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[PLATES 14–16.]

RESEARCHES

ON THE

STRUCTURE, ORGANIZATION, AND CLASSIFICATION

OF THE

FOSSIL REPTILIA.

I.—ON PROTOROSAURUS SPENERI (VON MEYER).

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IX. *Researches on the Structure, Organization, and Classification of the Fossil Reptilia.**—I. *On* Protorosaurus Speneri (von Meyer).

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[Plates 14–16.]

Protorosaurus Speneri, one of the earliest known fossil reptiles, has been already studied and described by Baron Cuvier, Hermann von Meyer, Sir Richard Owen, and Professor Huxley. Occurring in the Kupferschiefer, and therefore of Primary age, the exact determination of its structure and affinities has become of some interest in relation to the great development of Reptilian life which characterises the succeeding Triassic period.

The most interesting example of *Protorosaurus* is that originally obtained by Spener, which he described and figured in 1710, and regarded as the remains of a Crocodile.† His view was confirmed by Link. But Kundmann of Breslau in 1737 interpreted the remains as those of a new type of large-headed fossil-lizard. This conclusion was substantially adopted by Cuvier, who in 1808 made the animal universally known as the fossil Monitor of Thuringia.‡ Cuvier had never seen a specimen; and was dependent upon the figures published by Spener, Link, and Swedenborg, and a drawing, which he published, of a specimen preserved in the Royal Museum at Berlin. He remarks that the head is not without resemblance to that of the Nilotic Crocodile, and, as Spener only knew drawings of the exterior of

* Some time ago the Royal Society did me the honour to place at my disposal grants from the Government Grant Fund, for the investigation of the Fossil Reptilia. They enabled me to make studies and preliminary descriptions of a large mass of materials in Continental and English collections. Some of these, which were chiefly of geological interest, were laid before the Geological Society. Others needed further work before they could be used to elucidate the structure, organization, and classification of the Fossil Reptilia. The general results to which the researches have led are necessarily connected with the detailed evidence on which they rest; and I now propose to submit to the Roal Society any account of such genera and ordinal groups as fall within this field of work, as well as discussions of the distinctive osteological organization which some orders have in common, before summarising the classification.

† 'Miscellanea Berolinensia,' Berolini, 1710, T. 1, p. 99. "Disquisitio de Crocodilo in Lapide, &c.," figs. 24, 25.

‡ 'Annales du Muséum,' T. 12, p. 79, Plate 10.

the Crocodile, his identification was excusable. CUVIER goes on to argue that the number of teeth in the lower jaw of a Crocodile is at fewest fifteen, while in the upper jaw there would be seventeen or eighteen extending back to the middle of the orbit, whereas the fossil has only eleven teeth, which reach back to the anterior angle of the orbit. On this evidence the skull is interpreted as that of a Lacertilian, allied to the Monitor. The author goes on to show that other parts of the skeleton confirm the inference from the skull. Thus the hind limb has five digits, with the number of phalanges in them successively 2, 3, 4, 5, 3, which agrees with the Monitor. The correspondence extends to the larger bones of the extremities. CUVIER only detected two differences of specific value: first, the spinous processes of the dorsal vertebræ are much more elevated than in Monitors; and secondly, the foreleg is relatively longer in proportion to the femur and the foot. It is unnecessary to offer any detailed discussion of this interpretation, for the figure now given, when compared with SPENER's figure, shows that CUVIER had not the evidence fairly before him.

VON MEYER also studied the published figures, and came to the conclusion that the fossil was neither a Crocodile nor a Monitor; but that it was an extinct type which differed by remarkable modifications and peculiarities from the Saurian group. In consequence he founded the genus *Protorosaurus* in 1830, and described the species as *Protorosaurus Speneri* in 1832.* CUVIER's influence, however, continued to govern the views held as to the affinities of this animal, although VON MEYER's name was adopted in OWEN's 'Odontography.' Eventually VON MEYER, finding in various museums twenty-one specimens which appeared to him referable to *Protorosaurus*, made these fossils the subject of an elaborate monograph with nine folio plates, published in 1856.† Nearly all these specimens were studied and measured by the author. But unfortunately the type, which passed into the collection of JOHN HUNTER, was unknown to him, and he reproduces in outline SPENER's unsatisfactory figure of 1710. Yet such was VON MEYER's confidence in the figure that he supposes the soft parts about the mouth to be preserved. Nothing of value, therefore, is contributed to knowledge of the skull. The whole of the specimens are referred with some doubt to one species; and a detailed anatomical description is given of the several regions of the skeleton. The neck is suggestive of the vertebræ of Ornithosaurs and of the Giraffe, but is not compared with that of a Bird because the number of cervical vertebræ recalls that of the Crocodile. The dorsal vertebræ are more numerous than those of the Crocodile, but their shape differs from that seen in all living Saurians [as then known]. The ribs on the whole were Lacertilian. The absence of lumbar vertebræ was regarded as conclusive against affinities with Monitors. The sacral vertebræ in the several examples are considered to number two, three, or four. The tail vertebræ are distinctive in having the neural spine divided. In the shoulder-girdle some resemblances are seen to Archægosaurus. No important

* 'Palæologica,' 1832, pp. 109, 208.

† 'Fauna der Vorwelt,' "Saurier aus dem Kupferschiefer der Zechstein-Formation."

conclusions are drawn from the larger bones of the limbs. And the hand and foot both show Lacertilian characters. There is no dermal skeleton. This description is the basis of most accounts of the animal which have been published. I find no difference from VON MEYER possible except perhaps as to the reference of the remains to one species, and as to the absence of a dermal skeleton.

