in 1896, when he described and figured the elements composing the dorsal surface of the skull of *D. magnicornis*, correct in all details, except that he failed to recognize the obscure suture separating the premaxilla and lachrymal, and thus identified the lachrymal as the nasal. He likewise made some observations as to the palatal region, but did not make out any of its elements.

Broili (1902, 1904) gave a thorough description of the anterior vertebrae, which Cope had described but briefly. He described the clavicle and interclavicle and figured several skulls, but could not make out their elements. He proposed two new species, *D. copei* and *D. pusillus*, both from the Texas Permian.

Jaeckel (1903) discussed the relationship of *Diplocaulus*.

Williston (1908) made out most of the sutures on the dorsal surface of the skull of *D. magnicornis*, confirming Cope's description. He figured correctly the under surface and made out some of the sutures. He showed for the first time the presence of small limbs, figuring clavicle, interclavicle, coracoid, and numerous limb bones.

Case (1911) made a general morphological study of *Diplocaulus*, confirming in most respects the conclusions of Cope and Williston. He first determined the sutures of the dorsal surface of the skull of *D. limbatus*. He identified a suture separating the premaxilla of Cope into two bones, the posterior of which he called the nasal. He identified a few sutures on the ventral surface.

Moodie (1912) concluded that a postorbital was present and that there was no pineal foramen. He also figured the ventral surface of the skull, showing the sutures, not all of which, however, are correct. Moodie raised *Diplocaulus* to the rank of an order.

Von Huene (1913) described and figured the lower jaw of *Diplocaulus*. The present studies, however, show him to be in error in most of his determinations. In a later paper he described and figured the dorsal surface of the skull, but added nothing new.

II. ANATOMY

A. *The skull.*—The general form of the skull of *Diplocaulus* is too well known to need verbal description; the several outline drawings here given (Figs. 1, 6, Plates I, II) should be sufficient. It should be stated, however, that the skull is not depressed in the parietal region, as described by Case. Some of the skulls at hand show this condition, it is true; but it is quite evident that it is due to crushing. The better preserved skulls show no depression. Attention should be called also to the fact that the center of gravity of the skull is located between the occipital condyles in *Diplocaulus limbatus*, at least in the skull in the University of Chicago collection, while in *D. magnicornis* it is located only slightly anterior to the condyles. This suggests that one purpose of the posterior lateral horns may have been to balance the heavy anterior parts of the skull, thus making control of the head easier. This matter is taken up more fully on page 24.

The asymmetry of the skull with reference to the parietal and postparietal deserves mention. Unfortunately the posterior median part of the skull is usually lost or damaged; but all reliable specimens at hand, as also the figures of Cope, Case, and von Huene, show that the suture separating the parietals is always to the right side of the median line, though to a variable degree, being especially so at the posterior end of the parietals. Apparently the asymmetry of the skull is confined to these elements, though perfectly preserved skulls might show others. The writer has no explanation of this condition to offer.

Skulls of *Diplocaulus* exhibit a wide range of variation in size and form after corrections have been made for distortion. In Fig. 7 are shown the different types known. The differences, aside from size, are chiefly as to form and position of the lateral cornua, the relation of length to width, and the position and size of the orbits. The size of the orbits had little significance, however, since they are often greatly altered in preservation. Otherwise the skulls at hand seem to have suffered but little from distortion and to represent practically the condition found in life. That some of these differences represent specific characters seems not improbable. For the purpose of the present paper, however, it seems best to regard them as belonging to two species, *D. limbatus* and *D. magnicornis*. The subject of specific recognition is treated on page 34.

The elements forming the dorsal surface of the skull have been figured and discussed repeatedly; hence a general description here would be needless repetition. Fig. 1 represents the conditions found, which, it will be seen, agree essentially with the findings of Cope, Williston, and Case. A few special points only will be discussed here.

Moodie (1912) figured a postorbital bone, lateral to the postfrontal, and von Huene (1913*a*) recognized the same element. A careful examination, however, of one reliable skull of *D. limbatus* and of five of *D. magnicornis*, as likewise of the skull studied by Moodie, convinces the writer that no such element is present—that there is but one bone between the frontal and jugal. What Moodie identified as a portion of a suture is evidently a fracture. Watson's description of *Batrachiderpeton*, moreover, shows clearly that the bone that has been called the supratemporal and other names is really the postorbital dragged out of the orbit (see page 39 of this article).

Moodie thought that there was no pineal foramen in the specimen he studied (now in Stuttgart Museum), but, since the region where it is located is missing in this skull, the statement carries no weight. The specimen shown in Fig. 1 has unquestionably a pineal foramen in the position described by earlier investigators. Unfortunately this region, one of the weakest parts of the skull, is missing from most specimens; but the presence of the pineal foramen in the specimen indicated cannot be questioned.

Case (1911) states that the frontal bone of *D. limbatus* extends but little anterior to the orbits, making this therefore a specific character separating it from *D. magnicornis*. Von Huene's figure (1913*a*) shows, however, the same condition as in *D. magnicornis*. Likewise, a specimen at hand, which is identified as *D. limbatus*,

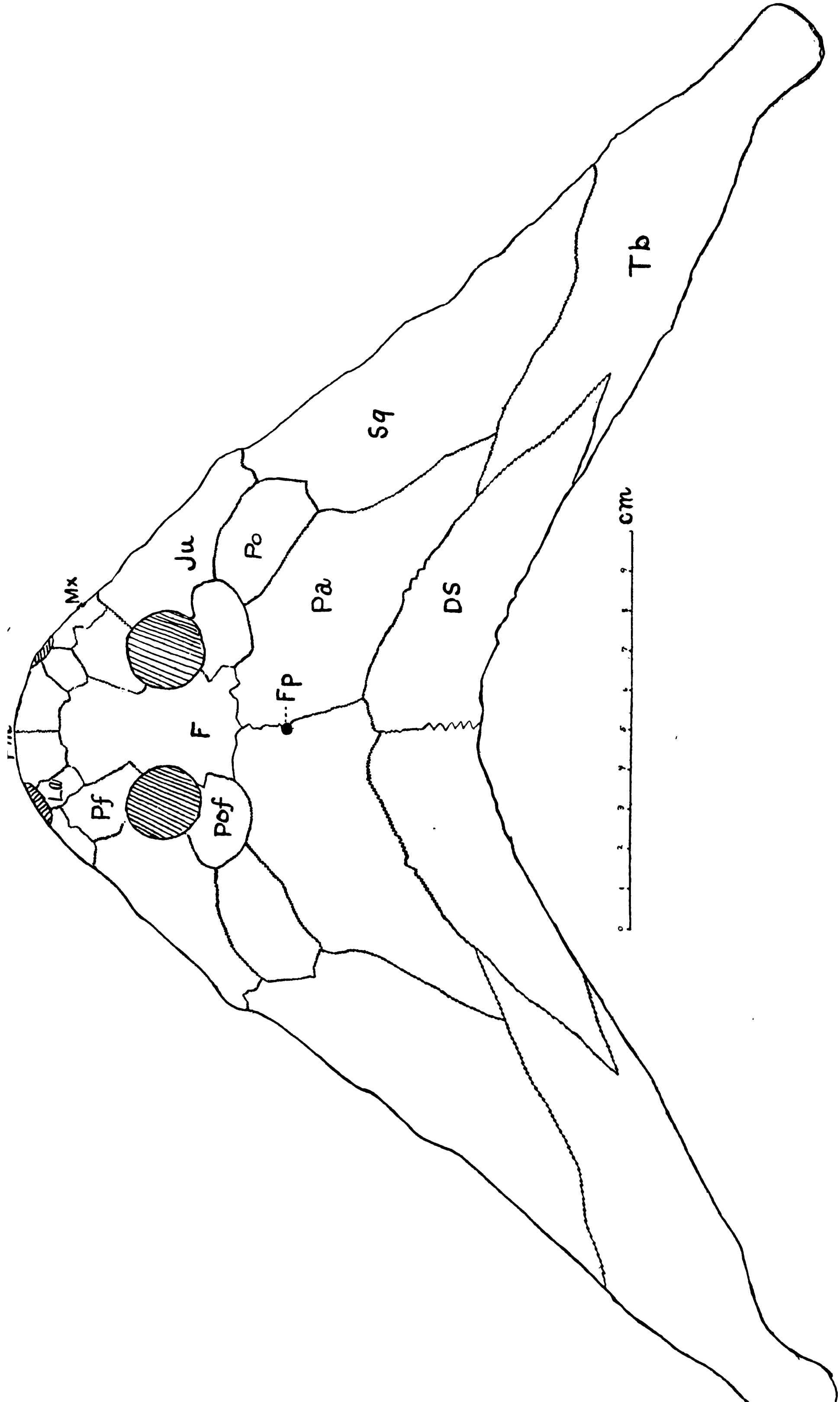

FIG. 1.—Skull of *Diplocaulus magnicornis*, dorsal view. *Fp*, pineal foramen; *F*, frontal; *Ju*, jugal; *La*, lachrymal; *Mx*, maxilla; *Pa*, parietal; *Pmx*, premaxilla; *Po*, postorbital; *Ds*, dermosupraoccipital; *Prf*, prefrontal; *Pof*, postfrontal; *Tb*, tabular; *Sq*, squamosal.

shows that the frontal extends every bit as far forward as in *D. magnicornis*.

The arrangement of prefrontal (lachrymal) and lachrymal (adlachrymal) fails to agree with the descriptions of Case and von Huene in four well-preserved skulls, but agrees rather with the descriptions of Cope (1896, lachrymal called nasal).

The probable cause of these discrepancies is revealed by a comparison of the outlines of the skulls studied by Case and von Huene with those of the University of Chicago collection. The drawings by Case and von Huene show the region in front of the orbits to be very much shorter than it is in the specimens at the University of Chicago. It seems probable that this difference is due to distortion, which would alter the condition of affairs greatly.

Case identified a suture dividing the premaxilla of Cope into two elements, the posterior of which he called the nasal. Three specimens at hand show conditions that might be so interpreted; but two unusually well-preserved snouts show no traces whatsoever of such a structure on either side. The conspicuousness of other sutures on these specimens (Nos. 636 and 1035) and the good state of preservation in the region where such sutures would occur convince the writer that they are not present. Moreover, the very small nasals in *Batrachiderpeton*, which is apparently ancestral to *Diplocaulus*, tell us that the nasals have disappeared in the latter. The explanation of the apparent sutures in some specimens is found if we consider that they occur at the angle formed by the junction of the anterior and dorsal surfaces of the skull—a place which would be the first to fracture.

Specimen No. 636 of the University of Chicago collection (*D. magnicornis*) has the under surface of the skull preserved in a practically perfect condition (Plate I) and with practically every suture visible. This and several other skulls which have the under side partly preserved agree completely with each other. They disagree, however, in most particulars with the determinations made by Moodie (1912). The skull upon which Moodie based his description has only a small part of the central surface preserved, but agrees with the account given here in every particular that could be made out.