Sir RICHARD OWEN first noticed *Protorosaurus Speneri* in his 'Odontography,'* and subsequently, in his 'Catalogue of the Fossil Reptiles and Fishes in the Royal College of Surgeons' (1854, p. 80), mentions that the specimen there preserved is SPENER'S type, which passed into the collection of Dr. JOHN WOODWARD, and was purchased by JOHN HUNTER at the sale of Humphrey's Museum.† In Sir RICHARD OWEN'S 'Palæontology'‡ it is stated that the head equals one-third the length of the neck and trunk, and resembles in shape a long, slender, obtusely-pointed cone. It has strong straight jaws, armed with sub-slender, sub-equal, straight, conical, sharp-pointed teeth; about eighteen on each side of the upper, and sixteen on each side of the lower jaw, implanted in a single close-set series of sockets. After describing the remainder of the skeleton, it is remarked: "Of existing Reptiles the largest carnivorous Varanian Monitors (*e.g.*, *Varanus*, *Hydrosaurus*) offer most resemblance to the *Protorosaurus*, which had evidently the same powers of progression, as well on land as in the water. But this oldest known Lizard presented a more powerful and complex framework. The neck is longer and stronger, the vertebræ rivalling in proportion those of Pterodactyles; the head is relatively larger and with more firmly fixed teeth; the dorsal spines are loftier and larger than in modern Monitors; the larger sacrum accords with the relatively larger and stronger hind limbs. The more numerous diverging processes for the attachment of the tail muscles bespeak the more vigorous actions of that part. All the vertebral bodies have sub-concave articular ends, and it may be concluded from the length and strength of the tail, from the peculiar provision for muscular attachments in that part, and from the proportions of the hind limbs that the *Protorosaurus* was of aquatic habits, and that the strength of its neck and head, and the sharpness of its teeth, enabled it to seize and overcome the struggles of the active fishes of the waters which deposited the old Thuringian copper slates." This animal was referred provisionally, and with doubt, to the order Thecodontia. But some evidence has since been adduced by Professor HUXLEY to show that *Thecodontosaurus* and *Palæosaurus* may be classed with Dinosaurs; so that, if the Thecodontia should be sustained as a group distinct from the Parasuchia, which appears to be synonymous, the suggested affinities would indicate that *Protorosaurus*, although written of as a Lizard, was regarded as approximating to Dinosaurs and their Crocodilian allies. I find myself, however, differing from Sir RICHARD OWEN as to the condition of the teeth, for I can detect no conclusive

* Vol. 1, p. 269.

† 'Descrip. Cat. Fossil Rept. and Pisces,' 1854, p. 80.

‡ P. 280, 2nd ed., 1861.

evidence that any were contained in sockets. And, if so, the evidence disappears which would refer the animal to the Thecodontia. The other characteristics mentioned are essentially a summary of the views of CUVIER and VON MEYER, unsupported by new evidence.

Professor HUXLEY discussed this animal in his 'Anatomy of Vertebrated Animals,'* classing it with Lizards, in a position intermediate between the fossil group Homœosauria and the Platynota, which comprises the Old World Monitors. VON MEYER's suggestion that it is the type of a new group is adopted, and the group is named Protorosauria. The skull is said to be of moderate size, preserved in one specimen only; and in that it is in such an imperfect condition that the details of its structure cannot be made out. The teeth, however, are nearly straight, conical, and sharply pointed, and seem to have been implanted in distinct sockets, though there may be some doubt on this point. The tail is long and slender, and the limbs well developed, as in the existing Monitors. In the abdominal region numerous short and filiform bones appear to represent and correspond with the abdominal ribs of Plesiosauria and Crocodilia. Beyond the middle of the tail the spinous processes bifurcate, so that each vertebra seems to have two spinous processes, a peculiarity unknown in other Lacertilia. The large chevron bones are articulated between the bodies of the caudal vertebræ, as in Crocodilia, but also as in some Lacertilia, such as the *Geckos*. In the pes the number of phalanges is characteristically Lacertilian, and so is the form of the metatarsals. The tarsal structure is compared with that of the *Geckos*. I find the skull crushed and badly preserved, but perfectly intelligible.

A specimen from Durham, described by Messrs. HANCOCK AND HOWSE, adds nothing to the scientific history of the type, beyond its presence in a British Permian deposit.

In these several studies there are substantially only two interpretations of *Protorosaurus;* first, CUVIER and HUXLEY class it unreservedly with Lizards; secondly, VON MEYER and OWEN refer it to a new Reptilian type. VON MEYER affirmed that it is neither Lizard nor Crocodile; but saw in it resemblances to those animals, as well as to *Archægosaurus* and Pterodactyles. The difficulty in harmonising these different views has been partly in want of knowledge of the skull.

Professor CHARLES STEWART, Conservator of the College of Surgeons Museum, having recently rearranged the Reptilia, and placed SPENER's fossil in an accessible position, I have been able to make some notice of its structure. And I have to thank the President and Council of the College for permission to obtain drawings of the remains; and to thank Professor STEWART and Dr. GARSON for facilities afforded me in making the following description of the type of *Protorosaurus Speneri*.

* P. 226, 1871.

Part II.

The Specimen in the Museum of the Royal College of Surgeons.

As figured by Spener, the skull is represented as having a blunt conical snout, which overlaps parts of some vertebræ, so as to terminate at the junction of the centrum and neural arch. The extremity of the jaw for a length of 12 or 13 millims. has been destroyed since that figure was drawn (Plate 14), so that, though the skull, as preserved, is 7 centims. long, it may originally have been $1\frac{1}{2}$ centims. longer. This destruction of the anterior end of the jaw makes it impossible to determine whether the anterior nares occupied a terminal position as in Crocodiles, or whether they are to be sought in the small ant-orbital vacuities, which we shall find situate, like the nares, in *Ichthyosaurus*. This uncertainty affects the interpretation of the bone which carries the teeth. It may be either pre-maxillary or maxillary; but can only be maxillary on the hypothesis that the pre-maxillary bones are lost. But Spener's figure gives no indication of the nares having been terminal, and so far is evidence against that condition; and the position of the nares must be inferred from their condition in the animal types to which the fossil may prove to approximate.

The skull is crushed and flattened obliquely, so as to display its left side, together with the roof bones of the head. It is displaced from connection with the vertebral column, and its hinder lateral region is covered up by the anterior cervical vertebræ, which obliterate the bones which would demonstrate the affinities of the animal.

The cranial bones are all remarkably dense and thin, in harmony with the large medullary cavities and thin walls of the limb bones; and this osseous condition approximates to that which characterises the bones of Ornithosaurs and Birds. Some approach to this condition is seen in the limb bones of Lacertilia, and in Crocodilia and Dinosauria, though some American fossils referred to the Dinosauria, such as *Megadactylus polyzelus* (Hitchcock),* have the walls of the limb bones thinner. The solid character of the articular ends of bones in *Protorosaurus*, however, would indicate a method of ossification by conical terminal epiphyses descending into the shaft, like that which characterises the Batrachia, Plesiosauria, and certain Chelonia; so that the evidence of affinities must be fully stated before any conclusions can be based upon the thinness of the cranial bones.

The brain-cavity.—The region of the brain is seen to be very narrow from side to side posteriorly towards the occiput, and to widen transversely as it extends forward towards the orbits. Portions of the parietal and frontal bones are lost, and their removal shows that the cerebral hemispheres were well developed. They are convex in length, broad, defined anteriorly by a groove in the matrix, and rounded anteriorly as though the brain case were closed anteriorly by bone. The lateral compression of the

* Cope, 'Trans. Am. Phil. Soc.,' vol. xiv., Plate 13, p. 122A.

part of the parietal region which is posterior to the cerebral hemispheres shows, I believe, that the cerebellum was relatively narrow and thrust downward in the way seen in Birds, Ornithosaurs, and Dinosaurs. The length of the cerebral region is about 15 millims., so that the head would be $5\frac{2}{3}$ times as long as the brain. The cerebrum may occupy 11 to 12 millims. in length; its width is less evident, but appears to have been about 7 millims. The hemispheres were high, and flattened at the sides, so that on the whole, in so far as the brain differed from that of an Ornithosaurian, it appears to have approximated to that of a Dinosaur. There appears to be a small parietal foramen placed far back, and in advance of it there is a slight oblong inflation of the cast of the cerebral cavity. I describe in succession the median roof bones of the head.