The under surface of the skull of *D. magnicornis* is characterized by several elevations and depressions or openings. Extending backward along the edges of the skull from in front of the quadrate to the middle of the lateral cornu is a prominent central ridge, which in a full-sized specimen is $2\frac{1}{2}$ cm. wide by 9 cm. long, and which projects downward 2 cm. It is composed entirely of the quadratojugal bone, which thus lies mostly behind the quadrate. At its posterior end it projects free beyond the base, forming a notch, which, as Williston has pointed out, corresponds to the notch between the squamosal and tabular in other Stegocephali. Here, however, the backward growth of squamosal and tabular has changed the relations, causing the notch to lie between squamosal and quadratojugal. In its middle portion this ridge is undermined from both sides, but especially from the inner, where a deep cavity is roofed over. This ridge projected downward in life and was invisible from above; but it is often crowded laterally in preservation.

The quadrate, and the portions of squamosal and pterygoid which cover it, likewise project considerably below the rest of the skull. The pterygoid and squamosal slope abruptly away from the quadrate.

The ventral surface, except in the lateral cornua, is formed by a series of bones which are separated by an interval from those composing the dorsal surface except for a bridge between pterygoid and parietal. In four places on each side are spaces in this ventral series through which the bones of the dorsal surface are visible. These are as follows:

Near the posterior edge on either side, and paralleling the border, is an oblong space, with steep or overhanging sides, which in a full-sized specimen measures 5 cm. long by 1.8 cm. wide. It begins about 3 cm. laterad of the median line, lying, therefore, within the lateral cornu. Its borders are formed by the pterygoid, exoccipital (paroccipital portion), tabular, and squamosal. Broili has called this the "Ohrenschlitzgrube," in which designation he is probably correct.

The palatine vacuities are large spaces in the anterior part of the skull, separated from each other by the anterior limb of the parasphenoid. They extend from the anterior end of the orbits to the body of the parasphenoid just anterior to the level of the quadrates. The orbits open into a little less than the anterior half. They are bounded by vomer, palatine, pterygoid, and parasphenoid.

Laterad to the palatine vacuities and separated from them by a bridge formed by the palatine and pterygoid are deep depressions which extend beneath the other structures posteriorly and medially. Into these cavities the ends of the lower jaw fitted, and without doubt the remainder of the space was filled with the muscles which controlled the jaw.

Anterior to the orbits are the large internal nares, whose boundaries are formed chiefly by the vomer and palatines and partly also by the maxilla and premaxilla.

The premaxilla forms but a small portion of the border of the external nares, and a still smaller portion of the internal nares. It bears 11 teeth in a single row along its anterior border. With the vomers the two premaxillae surround a small median foramen.

The maxilla forms a narrow strip along the margin of the jaw from premaxilla to jugal. It bears 20 teeth, which are arranged along the entire length in a continuous row.

The palatine is considerably broader than the maxilla. A narrow prolongation extends nearly to the premaxilla, forming the anterior border of the internal naris. A second, larger arm forms most of the posterior border of the naris, meeting a similar arm from the vomer. At the level of the posterior end of the maxilla the palatine bends mediad to meet the pterygoid. Beyond the maxilla it is bounded laterally by the jugal. It bears about 33 teeth in a continuous row along its lateral border. In some specimens the palatine extends farther posterior by several millimeters than in others.

There is no evidence of a transverse bone in the position recently described by Moodie. Three skulls which have this region well preserved have no evidence of such a condition. What Moodie identified in the specimen he studied, as a suture between the palatine and maxillary on one side and the transverse on the other, is evidently a fracture. The sutures in this region are visible in this specimen and are seen to agree fully with other specimens.

Williston and Case interpreted as transverse bone or ectopterygoid the portion of the skull lying immediately posterior to the maxilla and lateral to the palatine. Four well-preserved skulls at hand, however, seem to show that this region is a part of the jugal and that the transverse is not present in *Diplocaulus*.

The vomers occupy the space between the internal nares and extend slightly posterior to them, forming part of the bridge between naris and palatine vacuity. Each vomer bears 11 teeth, which in all specimens at hand are in a straight line, those of the two vomers forming an inverted V. Case described these teeth as arranged in a semicircle in *D. limbatus*, recognizing this as a character distinguishing this species from *D. magnicornis*. Specimen No. 637, however, which I am compelled to call *D. limbatus*, shows the teeth arranged in an inverted V. It seems probable, therefore, that the condition described by Case, as also by Broili, is due to distortion.

Joining the posterior end of the vomers is the large anterior prolongation of the parasphenoid, which lies in the median line, separating the two palatine vacuities. The suture between parasphenoid and vomer could not be made out, though there can be no doubt as to its location, if present, as it probably is. Just anterior to the level of the condyles this anterior arm joins the main body of the parasphenoid, a large, roughly square structure lying between the pterygoids.

The pterygoid lies lateral to the parasphenoid and exoccipital. Near its lateral end it divides into two branches, the anterior of which goes forward to meet the palatine, while the other extends laterally over the ventral surface of the quadrate to meet the squamosal. It was not possible to ascertain absolutely the sutures marking the lateral limits of this element where it meets the squamosal. It is absolutely certain, however, that the anterior end reaches no farther than the posterior end of the palatine, the palatine thus lying between it and the vomer.

A curious bone, of whose identity the writer is at present in some doubt, lies halfway between the mandibular condyle and the median line. It forms a heavy transverse pillar between pterygoid and parietal, being united by a broad base to each. In life it must have acted in a very serviceable manner to strengthen the weak parietal region of the skull.

An element in this position would of necessity be a cartilage bone. Of paired cartilage bones this might conceivably be one of the following: proötic, orbitosphenoid, alisphenoid, and epipterygoid. Proötic we should not expect in this position. Orbitosphenoid and alisphenoid have not been reported for amphibians. This is, however, no valid objection. Since the optic nerve must have been anterior to it, the orbitosphenoid is ruled out. Alisphenoid it might be. The writer is of the opinion, however, that it represents the epipterygoid of lizards and some other animals. Its presence here is surprising, for such a structure has not before been recognized for an amphibian. If it is the epipterygoid, then this is a primitive tetrapod element and is a belated survival in lizards. Since the writer plans to take up a study of the homologies of all the cartilage bones of the skull soon, further consideration of this matter is omitted here.

The exoccipital extends laterally along the whole length of the auditory groove, forming its posterior border. A large foramen lies between exoccipital and postparietal, just lateral to the foramen magnum. A smaller one, no doubt for the vagus nerve, pierces the exoccipital just anterior to the lateral end of the condyle. It will be seen that the exoccipital as thus described includes also the paroccipital or opisthotic, which is fused completely with it.

A small basioccipital is present, and also a long slender element anterior to it, mostly overlaid by the parasphenoid, Fig. **6,** 14, 15. In conformity with the usual nomenclature for the Amphibia, I have called this element the sphenethmoid. It is possible that it is separated into two or three elements, as in higher animals, but there is no evidence to support this conclusion in the specimens examined. The supraoccipital is absent. The alisphenoid has been mentioned above.

The presence of the basioccipital is rather unexpected. So far as the author is aware, it has not previously been reported for any holospondylous stegocephalian, and it seems certain that it is absent in most. However, it may be present in others, for it was not long ago that it was believed to be absent in the Temnospondyli, though it seems probable now that all of these possess it. If the presence of the basioccipital is a primitive character, as is the opinion of the writer, it would serve to indicate that *Diplocaulus* separated early from other holospondylous Stegocephalia.

The proötic seems to be absent, as a careful search failed to yield any indications of it. The quadratojugal is practically coextensive with the prominent ventral ridge (page 9) which lies along the edge of the skull. It meets the jugal in a transverse suture anterior to the quadrate. It covers the lateral portion of the quadrate, posterior to which it forms a downward projection from the squamosal, from which it is separated by a distinct suture.

The quadrate is hidden from view by the pterygoid, squamosal, and quadratojugal, except for the hourglass-shaped condyle which projects from beneath these anteriorly. A considerable cavity, which no doubt contained muscles for the operation of the mandible, extends backward beneath the quadrate.

The squamosal has about the same extent ventrally as dorsally. Its associations with the other bones of the ventral surface have already been mentioned.

The tabular has nearly the same distribution on dorsal and ventral surface and needs no special description.

The postparietal (dermosupraoccipital, dermoccipital, interparietal) is visible from below as a narrow strip along the posterior margin.

B. *The lower jaw.*—The collection of the University of Chicago contains several complete or nearly complete lower jaws of *D. magnicornis*, together with a great many smaller portions, all of which are in an excellent state of preservation and have the sutures unusually distinct. From this material I have been able to determine exactly all the elements except the coronoid and to verify each point on at least a half-dozen specimens, Fig. 2. The account here given differs in most particulars from the descriptions of von Huene (1913). Since the sutures are so clear in the specimens at hand and show absolute uniformity in all the specimens, I can only conclude that von Huene's account is inaccurate. This seems the more probable, since von Huene had half of one specimen at his disposal for study.

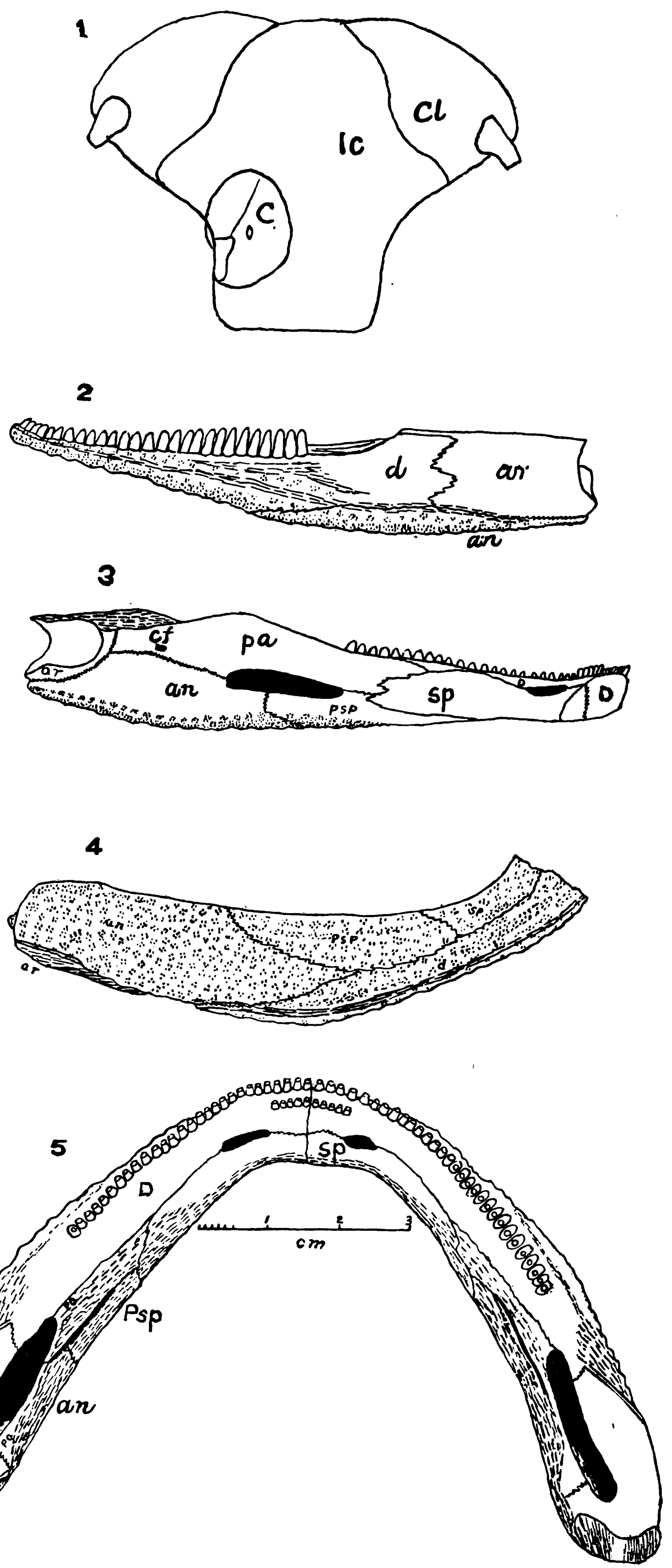

FIG. 2.—*Diplocaulus*. 1, pectoral girdle, dorsal side, *cl*, clavicle, *ic*, interclavicle *c*, coracoid (after Williston); 2, left mandible, external view; 3, left mandible internal side; 4, left mandible, ventral side; 5, mandible, dorsal side, *ar*, articular *an*, angular, *cf*, chorda tympani foramen, *d*, dentary, *pa*, prearticular, *psp*, post-splenia, *sp*, splenial.

Each half of the lower jaw is club-shaped, tapering gradually toward the anterior end, which has but half the circumference of the posterior. Near the anterior end each ramus bends abruptly mediad, the two rami thus meeting in the symphysis end to end—that is, not at an angle. The ventral and lateral surfaces are sculptured, except for the articular, which, however, also shows some sculpturing on the lateral surface in some specimens. On the ventrolateral angle of the jaw is a narrow groove which Moodie has no doubt correctly interpreted as a lateral line groove. The most conspicuous feature on the median surface is a long foramen, lying mostly in the posterior half of the jaw, which opens into Meckel's groove. Near the symphysis is a second conspicuous, but considerably smaller, foramen. These are the two usual Meckelian foramina of the Temnospondyli and some reptiles. The chorda tympani foramen is also present, though quite inconspicuous. Meckel's groove opens directly dorsal, extending from within a few millimeters of the articulatory facet to near the middle of the jaw.

The articular forms the bulk of the posterior end of the jaw. The facet, shaped to fit the hourglass-shaped condyle, is in the form of two hollowed-out depressions, which lie at nearly right angles to each other. The outermost of these faces backward, or slightly lateral, and the inner median. On the median and ventral side of the jaw the boundary of the articular is little more extensive than the surface of articulation. Laterally, however, it extends forward for 40 cm. in a jaw which is 95 cm. long. A considerable portion of it is overlaid by the jagged, irregularly outlined posterior end of the dentary. It forms practically the entire lateral border of Meckel's groove.

The angular extends from the posterior extremity of the jaw to beyond the middle. Posteriorly it forms the entire ventral surface of the jaw; anteriorly it ends in a point in the median line of the jaw, being bounded laterally by the dentary and medially by the postsplenial. It does not extend on to the lateral surface of the jaw, being separated from the articular and dentary by a suture that lies in the bottom of the operculomandibular canal. On the median surface it extends dorsal to meet the prearticular near the dorsal limit of the jaw. It forms a small portion of the boundary of a large median foramen which opens into Meckel's groove.

The dentary bone extends along three-fourths the length of the jaw. Anterior to the angular it forms about the lateral half of the jaw. It meets the anterior end of the angular in a diagonal suture on the ventral surface. Distally it overlies the articular laterally for a considerable distance, ending in a jagged, irregular manner. On the dorsal surface it extends but little posterior to the last tooth. The median surface is largely overlaid by this prearticular and the distal portion of the splenial. The dentary forms about two-thirds of the symphysis, the splenial forming the other third.

The dentary bears two rows of simple teeth. The one along the outer edge of the jaw contains about 30 teeth. Within this row, as first observed by Williston, is a second row of six smaller teeth, extending from the symphysis laterad. Von Huene believed these teeth to be borne on the splenial, but two well-preserved specimens show that they are borne upon the dentary.

The splenial forms about one-third of the bulk of the jaw at its anterior end, lying medial to the dentary. About 15 mm. from the symphysis it becomes reduced to a thin plate of bone, limited to the dorsomedial surface of the jaw. This portion overlies the dentary, postsplenial, and prearticular, reaching nearly to the middle of the jaw. With the dentary the splenial incloses a foramen of considerable size, which lies on the dorsomedial surface, not far from the symphysis.

The postsplenial (Williston, 1913) forms a direct continuation of the splenial, from which it is separated by a very distinct diagonal suture. Posteriorly a parallel suture separates it from the angular. It forms most of the ventral surface of the large foramen which opens into Meckel's groove, and anterior to this is overlaid by the prearticular, and anterior to this by the splenial. This bone is bounded by perfectly distinct sutures on all sides, and there can be no doubt as to its validity as a separate element.

The prearticular (Williston, 1903 = goniale, Gaupp, 1908) is a long, thin bone which extends along the upper median border of the jaw, from articular to splenial. It forms the median border of

Meckel's groove, in which region it projects dorsally as a thin, free plate. Ventrally it meets the angular and forms the roof of a large foramen opening into Meckel's groove. Between it and the angular is the small chorda tympani foramen. Anterior to Meckel's groove it becomes applied to the surface of the jaw, overlying dentary and postsplenial and finally disappearing beneath the end of the splenial.

The coronoid, one of the most persistent elements of the tetrapod mandible, must have been represented. Unfortunately, however, the region where it should occur has been somewhat eroded in all of the specimens at hand, leaving not even satisfactory proof that it was present. Such evidence as there is seems to indicate that it was a thin, loosely attached bone, 2 cm. long in adult specimens, reaching forward to the fourth tooth from the last. The appearance of the dentary anterior to this seems to indicate that the coronoid did not extend farther forward than this point and that inter-coronoid and precoronoid were not present.

As would be expected in an amphibian, the surangular is not distinguishable as a separate element. There seems to be no doubt, however, that the element is represented by the anterior prolongation of the articular on the lateral side of the jaw, the two bones being fused. On many specimens this region is sculptured like the angular and other membrane bones; and in all specimens at hand there is at least a faint sculpturing. It seems probable that this sculpturing is confined to membrane bones, and since it is exactly in the position the surangular would occupy if it were present, there seems no doubt that this portion of the articular represents this element.

C. *Vertebral column and ribs.*—The anterior vertebrae have been described in detail by Broili and later by Case; and they have been less completely described by Cope and Williston. To describe these vertebrae here would be superfluous, since one of these accounts will always be accessible. Attention is therefore given here only to the caudal region and to a few special points as to the anterior part.

Two specimens of the first vertebra, commonly called the axis, show a very prominent midventral keel, especially prominent at its posterior end. Broili's account is not available at the moment of writing this paragraph, but the drawings of Williston and Case show no indications of such a keel except at the extreme anterior end of the vertebra. Likewise, two specimens at hand show two long processes from the neural arch which extend over the upper surface of the succeeding vertebra nearly to its posterior end, as shown in Figs. 3, 4. Case and Williston also do not show these structures. The latter difference mentioned might be due to the processes being broken off in some specimens, but the former can hardly be so explained. It seems that it is another of the points in which *Diplocaulus* shows a wide range of variation, and it may represent a specific difference.

Specimen No. 1015 of the University of Chicago collection consists of skull, shoulder girdle, parts of limbs, and parts of vertebral column, lying in such a way as to show that the animal was preserved undisturbed in the position in which it lay at death. The first eighteen vertebrae when found were in six pieces, which fitted together and with the skull by clean, unworn fractures, leaving no doubt as to their identity. The centrum of the eighteenth vertebra bears two downward-projecting processes, which another specimen shows to be the bases of a heavy haemal arch on the posterior half of the centrum. This arch is considerably wider than the centrum or the succeeding haemal arches. It extends about as far ventralward as those following and is flat and rugose on its ventral surface. The difference between this condition and that described by Case for American Museum specimen No. 4472 is probably due to the haemal arch being broken off in the latter specimen. The ventral surface of the centrum is not flattened as described by Case, however, but rounded. Case is probably correct in designating this vertebra as the sacrum. He found it to be the seventeenth, while the specimen studied shows it to be the eighteenth. Such a difference might represent normal variation, or additional specimens may show that this difference represents a valid specific distinction between *D. limbatus* and *D. magnicornis*. However this may be, the two agree essentially as to the location of the posterior limbs.

Two other specimens of the University of Chicago collection, found within a few inches of each other, have no doubt complete vertebral columns. There is, however, a slight disarrangement in each column, and there are 41 vertebrae, showing the presence of another specimen; this is also shown by a portion of a third skull