Supra-occipital.—The supra-occipital region of the skull is imperfectly exposed, since only the portion is seen which lies above the occipital foramen. It looks obliquely upward and backward. It is defined anteriorly by the occipital crest. This crest is in two lateral portions, which meet mesially at about a right angle, and diverge outward and backward. The posterior surface of the bone is divided into two shallow, lateral, concave areas by a slight sharp median inclined ridge.

The parietal bones.—The parietal region is greatly compressed from side to side in its hinder part, so as to rise into a short sharp parietal crest (now broken away), which made the sides of the bone concave from the occipital crest forward. The length of this compressed area is only a few millims. On it the small ovate parietal foramen appears to be placed. In front the bone is lost, but I think the horizontally flattened state of the frontal bone anteriorly, and the comparatively flattened state of the mould of the cerebral hemispheres, together with the thinness of the bones, justifies a belief that the parietal bones became flattened superiorly as they widened and extended forward, and that the parietal crest was moderately elevated. There were two parietal bones, and the median longitudinal suture between them is seen as an elevated line on the mould beneath, where the bones are lost. The transverse suture between the parietal and frontal bones is at a distance of about 12 millims. in advance of the median angle of the occipital crest. This suture has a transverse saw-like edge, and admits the median extremity of the parietal bones to extend slightly forward between the hinder margin of the frontal bones.

The frontal bones.—The frontal bones are double, being united by a median suture. They exhibit an oblong surface, which was flattened horizontally. Their anterior extremities extend forward between the nasal bones in a V-shape, while the lateral parts of this suture diverge forward and outward. Posteriorly, the outer corner of the bone on one side is notched out by what appears to be the temporal foss, and, although the temporal arcade is not preserved, it may have extended backward from the narrow post-frontal process external to the notch in the manner seen in Ornithosaurs, Dinosaurs, Nothosaurs, or Anomodonts. The lateral borders of the frontal bones are concave, 15 millims. long, and are superior margins of the orbits. They are slightly

raised and transversely roughened. The least transverse measurement across the frontal bones at the middle of the orbital concavity was 11 millims. In the median line, behind the middle of the orbits, the frontal bones form a slight longitudinal median ridge, anterior to which a wide shallow median concavity extends forward, and is prolonged down the upper surface of the nasal bones.

Prefrontal and lachrymal bones.—There appears to be a slight channel above the anterior border of the orbit, which is increased by a slight displacement of the prefrontal bone. This bone forms the anterior border of the orbit. It widens as it extends forward and downward from the middle of the orbital border in the frontal bone to the dentigerous bone, which for the present may be premaxillary or maxillary. This bone is 15 millims. long by about a centim. wide where widest, in its lower third. It extends under the frontal bone above, and overlaps the dentigerous bone below. A suture divides it transversely, so the lachrymal bone is present as a separate ossification. In front of the lachrymal bone is a notch, which also indents the upper hinder part of the bone which carries most of the teeth. This foramen is led up to by a longitudinal channel in the dentigerous bone. The nasal bones would have reached the superior border of this foramen. Hence it is evidently an ant-orbital vacuity, but whether it is comparable to the ant-orbital vacuity of Teleosaurs, Dinosaurs, Ornithosaurs, and Birds, or to the ant-orbital vacuity of Ichthyosaurs, which is similarly placed, and forms on each side of the head the anterior narine, depends upon the interpretation of the bones which form its anterior borders.

The nasal bones.—The nasal bones roof over the head in front of the orbits, and are united by suture with the frontal bones behind. They are imperfect anteriorly, but as preserved are 3 centims. long. They are united by a median straight longitudinal suture, and form a shallow longitudinal concavity extending forward on the snout. They have a transverse width of 12 or 13 millims. posteriorly, and narrow anteriorly to a width of 4 or 5 millims. at the anterior fracture. Laterally, each bone makes an angular bend downward, so as to overlap and make a squamous union with the long dentigerous bone which runs parallel to it and forms the toothed margin of the jaw.

The question whether that bone is premaxillary or maxillary may now be examined. If the converging borders of the nasal bones were prolonged anteriorly, they would terminate one centim. in advance of the fracture, or half a centim. from the extremity of the jaw. Hence it is probable that if the nares were terminal they were small, though not smaller than in some Lizards. The large nasal bones, however, are not Lacertilian, and find no parallel so close as may be seen in *Ichthyosaurus*. And then the dentigerous bone would closely resemble the premaxillary bone in those Ichthyosaurs in which the nasal bones extend to near the end of the snout. A corresponding elongation of both nasal and maxillary bones is seen in Crocodiles; but the anterior groove, which in *Protorosaurus* runs up to the ant-orbital vacuity, is similar to that seen in Ornithosaurs and Birds; and this leads me to regard the ant-

orbital vacuity as probably nasal, and consequently the dentigerous bone as probably premaxillary, though the morphological data for the identification are confessedly slender.

The premaxillary bones.—This bone resembles the same element in *Ichthyosaurus* in steadily augmenting in depth as it extends backward. Its upper hinder margin is notched out by the vacuity which I am disposed to regard as nasal. The form of the bone is a long triangle with its narrow base towards the orbit. Its depth posteriorly, as exposed by the removal of the covering nasal bone, is about one centim. Its length as preserved is between 3 and 5 centims. There is a longitudinal groove above the bases of the teeth, like that seen in Belodon, and which indents the Ichthyosaurian jaw parallel with the base of the dental groove. The rough convex surface of bone between this groove and the alveolar border has been removed along its length, apparently to expose cavities like sockets which may have been for successional teeth, of which 18 are visible. Although these pits existed beneath the teeth which were in use, there is no evidence that those teeth were in sockets. The teeth were manifestly anchylosed to the jaw as in Lybyrinthodonts and some Lizards. A horizontal plate appears to have divided the base of the teeth from the quadrate cavity beneath. One tooth appears to be in one of these sockets. The teeth were closely set, but are nearly all wanting, and only indicated by the infra-dental cavities and by impressions of the crowns. There is no trace of successional teeth in any other of these infra-dental spaces. They are uniform in size and depth, and in most cases, but not always, immediately beneath the crowns. They are not circumstanced like cavities for successional teeth so far as these are known, and are apparently interior in position to the teeth on the alveolar margin. The crowns of the teeth appear to have been smooth, conical, pointed, with the base circular. One of the longest, in front, measures 5 millims. from the point to its anchylosis with the jaw, and about 7 millims. to the bottom of the infra-dental cavity.