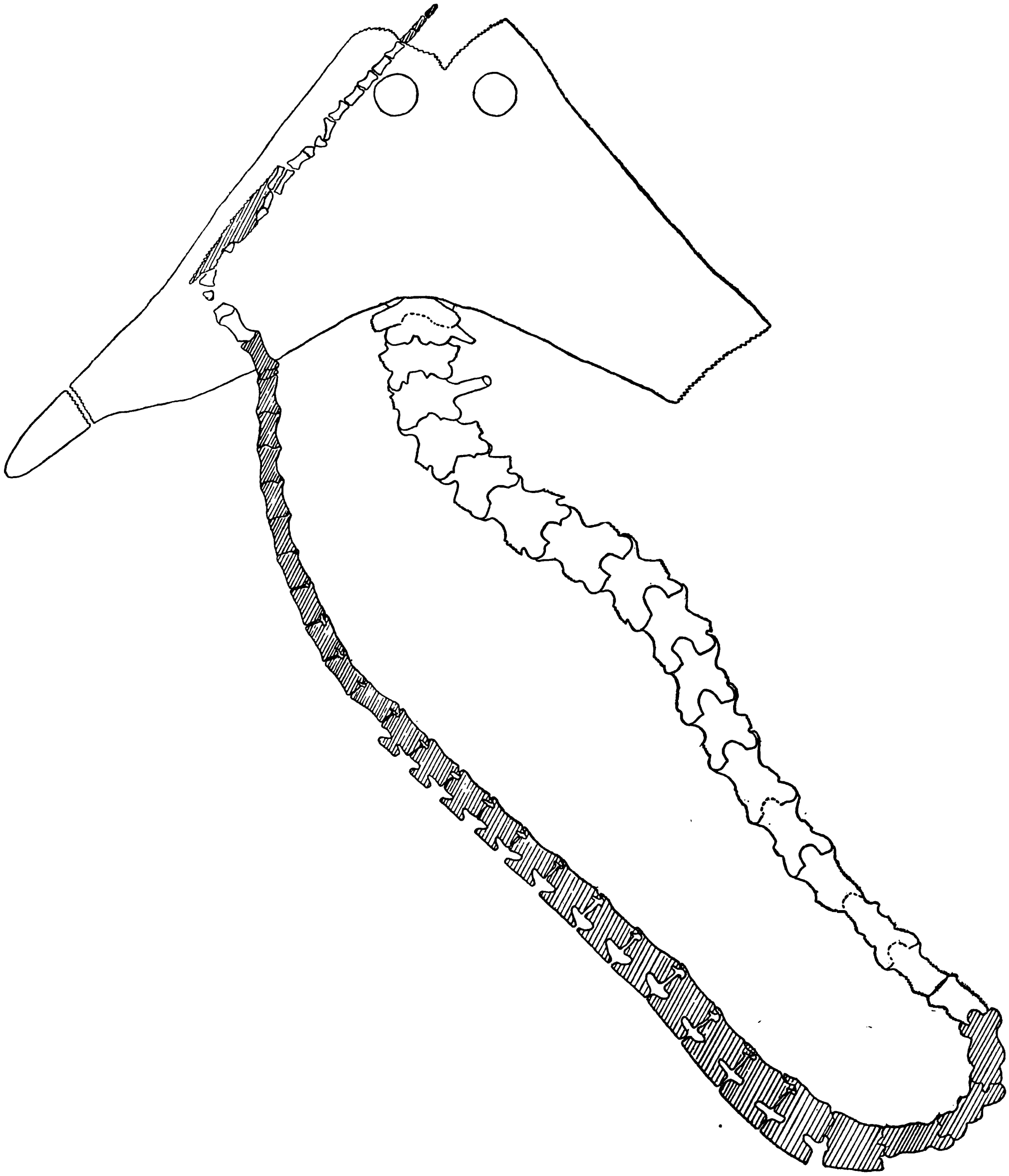

FIG. 3.—*Diplocaulus*, No. 1015, University of Chicago, showing skull, presacral, sacral, and caudal vertebrae, as preserved, the missing parts restored; some of the restorations are intercalated from other specimens (Nos. 11, 15, and first eight caudals).

and extra limb bones. It is not possible, therefore, to verify the number of vertebrae from these specimens, though both are probably complete and show practically no disarrangement.

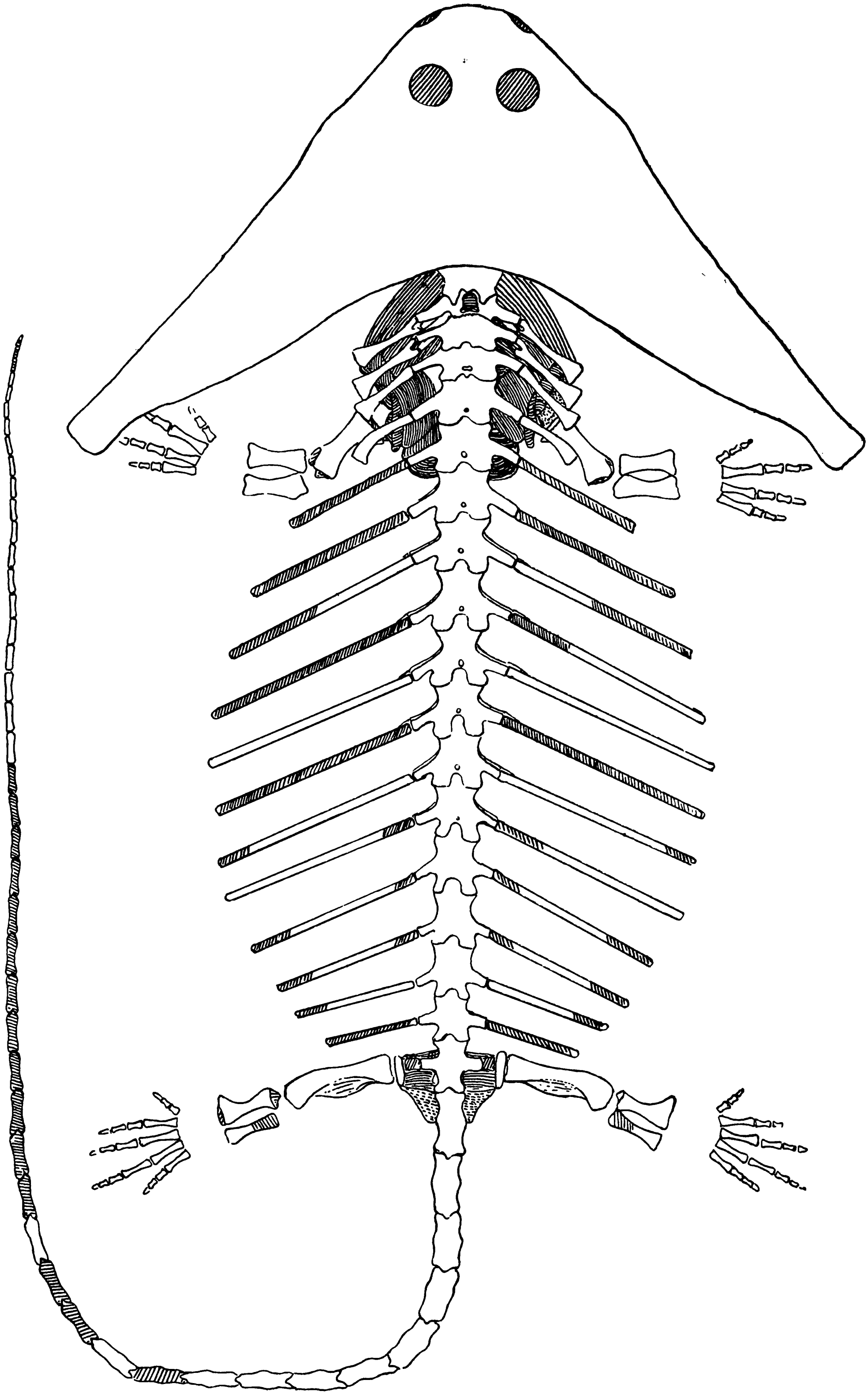

FIG. 4.—*Diplocaulus*, skeleton, restored. Barred parts restored. Pectoral

The vertebrae decrease gradually but considerably in size from the twelfth to the eighteenth. The centrum of the twelfth in the specimen at hand measures 20.5 mm. long by 10.5 mm. broad at the end, while the same measurements for the seventeenth are 17 and 8.5 mm. The centra usually are not flattened as described by Case, but strongly rounded; but some specimens have the centra as described by him. The differences are, to all appearances, not due to differences of preservation, and may well represent valid specific distinctions. This subject is discussed more fully on page 34.

The processes with which the ribs articulate, usually called diapophysis and parapophysis, both arise from the centrum, contrary to former descriptions. The writer has but two specimens before him at the time of making this examination, but this is certainly true of these, and can be made out positively for a dozen or more vertebrae, both in the anterior region, where they unite with the vertebrae separately, and in the posterior region, where they are joined at the base. The upper process, it is true, arises very near to the beginning of the neural arch, but is nevertheless distinctly borne on the centrum in at least a dozen specimens at hand.

The anterior ribs, as has been noted by other observers, are flattened at their outer extremity. They increase greatly in length posteriorly, all ribs being curved. Considering that they are borne on long processes, they extend very far laterally from the vertebral column. Their double-headed attachment must have made them rigid as far as any but anteroposterior motion was concerned.

Lying across the left side of the skull, in specimen No. 1015 are found also fifteen small caudal vertebrae in order, which are evidently from near the tip of the tail. Since the condition of all the other parts of the skeleton indicates that the animal was preserved undisturbed in the position in which it lay in death, it seems probable that the animal lay with the tip of its tail across its face. This would mean that the tail of *Diplocaulus* must have been unusually long and slender, longer than the rest of the body, and composed of at least 45 vertebrae. Fig. 3 shows the recovered parts of this specimen in which they were preserved, with the missing parts, as they are judged to have occurred, supplied.

It could be true, of course, that the caudal vertebrae belonged to a second animal, or that the tail, detached after death, floated forward to the position in which it was preserved; but opposed to the conclusion that there were two animals is the fact that, though the specimen was in more than a hundred pieces when found, all except a few small unrecognizable fragments fit together by clean, unworn surfaces to make one nearly complete skull with presacral vertebrae and other parts, occurring in such a way as to indicate that the carcass was preserved undisturbed. If two specimens are here represented, one would expect more of the one than these few caudal vertebrae.

It would matter but little, however, if these vertebrae did belong to another specimen, so far as our conclusions as to the length of the specimen are concerned. The slight differences in shape and size between the different vertebrae of this series indicates unmistakably a long, gradually tapering tail, whose total length could easily have been even greater than indicated in Fig. 3. There are, moreover, in the University of Chicago collection several specimens that show anterior caudal vertebrae, sometimes as many as eight continuous, but unfortunately always detached from the sacrum. It is evident from the very close similarity of all adjacent anterior caudal vertebrae in the collection that many of the intermediate vertebrae are missing. These facts, taken together, indicate an unusually long, gradually tapering tail.

Unfortunately the anterior caudals of the University of Chicago collection are all detached from the sacrum, so that it is not possible to determine their exact position in the column. Case states that the first caudal is longer and narrower than the presacral and possesses a haemal arch, which is narrowed anteriorly, but is as wide as, or wider than, the centrum posteriorly. There are vertebrae in the University of Chicago collection which fit this description. Other caudals show a much heavier haemal process than any figured by Case, no doubt indicating that the haemal processes at first increased in size posteriorly, which process was not accompanied by a flattening of the centrum. The series of eight caudals in specimen No. 1317 shows that the entire vertebra was afterward flattened, without any considerable reduction of other dimensions. Next, we see a quite gradual decrease of all dimensions of the vertebrae. It is certain that the ninth caudal has well-developed neural and haemal arches which extend for the full length of the vertebrae. Likewise, some detached caudals, evidently posterior to these, have the haemal arch but two-thirds the length of the centrum, and not so high. The neural arch meanwhile has become much reduced. In the last of these detached vertebrae the haemal arch seems to be on the verge of disappearing. These

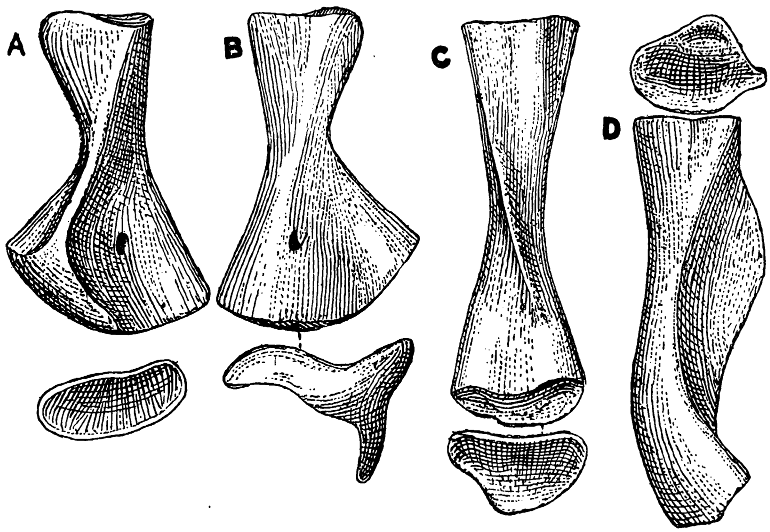

FIG. 5.—*Diplocaulus magnicornis*. *A*, *B*, left humerus, dorsal, ventral, and end views, natural size; *C*, *D*, right femur, ventral, lateral, and end views, one-half natural size (after Williston, 1909).

vertebrae as a whole have become much smaller, but are still considerably larger than the most anterior of the fifteen distal caudals of specimen No. 1015 (Fig. 3) when both have been reduced to the same scale. The caudals of this specimen show no trace of neural or haemal arch. The only conclusion is that the tail of *Diplocaulus* was very long and slender.

The more characteristic of these caudals, arranged in the order in which they seem to have occurred in life, may be seen in Fig. 3 (see explanation). Fig. 4 shows the probable appearance of the complete skeleton, with the missing parts supplied.

D. *The limb girdles and limbs.*—Although *Diplocaulus* was first described in 1877, and although the skull and anterior vertebrae have been fairly well known since Cope's description of 1896, it was not until 1902 that Broili showed the presence of a clavicular girdle, and not until 1908 were the limbs shown by Williston to be present. In the last few years, however, many specimens have been found with the limb-bones in unquestionable association, showing that *Diplocaulus* had small though nearly useless limbs. Practically every element of the skeleton of the limbs and girdles is represented in the University of Chicago collection, thus filling the last gap in our knowledge of the osteology of these forms.

Clavicle, interclavicle, coracoid, humerus, and femur all agree with the descriptions of Williston in four or more specimens and need only be figured here. The University of Chicago collection contains three scapulae and basal portions of several others. Several are associated with other parts of the shoulder girdle in the positions they occupied in life, leaving no doubt as to their identity or relations. Scapula and coracoid are not suturally united. They lie posterior to the clavicle, the coracoid lying upon the interclavicle. The ventral portion of the scapula is thickened considerably where it joins the coracoid. Dorsally and antero-dorsally it soon thins out to a thin plate, but the posterior border remains much thicker than the rest of the blade. The posterior border is strongly concave, while the anterior and dorsal are so convex as to form together a nearly perfect semicircle. A small foramen pierces the scapula near its base. There is no evidence of a glenoid fossa.

The cleithrum (Fig. **6**, 3) is about the same length as the scapula and humerus. In form it is a nearly straight bone whose width in the middle is a little over one-fourth its length. In cross-section it is T-shaped except at one end, where it is flattened and broadened out to double its usual width. The University of Chicago collection includes four cleithra. Specimen No. 221 has both preserved *in situ*. This specimen shows that the cleithrum in life embraced the dorsal lateral process of the clavicle, lying posterior to it, with the expanded end dorsalward. It lay, of course, just anterior to the scapula and was no doubt joined to it in life.

The radius and ulna are each represented in the University of Chicago collection by one complete specimen and many end

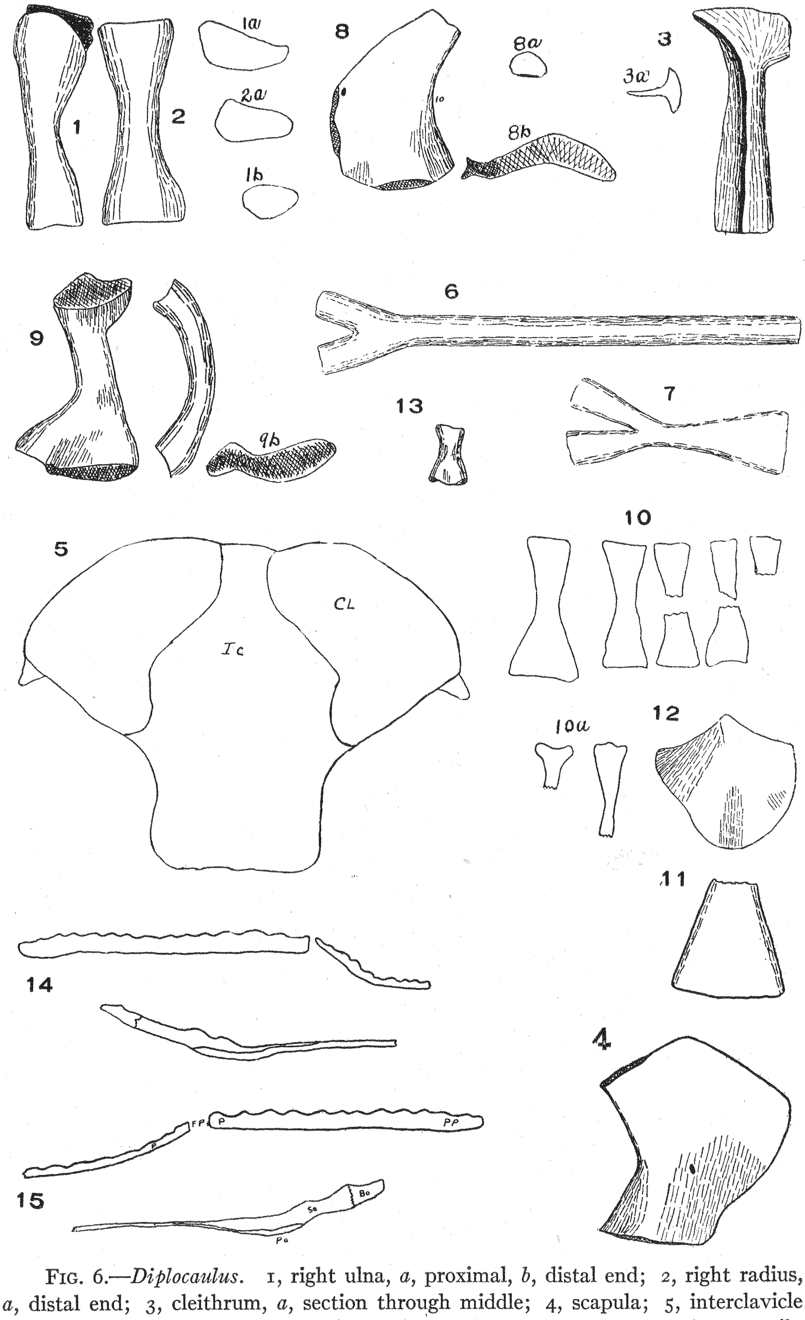

FIG. 6.—*Diplocaulus*. 1, right ulna, *a*, proximal, *b*, distal end; 2, right radius, *a*, distal end; 3, cleithrum, *a*, section through middle; 4, scapula; 5, interclavicle and clavicles (after Williston, 1909); 6, rib, tenth vertebra, posterior view; 7, rib, second, third, or fourth vertebra; 8, right ischium, *a*, proximal end, *b*, distal end; 9, tibia, posterior view, *b*, distal end; 10, right metatarsals, *a*, phalanges from same foot; 11, part of fibula; 12, ilium; 13, dissociated metapodial, probably first metatarsal; 14, 15, median sections through occipital region of skull.

portions. The ulna is preserved in direct association with the humerus, and the radius occurs attached to the mid-dorsal region of the specimen. Both are slightly shorter than the humerus. The radius is a short bone, about equally expanded at either end, the ends being about twice the width of the middle portion and flattened. The ulna is curved slightly and is considerably broader at its proximal than at its distal end. Fig. **6,** 2, 3, show these two bones apparently undistorted.

In specimen No. 1009, a small *Diplocaulus* whose skull measures only 4 cm. across the horns, a portion of the hand was found upon removing the matrix just below and behind the left cornu of the skull. Four fingers are clearly represented, each by two phalanges. There is also a fragment of bone that might seem to indicate the presence of still another finger (the fourth), but since no holospondylous amphibian is known to have five fingers, it seems best to interpret this fragment of bone as an intrusion. Numerous unassociated metapodials were found, which might belong either to hand or to foot.

The mesopodial bones were probably unossified. We should hardly expect to find them in an animal so thoroughly aquatic as *Diplocaulus* evidently was. Associated with some metapodials, however, are several small bony structures of unrecognizable form that may represent mesopodials. They are attached opposite, apparently, to the end which bore the phalanges. It seems safest, however, to interpret these unrecognizable structures as accidental intrusions.

The hind foot is represented in specimen No. 1317 by two complete metatarsals, five portions of other metatarsals, one phalanx and half of another, all found in close association with each other and with other remains of the hind limb. Other phalangeal and metapodial remains were recovered in this and other specimens in undoubted association. They are shown in Fig. **6,** 10, 13. The element shown in Fig. **6,** 13, apparently belongs to a first digit. These elements need no verbal description.

The tibia is represented by one complete specimen (Fig. **6,** 9) and halves of several others. The complete specimen is bent into a sharp curve, which is probably due to preservation, though the specimen is quite perfect and shows no evidence of distortion. It is greatly expanded at either end, especially at the distal, where it is three and a half times as wide as the shaft. The fibula is positively represented by but a single distal half (Fig. **6,** 11). These bones are not preserved in life relations with other bones of the hind limbs, but the only question that could possibly be raised would be whether they are not pelvic rather than epipodial elements.

Ileum, ischium, and pubis are each represented in the University of Chicago collection by two or more specimens, always in close association with each other and with the sacral region of the vertebral column. The elements are somewhat disarranged, however, so that it is by no means certain which should be designated ileum, which ischium, and which pubis.

The elements of the pelvis were not suturally united, and there is no evidence of an acetabulum. It seems certain that in life there was a considerable strip of unossified cartilage between the parts of the pelvis. We thus have a condition quite similar to that of the mosasaurs, due no doubt to the same cause—the degeneracy of hind limbs. Two of the pelvic elements are quite heavy, while the third is thin.

There are three ilia in the University of Chicago collection, two belonging to specimen No. 1317 and one to specimen No. 221. The lower margin is semicircular, while the upper is formed by two convex lines whose inner ends meet in a median projection (Fig. **6,** 12). The upper margin becomes thin and somewhat knifelike, while the entire lower semicircular margin is quite thick and gives evidence of having been continued in cartilage. The lowest anterior surface, where it probably united with the pubis, is flattened or perhaps slightly convex for a short distance. The corresponding part of the pubis is similarly shaped.

The ischium has the appearance of a short, broad cutlass with dorsal margin concave and the ventral and posterior even more strongly convex. Its anterior end is but one-fourth the width of the posterior. Its ventral border shows likewise that it was continued in cartilage while the dorsal border was complete (Fig. **6,** 8).