The maxillary bone.—The posterior part of the dentigerous border may be a separate bone, but if so the suture which defines the maxillary bone is not clearly made out. It probably is in front of the last two infra-dental cavities, above a depression which indicates a squamous overlap upon the premaxillary bone. As it extends backward below the orbit, three or four slender pointed teeth are seen to extend from it, but more may be hidden in the matrix. The bone terminates backward in an oblique suture which is below the middle of the orbit, and therefore presumably indicates the jugal bone, which is imperfectly exposed and apparently displaced downward.

Above the maxillary region the cervical vertebræ lie over the orbit and the back of the head. The violence which separated the vertebral column disengaged the lower jaw and separated its elements, and displaced the quadrate bone and bones of the palate, which lie scattered between the head and the lower jaw, not entirely free from matrix.

The sclerotic circle.—Below the orbit a structure exists which closely resembles the sclerotic armature of a Bird (Plate 15), which, when complete, may have approached a diameter of 2 centims. A circle of this size might have been contained in the orbit. It is inflated in the middle part, in the centre of which appears to be a smooth space of matrix; externally its border is concave. It appears to be formed of radiating thin plates in close contact; but the state of preservation does not admit of detailed description or absolute identification, for the mass may possibly be dermal armour.

The bones of the palate.—The bones of the palate are scattered. Their identification rests upon, first, the forms of the bones; secondly, their consecutive positions; and thirdly, the fact that the vomer, palatine, and pterygoid all carry minute teeth; while there can be no suspicion that these elements belong to the lower jaw, since the lower jaw is preserved.

Vomer.—Both vomerine bones are indicated, and both are partly imbedded in the matrix. They were very slender, 3 centims. long, and about 2 millims. wide where widest proximally. They carried minute teeth, densely placed along the margin. The crowns are enamelled, enlarged and pointed, with lanceolate form.

Palatine bone.—The palatine bone is a long triangle, notched out on the inner anterior margin for the reception of the vomer. The bone is 3·2 centims. long, and 8 millims. wide posteriorly, tapering away in front. The external border is straight. The posterior border is straight and truncated, but rounds into the inner side, which is depressed where it received the anterior limb of the pterygoid. The surface of the bone is rather convex till it becomes channelled with the groove which leads forward to the notch for the vomer. The vomer probably extended along much of its inner margin (fig. 1, p. 19). Along the external margin of the palatine bone a row of teeth extended. They were rather larger than those on the vomer, though only one or two are preserved.

The pterygoid bone.—The outline of the pterygoid bone is not easily traced. The bone is in accidental contact with the palatine bone, and probably in natural union with the quadrate bone. It is stronger than the palatine bone, short and broad posteriorly, sending a long sharp process forward which I regard as extending interior to the palatine bone (fig. 1, p. 19). This process or bone is 1·6 centim. long, 3 millims. wide at the base, and tapers to a point. It carries a few minute teeth, some of which appear to be barbed. The interpretation of the posterior part of the bone is more difficult, because the bone originally extended in more than one plane; and it is impossible to determine with certainty whether the expanded transversely oblong plate which is in contact with the quadrate bone is in natural union. I assume the connection to indicate the true relation of the bone. Then it follows that the oblong truncated expansion of the bone which is at present in contact with the palatine must be internal, and either have articulated with the basi-sphenoid, as in Lizards and Anomodonts, or else with the corresponding surface of the other pterygoid bone, as in Dinosaurs. Then there would be no lateral plate for the internal pterygoid muscle

such as is seen in Crocodiles and Lizards, but the great oblong plate which extends outward to the quadrate bone must have been attached along much of the length of that bone.

The quadrate bone.—Posterior to the pterygoid bone is a much stronger bone, imperfect at both ends, which I regard as the quadrate bone. As preserved, it is 1·4 centim. long. It is somewhat compressed, constricted in the middle, and expands proximally to a width of 4 millims. It has an internal expansion which is not fully seen, which is wide, thin, and oblique, and appears to be the pterygoid process. The surfaces of the quadrate bone are smooth, and concave in length in every direction in which exposed.

The lower jaw.—The lower jaw has its constituent bones displaced. As preserved, it is about 9 centims. long, and measures 8·5 centims. from the articulation for the quadrate bone to the extremity of the dentary bone. There is no indication of a coronoid process. It is long and narrow, increasing a little in depth as it extends backward, but becomes less deep again towards the posterior articulation. The outline is straight along the dentary border, and slightly convex below. Both dentary bones are present, and show that they had only a narrow union at the extremity of the jaw, and were not anchylosed together. The extreme length of the dentary bone was probably about 6·5 centims. The angular and surangular were both elongated bones. The splenial bone appears to have lapped along the inner side of the jaw and extended forward to near the extremity of the dentary bone. The articular bone is lunate, 8 millims. long; not unlike this bone in the Crocodile, with a transverse concave articulation. The bone, though now exposed, was probably imbedded. Twenty-seven teeth can be counted apparently anchylosed to the dentary bone, extending along a border of more than 4 centims. Other teeth may have been present further back.

Hyoid bones.—Between the articular end of the lower jaw and the displaced quadrate and pterygoid bones are slender, delicate, straight, cylindrical bones, very imperfectly displayed, which are jointed. Their slenderness and position are suggestive of the hyoid elements. The length exposed is 2·2 centims. The structure apparently consists of a rod measuring 1·8 centim. and two short joints of about 2 millims. each. The terminal joint is conical.

The vertebral column.—The vertebræ extend in a continuous curve, with the neck bent round so as almost to meet the sacrum; beyond which the tail extends, at first gently curved, and then almost straight. About 59 centims. of the vertebral column are preserved, but a portion of the tail, of unknown length, is lost.

The cervical vertebræ.—The cervical vertebræ are conspicuously elongated (Plate 14, 2–7). Six are preserved in connected sequence. Measured round the curve, they have an aggregate length of 13 centims. The Atlas does not appear to be preserved, or, if preserved, is broken, and the fragment out of position and imbedded in matrix. As the first of the series is the short Atlas, this animal appears to have had seven cervical vertebræ. Being in close union by means of the several articular processes,

the forms of the articular ends of the centrum are imperfectly seen, but the condition displayed by the third vertebra of the series (Plate 14, 4) appears to show that the intercentral articulation in that vertebra, at least, was opisthocœlous.