The pubis is probably represented in specimens Nos. 1019 and 1317 by incomplete structures so badly crushed that their extents are not determinable. They are flat and thin, much thinner than ileum and pubis, and measure at least 2 cm. each way. More than this could not be made out.

III. THE FORM AND HABITS OF *Diplocaulus*

Reviewing briefly those structural features of *Diplocaulus* which are indicative of habits and form we find: (1) an unusually large head (Fig. 4), with posterior lateral horns which bring the center of gravity of the skull back to the level of the condyles in *D. limbatus* and nearly so far in *D. magnicornis;* (2) an unusually flat skull, a skull 37 cm. wide being in no place 3 cm. deep, and in most places 1 to 2 cm. in depth; (3) an absurdly short and stumpy trunk, and a flattened tail longer than head and trunk together; (4) low vertebrae, with very low neural spines; (5) very slight opportunity for muscular attachment on any part of the skeleton, indicating an almost unbelievable weakness so far as the commonly used muscles are concerned; (6) zygosphene articulations and interlocking neural arches in the presacral region, allowing only lateral movement in the trunk region; (7) unusually long, straight ribs, joined to the vertebrae by two widely separated heads; and (8) small limbs that would have been of no use for locomotion on land.

One purpose, at least, which the posterior lateral horns of the skull served is evident. Without them *Diplocaulus* would have found it an extremely difficult task to control the enormous portion of the head anterior to the condyles, even in an aqueous medium. Even if the head and vertebrae had been of considerable depth, as in other large-headed Stegocephalia, the task would have been difficult enough; but with the flattened head, the vertebrae almost devoid of neural spines or other structures giving advantage for muscular attachment, the task would have been well-nigh impossible, even in the water, without the heavy posterior lateral horns, which bring the center of gravity back to the level of the occipital condyles, or at least nearly so far.

Even though we grant, however, that this was the purpose of these horns, we have yet to explain why the head as a whole should have been so large, for even without them the head was still enormous, and since it contained so much bone, it must have been very unwieldy. It is hard to conceive of any mode of life in which such a head would have been anything more than a burden to be borne. It seems most probable that the growth of the head took place regardless of the welfare of the animal, as the result of some internal metabolic derangement, as suggested by Case. Indeed, all of the known Stegocephalia seem to have been in the same decadent condition that the dinosaurs were in the latter part of the Mesozoic.

That *Diplocaulus* was incapable of moving upon land seems certain. With its extremely slight development of trunk and appendicular muscles, as indicated by the smoothness of the bones and the absence of neural spines or other opportunities for muscular attachment, with its very heavy head, with its trunk just equal in length to the width of the skull, and with its poorly developed limbs and pelvis, *Diplocaulus* could not have been equal to the feat of lifting its head from the ground on land. Nor could it have lifted its snout, since the posterior horns, pressing against the ground, would have prevented this. Progress upon land by pushing the head before it would have been impossible. Only in an aqueous medium could it have moved at all, and, indeed, the long, flattened tail clearly indicates that such was its habitat, as do also the large rugose pectoral girdle, the great development of the lateral line system, the anterior and dorsal position of the eyes, and the incompletely ossified pelvis.

Contrary to what we should expect in an aquatic animal, however, the ribs were sturdy and had two well-developed heads. Aquatic life almost universally results in the weakening of the ribs in every way, especially in that they tend to become single-headed. So far as the author is aware, *Diplocaulus* is the only example, except some ichthyosaurs, of an aquatic animal with double-headed ribs.

It seems probable, however, that the usual condition in aquatic animals is due, not to adaptation, but to that law of nature which permits no animal to keep a structure that it had no need for. In a dense medium the control of the ribs is a much easier task, and an aquatic animal usually has no need for two heads. But if *Diplocaulus* was flat, as it must have been (page 30), the double-headed ribs would have become a necessity in order to counteract the weakening effect of the flattening process. An animal with the flatness of *Diplocaulus*, without strong ribs, would be like a floor without joists.

The problem of the form of the body which clothed this remarkable skeleton has called forth about as many theories as there have been investigators. The following facts seem significant as indicating the shape of the body:

1. The vertebrae exhibit zygosphene articulations and interlocking neural arches, thus inhibiting dorsoventral motion.
2. The neural spines are very low and smooth.
3. The ribs are unusually long and are borne upon long processes upon the vertebrae. They are straight and with two heads, one directly above the other and separated from each other by a considerable distance, which would have made them rigid so far as up-and-down motion was concerned. Their great length, likewise, would have made lateral motion of the trunk impossible; hence the trunk must have been rigid.
4. The clavicular girdle was at least nearly flat.
5. The head was unusually wide and flat.
6. The position of the orbits was such that the animal could see only directly above itself.

All the structural features of *Diplocaulus* are such as we should expect to find in an animal whose body was unusually flat, like that of the modern rays or skates (Batoidea). Its ribs and interlocking vertebrae would give just the rigidity necessary for so very wide and flat a body. Perhaps the animal depended for locomotion entirely upon its long, slender tail, but it seems more probable that the animal moved for the most part by flapping up and down the lateral portions of the body, beyond the extremities of the ribs. The very heavy head, with its dense bones, would seem to indicate that *Diplocaulus* lay at the bottom when not active. No doubt it was able to crawl over the bottom somewhat by means of its small limbs, perhaps assisted also by the lateral portions of the body. By a comparison with the rays, it will be seen that the head and tail, especially of the *sting ray*, are almost exactly similar to those of *Diplocaulus;* and the wide, flat body of both is just such as the form and length of the ribs of *Diplocaulus* would serve to indicate as to its form. The hind legs probably extended posteriorly and laterally, as do the fins of these rays. The front limbs, if the trunk was wide anteriorly, must have been entirely ventral; but the anterior end of the trunk may have been no wider than the clavicular girdle and anterior ribs. The legs were probably of use in helping to crawl over the bottom and in turning. The eyes, as has been mentioned, looked directly upward, as in soles and skates.

Such a conception of the form of *Diplocaulus* is most in accord with the general unfitness of the bones for muscular attachment. In such an animal, with rigid head and trunk, the active muscles would have been those of the lateral trunk region, which would not have been attached to any bones, but to fascia and to each other. It seems impossible that *Diplocaulus* could have moved about at all with the ordinarily used trunk muscles, considering how slight the development of these must have been.

The teeth of *Diplocaulus* indicate a soft animal or vegetable diet. Delicate, small, conical in form, and rather few, they could not have been of service in crushing shellfish, nor could they have been of service in taking active prey from the water. To this last source of food the entire make-up of the animal seems ill adapted. *Diplocaulus* was apparently not adapted to any method of making a living, but it seems to have been least poorly adapted to a soft animal or vegetable diet, such as are most of the rays. The writer is of the opinion that it was a bottom feeder, possibly plowing through the soft mud of pools and streams in search of annelids and other soft-bodied animals. The large proportion of bone in the skull of *Diplocaulus*, moreover, would have caused it to sink to the bottom when at rest, a circumstance that seems to suggest that it was a bottom feeder.

We have no knowledge of gills in any adult stegocephalian; but gills in the adult of any thoroughly aquatic stegocephalian would seem even more probable than in a modern urodele. If *Diplocaulus* was aquatic and a bottom feeder, it would seem very probable that it was so provided. In a flat-bodied animal crawling over the bottom external gills would suffer greatly from abrasion; and, whether or not it searched for its food in the soft mud, it would find respiration very difficult. In *Diplocaulus*, however, the downward-projecting quadratojugals, extending halfway along the lateral horns (Plate II), would act in a very serviceable manner to prevent abrasion and to provide a chamber just large enough for the gills. It is even better adapted than this; for the quadratojugal projects medioventrally so as to inclose a cavity, open only on the median side, which would serve admirably as a chamber into which gills might fit and so be protected on three sides and have always a chamber of water about them. This use has been suggested by Williston and others.

Aside from these points there is some doubt as to the further faunal relations of *Diplocaulus*. It has been asserted frequently, and is perhaps generally held, that the remains of *Diplocaulus* are found associated with those of the shark *Pleuracanthus* (*Diplodus*). The writer's brief experience in the field, however, has failed to show any significant association. True, they are found together in various bone beds, as at Orlando, Oklahoma, and Danville, Illinois; but the fragmentary condition of the material at these places and the mixture with a host of other forms would suggest that these beds represent dumping-grounds—probably deltas—which indicate nothing as to the associations in life of the animals found in them. In those places where the writer has observed remains of *Diplocaulus* in such a condition as would seem to show that the animals were preserved undisturbed where they had lived, *Pleuracanthus* is conspicuously absent; and likewise, where *Pleuracanthus* occurs, *Diplocaulus* is not found, except in beds of mixed fragments of all sorts. For instance, over the region of Briar Creek and Godwin Creek valleys, east of Seymour, Texas, one may expect to find teeth of *Pleuracanthus* everywhere, but little if any remains of *Diplocaulus*. From Pony Creek and westward, on the other hand, many good specimens of *Diplocaulus* have been taken, perhaps more than half of the specimens ever found, but I do not know that *Pleuracanthus* has ever been found here.

In one place not over 6 meters square, in Pony Creek valley north of Seymour, Mr. Miller and others have found at least ten skulls or skeletons of *Diplocaulus* and fragments of perhaps a hundred other specimens, but no trace of other animals except one skull of *Trimerorhachis*. A quite similar deposit was found last summer by Mr. Miller several miles west of this locality. It seems from the condition of the remains that the animals were preserved undisturbed in the place where they lived, a shallow pool, most likely inland, which in this case filled up so rapidly that the remains did not have time to become scattered. *Diplocaulus* probably lived in just such inland pools, probably also in streams, for the most part on the bottom, but it was capable also of swimming through the water.

IV. THE SPECIES OF *Diplocaulus;* THE POSITION OF THE GENUS

Cope designated three species of *Diplocaulus: D. salamandroides* (1877), *D. magnicornis* (1882), and *D. limbatus* (1896). The first of these was based upon a few vertebrae and a portion of a lower jaw, now in the collection of the University of Chicago. Case doubted the validity of this species, but retained it because the centra are round on the lower surface instead of flat, and because of the distinctly smaller size and lack of knowledge of intermediate sizes. Specimens of *D. magnicornis* of the University of Chicago collection show, however, that the anterior and posterior presacral vertebrae have the centra rounded beneath, when not flattened in preservation; and the vertebrae from the middle of the presacral region are not greatly flattened. The difference in size, moreover, between the vertebrae referred to the two species is bridged over completely by specimens of the University of Chicago collection, there being no gap of as much as one millimeter in any measurement. There is still one character, however, upon which *D. salamandroides* seems entitled to recognition as a separate species. None of the vertebrae referred to this species in the University of Chicago collection has a centrum more than three-eighths as wide as long at the widest part. In *D. magnicornis* and *D. limbatus*, on the other hand, many of the vertebrae are wider than long, and none are over twice as long as wide. On this ground *D. salamandroides* seems entitled to provisional recognition.

D. magnicornis and *D. limbatus* can be distinguished from each other only by the posterior lateral horns of the skull. The other characters indicated by Case fail to hold true for specimens of the University of Chicago collection, as has already been shown. Even this character is one upon which it is not always possible to identify positively a given skull. There seems no reason, however, for questioning the distinctness of these types.

Broili (1904) has designated two other species, namely, *D. copei* and *D. pusillus.* At the time these were proposed *D. limbatus* was known only by an unsatisfactory, largely erroneous verbal description. The descriptions since made by Case for *D. limbatus* show, however, that there is not a single point in which the two are different. *D. copei* should be dropped, therefore, as a synonym. The distinctness of *D. pusillus* cannot be questioned; the only question is as to the propriety of placing it in the genus.

The collection of the University of Chicago shows a wide range of variation. Were the different types of lateral horns accepted as valid specific characters, it would be necessary to make a separate species for nearly every skull in the collection. There are also pronounced differences as to the angle at which these horns are joined to the rest of the skull. Fig. 7 shows the more important of these types, as also those figured by other investigators. In these figures peculiarities which have the appearance of being due to distortion are either omitted or corrected.

Other differences were observed, such as the posterior extent of the palatine, the shape of the postparietal, the shape and position of the dorsal process of the clavicle, the form of the atlas, the flatness of the centrum, and other characters. Unfortunately, however, there is not enough material of any one of these structures to judge of their constancy, association, etc.

That some of the differences here presented are of specific rank seems probable. There is probably significance also in the fact that certain types are found several together and well preserved and not mixed with other remains, as if they had lived several together in small sheltered pools; and others have never been found except singly, as if they had lived more in open waters or streams. I cannot agree, however, that separation into species would be more than guesswork, unless the investigator had before him much more material than even the University of Chicago collection affords, in order to determine the association of these characters with each other and their stability. Such guessing not only contributes nothing to the advancement of science, but does harm by burdening the literature with a lot of meaningless names. It has been shown

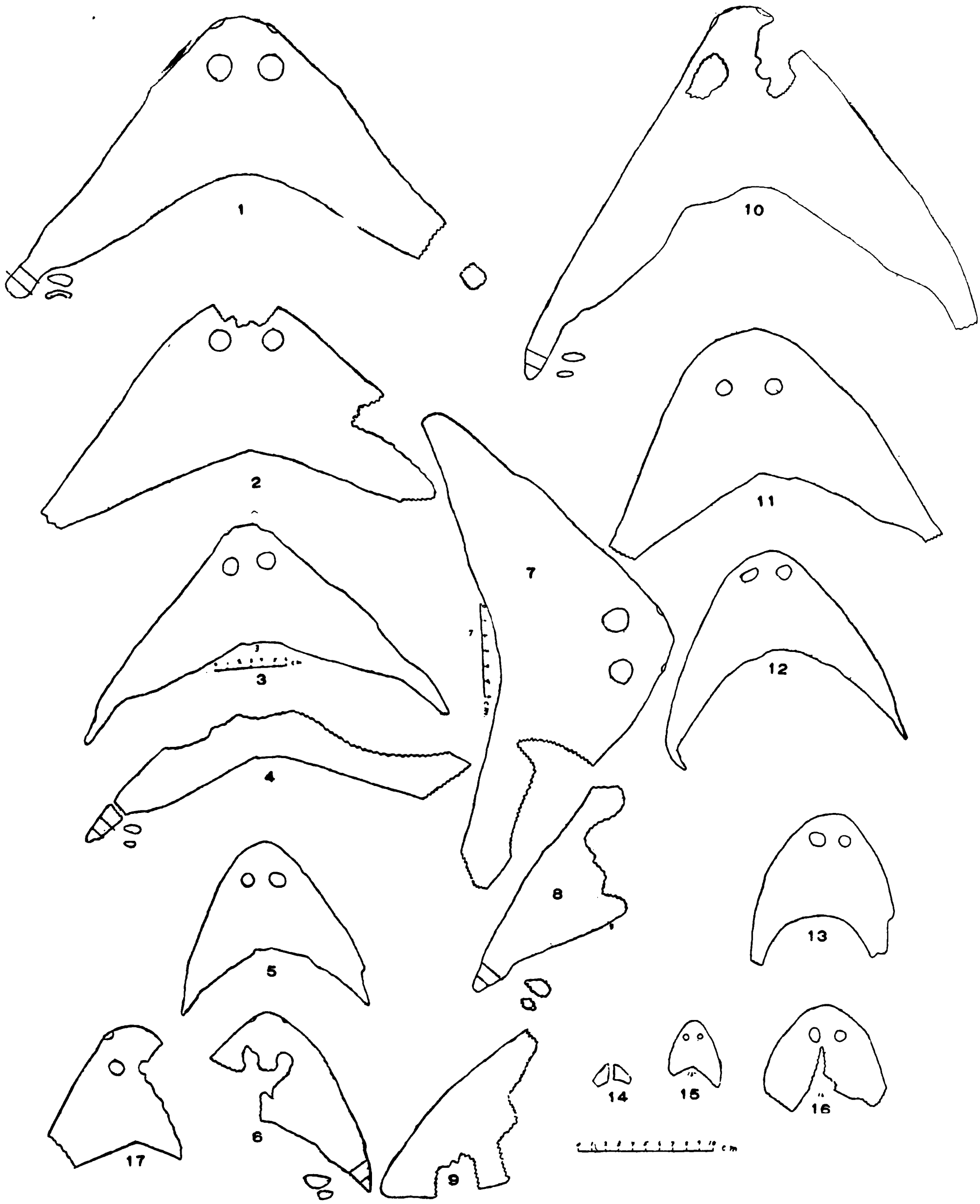

FIG. 7.—Variations in the form of the skull of *Diplocaulus*. All except Figs. 3, 7, and 12 drawn to same scale. Fig. 26, after Case, No. 4467 American Museum. Fig. 13, after Case. Figures 10, 11, 12, *D. limbatus;* Fig. 13, *D. limbatus* (*Copei*). All other, *D. magnicornis*.

in this paper that most of the characters supposed to distinguish the different species of *Diplocaulus* that have been proposed do not hold true. In all departments of biology we are hampered by poorly defined species, based often upon a single specimen or a fragment of one, which too often are the result of the personal ambition of the investigator rather than a desire to increase our scientific knowledge. The question of the number of species in a genus—even well-defined species—is utterly unimportant as compared with the other problems of biology. Especially is this true in the field of vertebrate paleontology. In this field morphology, phylogeny, and ecology are vastly more important, and the making of a lot of unrecognizable species only serves to draw attention from the really important problems. When we have secured enough material to make such efforts more than guesswork, we can take up the question of determining species. The materials at hand are here treated as representing the three species (or four) above mentioned.

In addition to those characters which mark *Diplocaulus* as one of the most bizarre tetrapods that ever lived, such as its flatness, the development of the posterior lateral horns, the small size of the limbs, and the very long, slender tail, there are other characters equally significant which show that *Diplocaulus* was a highly specialized animal, with no very close kinship to the other known Stegocephalia. These other characters, briefly, are as follows:

1. There was a single, unpaired frontal bone, which helped to form the orbits.

2. The nasal, supratemporal, and transverse bones were absent.

3. The ribs had two heads, which attached to long processes from the middle of the centrum.

4. The vertebrae had well-developed zygosphene and zygantrum articulations and interlocking neural arches (true also of *Urocordylus* and *Crossotelos*).

5. There was no coronoid, or at least only one small one.

6. The eyes were small, dorsal in position, and apparently degenerate.

7. The teeth were small and somewhat degenerate.

8. The pineal foramen was quite small.

9. The postparietals and possibly parietals were asymmetrical.

10. The pterygoids reached forward only to the palatines.

11. The feet were very small and poorly developed.

On the other hand, the presence of the basioccipital, which has not been shown before in any holospondylous amphibian, and of the epipterygoid, which has not been recognized in any amphibian, are decidedly primitive characters. The large size of the post-splenial and splenial are likewise primitive characters. It is evident, however, from this review that *Diplocaulus* had departed widely from the stock of ancestral Tetrapoda, in the way both of specialization and of degeneracy. Its occurrence in the very base of the Permian, perhaps in the Upper Carboniferous, is another proof of the generally accepted view that they had their origin much farther back than we have any remains of them preserved, and that all of the Amphibia that we know were decadent. The presence of the basioccipital and epipterygoid is unusual; but when we consider, however, that only a few years ago we believed that the Temnospondyli did not have several of the cartilage bones since shown to be present, the facts lose much of their remarkableness. These primitive characters would seem to indicate that the phylum which includes *Diplocaulus* separated very early from the other holospondylous lines, or else had a separate origin from the Temnospondyli.

Watson has given us recently an interesting description of a carboniferous amphibian, *Batrachiderpeton lineatum*. His account of the skull is quite complete and bears all the marks of being thoroughly reliable. He recognized a close similarity to *Diplocaulus*, which he interpreted as proving genetic kinship. With this conclusion I am fully in agreement. The following discussion is in the writer's own words, but most of the facts have been pointed out already by Watson.

The close kinship of *Batrachiderpeton* and *Diplocaulus* is proved by the following similarities:

1. The general shape of the skull and clavicular girdle is quite similar.

2. The general arrangement of elements on the dorsal side of the skull is practically the same. The differences are such as we should expect between ancestor and descendant.

3. The nasals are quite small in *Batrachiderpeton* and absent in *Diplocaulus*.

4. The mandibular condyle shows the same double nature in both.

5. The dentition shows similarities (discussed later).

6. The postorbital is almost excluded from the orbit in *Batrachiderpeton*, entirely so in *Diplocaulus*.

Of structural differences between *Diplocaulus* and *Batrachiderpeton*, they are of two sorts: primitive characters of *Batrachiderpeton*, which we should expect in an ancestor of *Diplocaulus*, and those characters which show that *Batrachiderpeton* had diverged from the direct ancestral line.

The characters of *Batrachiderpeton* which we should expect to find in an ancestor of *Diplocaulus* are as follows:

1. Small nasal bones are present.
2. The frontal is paired.
3. The frontal is excluded from the orbits.
4. The orbits are not dorsal, but lateral.
5. The posterior lateral horns of the skull are smaller.
6. The quadratojugal is small, lying almost entirely anterior to the quadrate.
7. The otic notch is intermediate in position between that of *Diplocaulus* and the normal position in the Stegocephalia.
8. The pterygoids were large (discussed below).
9. The postorbital is not quite excluded from the orbit (discussed below).

Of specialized characters excluding *Batrachiderpeton* from the direct ancestral line I can see but one—the matter of dental distribution. Watson's drawing shows but two teeth on each vomer (prevomer), and these occur in a different position from the eleven of *Diplocaulus*. The teeth on maxilla, premaxilla, and palatine are also much fewer. The pterygoid teeth, on the other hand, are absent in *Diplocaulus*.