The first vertebra, which is very imperfectly preserved, has the centrum 1·9 c.m. long. The second is of the same length. The third vertebra is the longest, and measures 2·5 centims. The fourth is about a millim. shorter. The fifth measures 2 centims.; and the sixth, which is badly preserved, is about 1·8 centim. long.

In relative elongation as compared with dorsal vertebræ, these cervical vertebræ show a character which is most closely paralleled among Ornithosaurs, but is also met with in various existing Birds and Mammals. Some Chelonians have the cervical vertebræ of a similarly long form; and in the fossil the zygapophyses have a development which is scarcely equalled among Chelonians. The strong, broad, elevated neural spine is distinctive.

The external layer of bony tissue in these vertebræ appears to be as thin as in an Ornithosaur, or a Dinosaur like *Cœlurus*, as though the centrum were occupied by an air-cell. But, although there is a small foramen in the middle of the side, in a position which might coincide with the junction of the centrum and the neural arch, it is scarcely larger than the ordinary nutritive foramen, common in such a position, and gives no indication of a pneumatic function. The forms of the articular surfaces make the inferences probable that the neck was carried or capable of being carried in a vertical position, as in the Galapagos Tortoises. Only the side of the vertebræ is exposed.

In the third vertebra (Plate 14, 4) the centrum is marked with three narrow, sharp, sub-parallel ridges which extend in curves between the anterior and posterior articulations; they are but little elevated, and give a channelled aspect to the side of the centrum. The anterior articular ball of the centrum appears to be well ossified; it is about 6 millims. deep, and hangs obliquely forward. There is a less obliquity in the posterior cup, which is somewhat deeper, and is defined by a sharp margin. The neural arch extends along the centrum. The anterior and posterior borders of the neurapophysial lamina which margins the intervertebral neural foramina are concave from above downward, convex from within outward. The antero-posterior distance between them is 2 centims., and the arch, as usual, ascends from the centrum close to its anterior end, just over the anterior articulation. From the upper side of the neural canal the prezygapophysis extends forward and upward. It is 8 millims. long and 2 millims. wide, and its upper surface is 1 centim. above the base of the centrum. Immediately behind it is a strong ridge or slight transverse process which connects with the posterior zygapophysial process. Its transverse extension outward is broken away. The extreme measurement between the extremities of the zygapophyses is 3·1 centims. The neural spine is sub-quadrate, compressed from side to side, rising about 9 millims. above the interzygapophysial ridge. The upper border is truncate, slightly rounded from the post-zygapophysis behind, as it extends forward and upward. The front border of the neural spine leans a little forward. In the fourth vertebra the

neural spine has its anterior border more vertical, but in both the posterior border is inclined obliquely backward, so that the spine becomes less high towards its posterior extremity.

Slender cervical ribs are attached to the anterior extremities of the sides of the centrum. The ribs are straight, slender, pointed behind, are as long as the vertebræ to which they run parallel, and have thickened heads for attachment.

Near these cervical ribs are several slender, long, tendenous ossifications, such as are often met with in the vertebral column in Birds and Mammals, and are common in the caudal region of the Bernissart Dinosaurs.

Dorsal vertebræ.—There appear to have been sixteen dorsal vertebræ in the 19 centims. between the neck and sacrum. None of these vertebræ are so preserved as to be worth description. They give little information about the centrum, but show that the neural spines were 9 millims. high in the anterior vertebræ, vertical, 6 millims. wide, with the anterior and posterior margins parallel, and the truncated superior outline convex. The ribs appear to have been attached to short transverse processes or tubercles given off from the neural arch. The centrums appear to be bi-concave or flattened at the ends.

The ribs are strong, curved, and compressed from front to back.

Sacrum.—The sacrum appears to have included two vertebræ. They are short, and had well-developed transverse processes, 12 millims. long, which expanded externally. But the bones are too badly preserved to demonstrate any other point of structure.

Caudal vertebræ.—Twenty-three caudal vertebræ are preserved. Each centrum is 1 centim. long. The body of the centrum is compressed from side to side, and rounded on the base. At about the level of the neuro-central suture transverse processes are developed in the earlier part of the series. Then the neural arch rises, and develops short zygapophyses on the level of the summit of the neural canal, and forms a short platform from which the high vertical neural spine rises. The measurement from the base of the centrum to the neural platform in the earlier caudal vertebræ is 1 centim.; and the height of the neural spine above the platform is 1·2 centim. The caudal vertebræ after the first two have long spathulate chevron bones, which are directed obliquely backward. They are at first very long, and then become gradually shorter. With their development the neural spine becomes constricted at its base and wider at the summit, so that it gradually assumes a wedge-like form. At about the 14th caudal vertebra, 11 or 12 centims. behind the sacrum, the summit of the neural arch is notched. The spine after this continues to decrease in height as the notch increases in depth, until after about six vertebræ the neural spine is completely divided into anterior and posterior parts, which have the spines obliquely directed backward and forward, with an increasing interval between them. As they are followed backward, the vertebræ diminish in all dimensions except length. And the neural spine decreases in height, while the transverse process, which at first is

strongly marked, soon sinks into insignificance, and appears to be lost before the neural spine becomes divided.

The hind limb.—There is no bone of the pelvis preserved.

The femur and bones of leg lie in natural position, with the head of the femur towards a transverse process of a sacral vertebra. That process (Plate 14, *sa*), as in other animals, is wedge-shaped, 11 millims. in transverse extension, and 9 millims. in antero-posterior extension on its external limit, as preserved. But it is imperfect, and may have been wider, and may not have been so much constricted where it joined the centrum as the present state of the fossil would indicate. These processes indicate a strong pelvis. Little of the strong straight femur now remains except the crushed impression of its outline, in which some fragments of bone still adhere (Plate 14, *f*). The length of the impression is 7·1 centims. The proximal articular surface does not appear to have been in quite the same plane as the distal surface. The proximal end is 1·6 centim. wide, with the head convex and directed laterally, but with a broad process or trochanter 6 millims. wide, which extends a few millims. proximally beyond the external border of the articular surface. If this fragment of bone is correctly interpreted, the articulation presents a condition which is only paralleled among Birds, Ornithosaurs, and Dinosaurs, though the proximal trochanter is less developed in Dinosaurs than in this fossil. The sides of the bone approximate so that the transverse measurement in the middle of the shaft is 8 millims., which width is preserved without appreciable diminution to the distal end of the straight shaft. The distal articulation is rounded from above downward, and slightly thickened on the posterior condylar aspect, as in a Lizard, Bird, or Ornithosaur. The bone was hollow, with a very large cylindrical cavity in the shaft, quite as much developed as in Wealden Ornithosaurs and many Birds, and with the bony tissue quite as dense, though Lizards make an approximation in both respects.

The tibia and fibula are imperfect distally, and only 4·7 centims. of the bones are preserved (Plate 14, *t*, *fi*). What remains of the bony tissue shows that the bone was thin in the middle of the shaft, with a large medullary cavity. The proximal end of the tibia is truncated, with rounded margins. Its transverse width is fully 11 millims., while the transverse measurement in the middle of the shaft is only about 3 millims. This proximal expansion is partly due to a general Bird-like or Dinosaurian massiveness of the proximal end of the bone, and partly to the development of a not inconsiderable cnemial crest, which speedily subsides distally, but forms a ledge against which the fibula rests. The proximal end of the bone is more solid than in existing Lizards. Where fractured, the bone is enlarging distally. The fibula is a more slender bone, with a slight sigmoid curve, nearly uniform in width, being 3 millims. wide in the proximal half, and a little narrower distally.

The foot.—In the region between the cervical and dorsal vertebræ remains of an extremity of a limb are displayed. A metapodial bone is 2·1 centims. long; extremities of other bones of a like character are exposed. Extending beyond them

are the impressions of four digits, which successively augment in length. They show the increasing number of bones, indicated by the formula 2.3.4.5. All the articular surfaces of the phalanges are perfectly ossified, and they are shaped as in Dinosaurs, but an approach to this perfect ossification is seen in the Homœosaurs and other fossils. The terminal phalanges of the digits are in the form of claws, curved and pointed, and compressed from side to side.

Armature of the skin.—In the region of the early dorsal vertebræ a fragment is exposed of a very thin plate of bone which was at least 3 centims. long. It is made up of a number of minute oblong bones, each 1 millim. wide, suturally united together into a shield across which a slight longitudinal keel runs. This plate I regard as a piece of dermal armour. (Plate 15, fig. 11.)

Part III.

Comparison between the Type in the Royal College of Surgeons Museum and other Specimens referred to Protorosaurus Speneri *by* von Meyer.

Before an attempt is made to explain the structure of this type of animal, it is necessary, on account of its imperfect preservation, to discuss its relations with the specimens figured by von Meyer. That great anatomist was disposed to regard the differences between the fossils as due to age and resultant differences in ossification, though he did not decide absolutely on the specific identity of the whole of the materials. Unless the specimens could be brought together, it would be difficult to determine their relations so as to assign its systematic place to each, for the animals have so much in common, and the differences between them are not at first obvious. Nevertheless, if the method of comparison is applied, I believe the result will show that von Meyer's species is really a family including several species, and more than one genus.

The available data for comparison in the type specimen are remarkably scanty. It has been shown that the femur is 7·1 centims. long, and that it is seven times as long as the caudal vertebræ, which are almost uniformly 1 centim. long. The cervical vertebræ also yield some characters in the form of the neural arch and the ridges on the centrum.

There is no other specimen with the femur so short, but the differences in the length of the bone are so slight that they might at first pass for gradations of growth, their lengths in centims. being 7·1, 8·3, 8·8, 9·7, 10. All the bones, however, do not vary in the same ratio.

I will first contrast the type with the specimen described by Link, known as the Waldenburg specimen. In that specimen (von Meyer, *l.c.*, T. 9) the caudal vertebræ augment in length from 1·3 centim. in the early caudal to 1·8 centim. at the twenty-fourth caudal, where the specimen is fractured. The femur is 10 centims. long, but it

differs from the type in being as long as five-and-a-half of the middle caudal vertebræ, and as long as six-and-a-half of the early caudals. Moreover, the two femora are of different type; that in T. 9 being more expanded transversely at both the proximal and distal ends. The 23 caudal vertebræ of the type specimen measure as many centims.; the first 23 vertebræ in the tail in LINK's fossil measure 38 centims. If, on the evidence of the femur, the proportions of size between these animals may be taken as 7 to 10, then the 23 caudal vertebræ of the type would have measured 26·6 centims., or almost a sixth longer than is the case.

In the type I recognise two sacral vertebræ; in LINK's fossil there are three, according to VON MEYER. In the type I can only count sixteen vertebræ between the neck and the sacrum, where they measure 19 centims. In LINK's fossil there are not fewer than eighteen vertebræ in this region, measuring 30 centims. Seven-tenths of 30 being 21, it follows that the dorsal vertebræ in the type, besides being fewer, are relatively rather longer. The neural spines in the type are 6 millims. wide; here the width is double. The neural spines of the dorsal vertebræ in the type are 9 millims. high; here the height is about 2·2 centims. This is such a difference as might be attributed to age, but the aggregate of the other characters seems to me of specific value. I accordingly separate LINK's fossil as a distinct species, which may be termed *Protorosaurus Linkii;* until the discovery of better materials shall determine whether it can remain in the same genus.

Among other characters seen in LINK's specimen are all the details of the fore and hind limbs, showing the humerus to be 7·4 centims. long; the ulna 6·1 centims. long; the longest metacarpal about 1·9 centim. long, and the longest metatarsal 4·3 centims. The cervical vertebræ are relatively massive, 2·7 centims. long, and have the upper border of the neural arch nearly horizontal, without any trace of the posterior attenuation seen in the type of *Protorosaurus Speneri.* The caudal vertebræ show no transverse processes.

I would next compare SWEDENBORG's specimen, figured by VON MEYER *l.c.* in T. 8. This is a smaller animal than LINK's, of less robust type. The cervical vertebræ resemble those of LINK's fossil in the contour of the neural arch, which is quite distinct from the College of Surgeons specimen, though there is more resemblance to the latter in the ridges on the centrum. VON MEYER's drawing, however, gives no indication of the possibly opisthocœlous articulation which appears to be indicated in the drawing of LINK's fossil. The shape of the femur is altogether Dinosaurian, and quite distinct from that in LINK's specimen, where it has a Crocodilian or Chelonian curvature. It is more than an eighth shorter than in LINK's type. The tibia is a sixth shorter. The metatarsus is a fourth shorter. The ulna is a fifth shorter. The cervical vertebræ are of the same length; the dorsal vertebræ one-eighth shorter; while the caudal vertebræ, which have transverse processes, have a uniform length of 1·1 centim., and are therefore relatively very short. The pelvic bones are badly preserved in SWEDENBORG's fossil; but if the large expanded bones which lie in the sacral

region of LINK's fossil, beneath the humerus, are, as I believe from evidence in the British Museum, to be accounted pelvic, then the distinction between the types is very marked, and with the other characters would indicate a difference from LINK's specimen of more than specific value. SWEDENBORG's type is manifestly more nearly related to SPENER's type. If, as before, the comparison is based on the femur, SWEDENBORG's animal is larger than SPENER's in the proportion of 88 to 71. If, then, the dimensions in the latter are augmented by one-fourth, it should give approximately the size of the former. Four caudal vertebræ should measure about five centims.; they actually measure 5·5 centims. The correspondence is equally close in the proportions of the dorsal vertebræ. The chief differences in the cervical vertebræ are in form of the neural arches; but in length of centrum the correspondence, bone for bone, is exceedingly close between the theoretical measurements and the actual measurements. These resemblances seem to me to warrant the identification of the Vienna specimen with *Protorosaurus Speneri*. This determination makes known the hinder extremity of that species, the distal end of the humerus, the ulna and radius, the carpus, and some portion of the metacarpus. And it shows the complete series of dorsal ribs, to the distal ends of which slender sternal or abdominal ribs are articulated, two or three in number being placed side by side in connection with each dorsal rib. As the remains lie, they give a depth of body in this specimen of about 10 centims.