The writer agrees fully with Watson that the type of pterygoid found in *Batrachiderpeton* which is typically reptilian is of the primitive tetrapod type, and that the amphibian type with the open space between the pterygoids is derived from this by reduction of these elements. If the amphibian palate be primitive, the open region between the pterygoids is the only part of the original skull or mandible covered by ectoderm which was not ensheathed by membrane bone. The entire dorsal, lateral, posterior, and anterior parts were so ensheathed, as was the mandible, except for Meckel's groove, where there was no ectoderm in contact. The roof of the mouth, which was lined by stomodeal ectoderm, we should certainly expect to act in the same way, and it cannot be denied that it did, over the rest of the roof of the mouth. The same dermal scales covered this region, and it would be contrary to the principles of homology for the scales in this region not to develop as they did elsewhere.

The writer agrees also with Watson that the element that has been designated as supratemporal is really the postorbital, dragged out of the orbit by the development of the posterior lateral horns of the skull. The clearly intermediate condition of *Batrachiderpeton*, in which the element is all but dragged out of the orbit, proves this beyond a reasonable doubt.

The mandible of *Batrachiderpeton* as described by Watson differs greatly from that of *Diplocaulus*. Since there can be no question that the mandible of *Diplocaulus* is quite primitive, and since the structure here presented is proved to be correct by several perfect specimens, the writer is of the opinion that a more thorough study of the mandible of *Batrachiderpeton*, with better material, will show that it is similar to *Diplocaulus*, except that there will be found, probably, a long coronoid or several small ones. The inner rows of teeth described by Watson for *Batrachiderpeton* were probably borne upon this element.

The question of the position of *Diplocaulus* has been discussed by Williston, Broili, Jaeckel, Case, Moodie, and Watson. It is probably universally agreed that they are more nearly related to the Microsauria than to any other order. Moodie, however, gave them the rank of a distinct order, the Diplocaulia, because of the presence of zygosphene and zygantrum, and because the ribs were attached to the middle of the centrum by two heads. Unfortunately we have not enough authentic information about the skulls of the Microsauria to permit of judgment as to the importance of the differences, or even to determine what are valid differences.

The writer's conviction is that *Diplocaulus* will be shown to be ordinally distinct from the Microsauria by still other characters than the vertebrae. With *Diplocaulus* should go *Batrachiderpeton*, *Ceraterpeton*, and *Diceratosaurus*. Personally, however, I am opposed to establishing new groups without a full knowledge of their characters. It seems better to leave *Diplocaulus* and its relatives with the Microsauria until the other Microsauria have been made more fully known.

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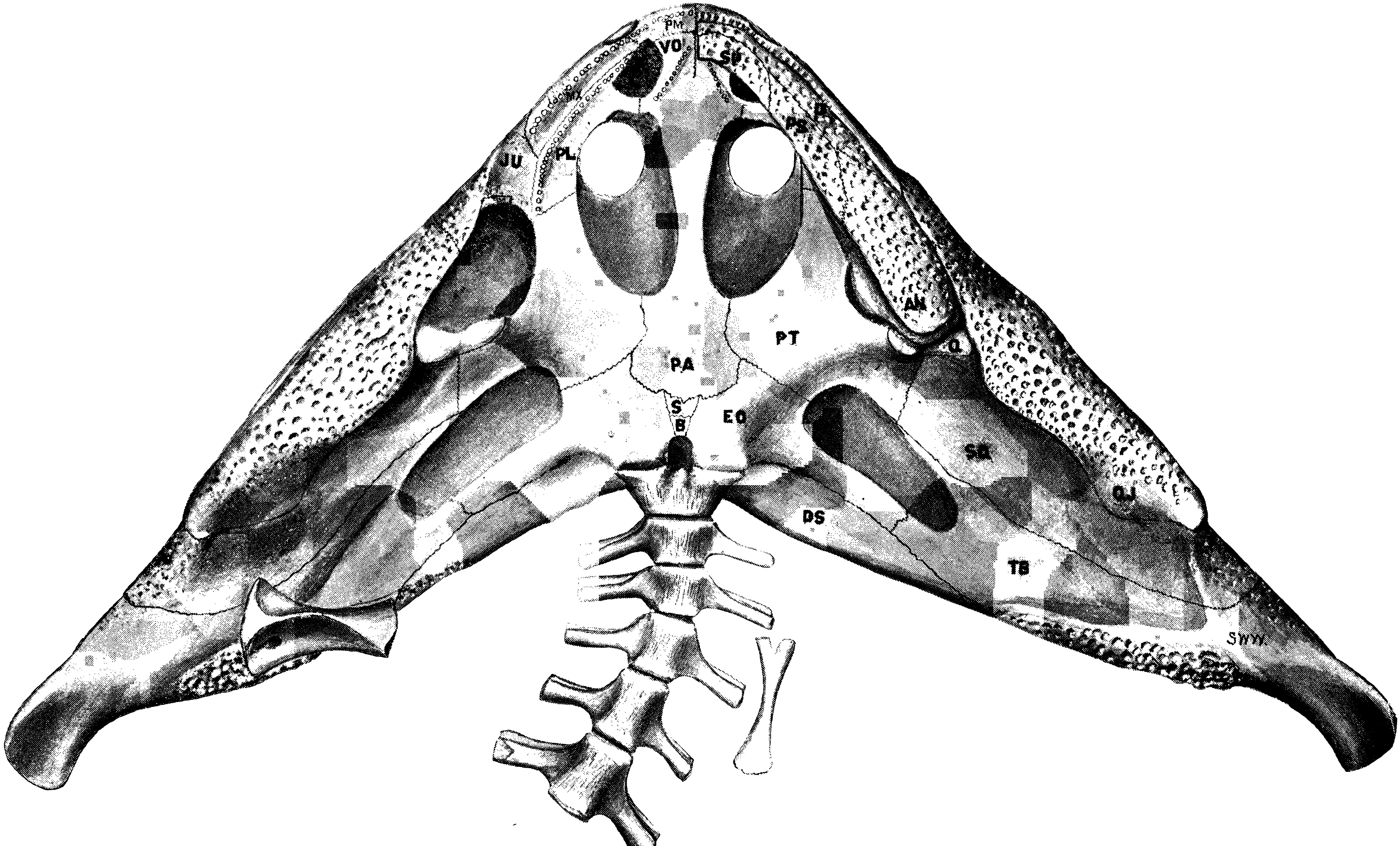
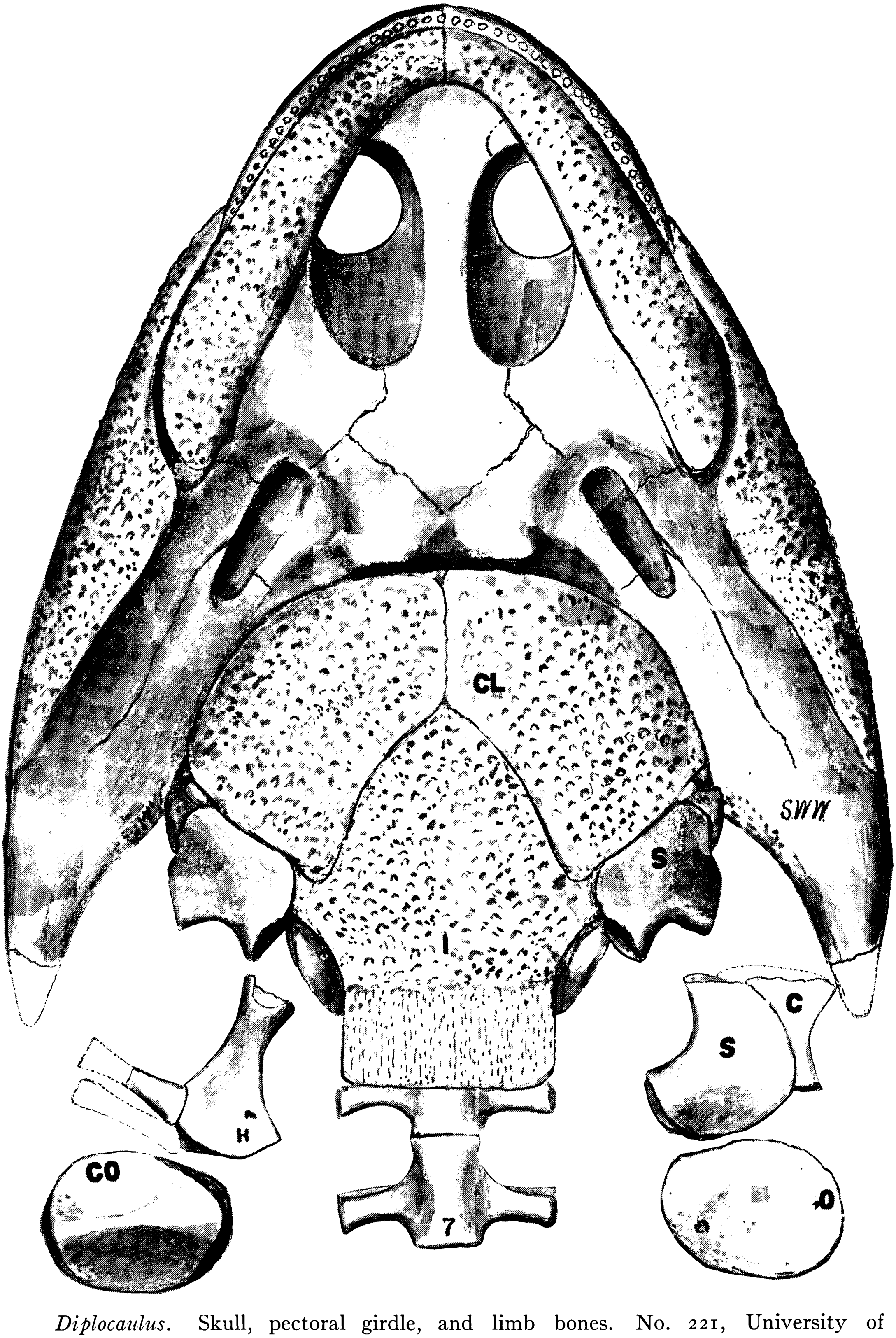


Diplocaulus magnicornis ventral view (after Williston, 1909, with modifications and additions). *An*, angular; *B*, basioccipital; *D*, dentary; *Eo*, exoccipital; *Ju*, jugal; *Mx*, maxilla; *Pa*, parasphenoid; *Pl*, palatine; *Pm*, premaxilla; *Ds*, dermosupraoccipital; *Ps*, postsplenial; *Pt*, pterygoid; *Qj*, quadratojugal; *Qu*, quadrate; *S*, sphenethmoid; *Sp*, splenial; *Sq*, squamosal; *Tb*, tabular.



Diplocaulus. Skull, pectoral girdle, and limb bones. No. 221, University of Chicago, seven-eleventh natural size, from below. *Cl*, clavicle; *S*, scapula; *C*, cleithru; *I*, interclavicle; *H*, humerus; *Co*, coracoid. (Drawing by S. W. Williston.)

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