The specimens figured by VON MEYER *l.c.* on T. 6, with the exception of his copy from SPENER's figure, all belong to the same genus as *Protorosaurus Linkii;* but whether the species is identical, as would seem probable, I have not made the necessary calculations to determine. The Munich specimen, figured by VON MEYER *l.c.* in T. 1, fig. 1, though very fragmentary, is sufficiently different in some of its proportions to be worth comparison. The cervical vertebræ are preserved in sequence. They are of the same character as in *Protorosaurus Speneri*. Their lengths are given in the following Table, for comparison, in centims.:—

	1st.	2nd.	3rd.	4th.	5th.	6th.	7th.
College of Surgeons	.	1·9	1·9	2·5	2·4	2·	1·8
Vienna	.	2·3	2·3	2·8	2·9	2·6	2·3
Munich	·6	2·0	2·6	3·1	2·8	2·8	2·3
Freiberg	.	.	.	2·5	2·5	2·3	2·2

From this it is evident that the vertebræ in the Munich fossil do not preserve a relation of proportionate length with those of *Protorosaurus Speneri*. Four dorsal vertebræ measure 5·9 centims., which is nearly the calculated length. The femur is 9·7 centims. long, has a rounded proximal end, and a slight sigmoid flexure, but is less massive at the ends and more slender than in *P. Linkii*, and not so straight or so wide at the proximal end as in *P. Speneri*. The humerus is imperfect, but the ulna

and radius are preserved. The width of the humerus corresponds very well with the SWEDENBORG specimen ; but the ulna in the Munich specimen is 4·8 centims. long, while in the Vienna specimen it is 5 centims., so that the bone should have measured in this fossil about 5·5 centims. if the specimen had belonged to *Protorosaurus Speneri*. Hence this animal appears to differ from that species in being longer in the hind-legs and shorter in the fore-legs. But I do not venture to suggest for it a distinct name. It is interesting, as showing the coracoid and scapula.

Another specimen, preserved at Freiberg, is figured by VON MEYER *l.c.* in T. 2. It is of about the same size as the SPENER fossil, but only shows cervical and dorsal vertebræ, pelvis, scapular arch, and fore-limb. The cervical vertebræ are contrasted in measurement with the College of Surgeons specimen in the foregoing Table, from which it appears that the last two cervicals are relatively longer. Four dorsal centrums measure 4·5 centims., which would correspond with the length in SPENER'S fossil. The bones of the fore-limb are slender and graceful in outline ; and both ulna and radius are remarkable for a slight sigmoid flexure and constriction of the middle of the shaft. The humerus is 5·5 centims. long ; the ulna and radius measure 4·6 centims., and the foot beyond the carpus about 5 centims. In the Vienna specimen the ulna and radius measure about 5 centims., and in the Munich specimen about 4·8 centims. ; and in both are strong massive bones with sub-parallel sides and different contours. This character is suggestive of a specific difference ; but, as the contours of the humerus are similar, and there is no fundamental difference in the form of the coracoid or of the pelvic bones, it seems to me more convenient to group the Freiberg fossil with *Protorosaurus Speneri* till it has been re-examined. It makes known the structure of a remarkable type of scapular arch, and gives some valuable details of pelvic structure.

The Berlin specimen, figured by VON MEYER *l.c.* in T. 4, has the femur 8·5 centims. long, while the tibia measures 9 centims. This reverses the usual relations of length between the leg and the fore-leg, and is probably a good specific character. The pelvic bones resemble those in the SWEDENBORG fossil, but differ in form. The femur is as long as six of the early caudal vertebræ. Further evidence is required to determine the systematic place of these remains. All the specimens hitherto compared are exposed in side view ; but there are two other fossils figured by VON MEYER. One, preserved at Hanover, shows the dorsal aspect of the dorsal and sacral vertebræ, pelvis, &c. ; the other exhibits the ventral aspect of the sacrum of a large animal preserved at Dresden. The Jugler fossil at Hanover has a femur of a massive oblong form, not unlike that in the Vienna fossil, but relatively much shorter and wider. It is about 5·3 centims. long and 2·2 centims. wide proximally, and is equal to the length of four dorsal vertebræ. In the Munich fossil the femur is equal to seven dorsal vertebræ, and the proportion is nearly the same in the Vienna specimen and in the College of Surgeons type. In the Waldenburg specimen, *P. Linkii*, the femur is as long as six dorsal vertebræ. But, although the relative shortness of the femur thus separates

the Jugler fossil from the others, the form of the femur is no less distinctive in its prop-like character and massive width. In *Protorosaurus Speneri* the bone is between four and five times as long as wide ; here it is between two and three times as long as wide. The dorsal ribs shorten towards the sacrum in a way of which the Vienna fossil gives no indication, and which is not paralleled in any of the specimens referred to *Protorosaurus Speneri* or *P. Linkii*, since the last rib hardly exceeds the length of a dorsal vertebra. The ilium is in the form of an arch, the extremities of which rest against the bodies of the vertebræ, and to the middle of the outer curve of the arch the femur articulates. If all the vertebræ between the extremities of the arch are regarded as sacral, the sacrum includes five or six vertebræ at fewest. These characters are very scanty evidence of the animal, but they indicate in my judgment that the Jugler fossil belongs to a new genus and species. Till the genus is named the fossil may be referred to as *Protorosaurus Meyeri*. There can be no doubt that the Dresden fossil belongs to the same genus as the Jugler example, but I cannot at present determine whether it is specifically distinct.

From this discussion it appears that *Protorosaurus Speneri* as defined by von Meyer included two or three genera and several species ; and that the materials available for the elucidation of the type of the genus make known, more or less perfectly, the parts of the skeleton which are missing from the College of Surgeons specimen. The Jugler and Dresden specimens make known a form of pelvis as strong as anything met with among Ornithosaurs and fossil Reptiles, and show that the strength of the bones in the sacral region is associated with shortness and strength of the femur.

I now propose to use this evidence, brought together by von Meyer in the discussion of the affinities and structure of the type of *Protorosaurus*.

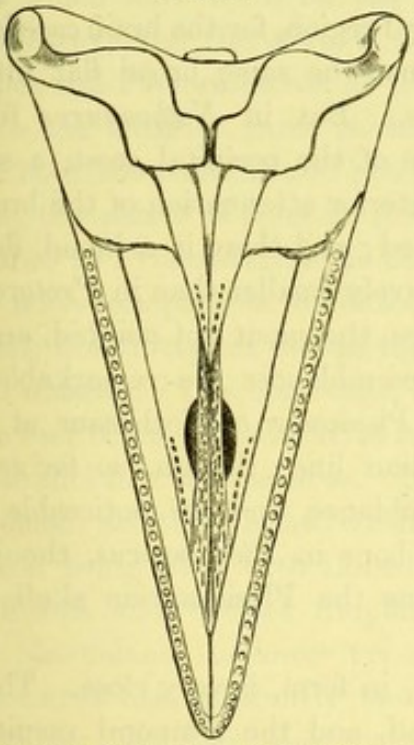
Part IV.

Comparison of Protorosaurus *with other Types of Animals.*

The skull.—Imperfect as is the preservation of the skull, it can be almost completely restored. The pterygoid bones, being still connected with the quadrate bones, furnish approximately the width of the palate in the transverse line of the quadrate articulation as not less than 4·5 centims., nor more than 6 centims. This is more than the width of the superior aspect of the back part of the skull as preserved, which would not have exceeded 2·5 centims., and if to this the width of the lost post-frontal and squamosal bones is added the width of the back of the skull presumably would still be less than the measurement over the condyles of the quadrate bones. The quadrate bones may have been inclined so as to converge upward, and thus have given an obliquely inclined aspect to the sides of the head, making its transverse section trapezoidal. If an attempt is made to reconstruct the palate (fig. 1), it is manifest that if the narrow internal facets of the pterygoid bones met each other

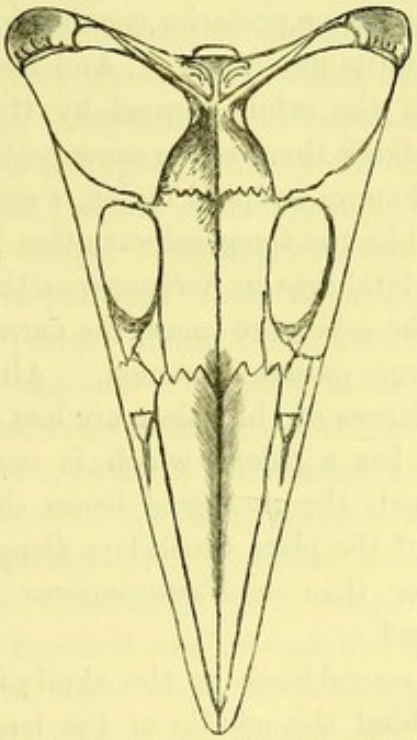
the bones diverged posteriorly. Hence I conclude that the sphenoid came between them after the type of *Ichthyosaurus*, and Lizards and Birds. The palatine bone shows some indication of having been slightly overlapped posteriorly as well as along one side of the anterior margin. The former character I take to indicate connection with the pterygoid bone, the latter with the vomer. We are entitled to infer on general analogy that the vomerine bones converged anteriorly. On this basis I reconstruct the palate with a slight median vacuity, less open than that of *Ichthyosaurus;* but there is no evidence whether there was a similar pre-sphenoid rostrum. There was a pair of lateral vacuities external to the pterygoid bones. The premaxillary bones and maxillary bones are necessarily external to the vomera and palatines, but their transverse width depends to some extent upon the

Fig. 1.



Partial Restoration of the Palate of *Protorosaurus Speneri*. Of the natural size.

Fig. 2.



Restoration of the Upper Surface of the Skull of *Protorosaurus Speneri*.

degree to which the vomer laps along the palatine. In the restoration this parallelism of the two is represented, so as to carry the vomer far back; its position may have been more forward, and then the palatal plate of the premaxillary would have been narrower. The distance from the condyle of the quadrate bone to the extremity of the snout is 8·5 centims., that being the length from the articulation in the articular bone to the anterior extremity of the lower jaw, which is inferred to have extended as far forward as the snout. As the bones of the side of the jaw give no evidence of lateral constriction, the outline of the skull was an isosceles triangle or sugar-loaf contour.

The restoration of the upper surface of the skull is constructed on the basis of the

contour of the palate, upon which the measurements of the bones already described are drawn (fig. 2). The orbits of the eyes were possibly larger than here shown, while the posterior border to the orbit is given on the hypothesis that post-frontal and malar bones were present, and that the malar united with the maxillary in the usual way. There is no evidence whether the malar arch connected with the quadrate bone. The characters shown by the skull are not to be found in one order of animals. In the first case I will assume that the position of the nares is in the small ant-orbital vacuity, and that they were not terminal as in the South African Theriodonts described by Sir RICHARD OWEN, and in Chelonians, or subterminal as in existing Crocodilia and Ophidia. There are several fossil types in which the external nares are quite as small and have as backward a position. In *Pistosaurus* from the Muschelkalk both these conditions are seen, and in many species of *Plesiosaurus* the nares, and other vacuities of the superior surface of the skull, are similarly placed. In true Plesiosaurians there is not the same posterior constriction of the cerebral region, for the brain case is always widest in its hinder part. And Plesiosaurs have not the same broad flat interspace between the orbits formed by the frontal bones. But in *Nothosaurus* from the Muschelkalk there is the same posterior divergence of the occipital crest, a similarly inclined supra-occipital region, a corresponding posterior attenuation of the brain case, which, like the temporal vacuities, is more elongated; and there is a broad, flattened, inter-orbital area in *Nothosaurus*, though it is relatively smaller than in *Protorosaurus*, while the orbits are small, the nares relatively large, the snout not pointed, and there is a large parietal foramen. Altogether the resemblances are remarkable. The resemblances of the palate are less obvious, for no Plesiosaur or Nothosaur at present known has a palate which is open in the median line; though, so far as form is concerned, the pterygoid bones show some resemblance, and are noticeable for the width of the plate which laps along the quadrate bone in *Plesiosaurus*, though it is narrower than in *Protorosaurus* in proportion as the Plesiosaurian skull is more depressed.

The resemblance to the skull of *Ichthyosaurus*, in form, is very close. The orbits are behind the middle of the length of the head, and the temporal vacuities and nares are similarly situate; but there is a fundamental difference in the minute size of the true frontal bones in *Ichthyosaurus*, in which genus they are excluded from the orbital margin by the intervening nasal, post-frontal, and pre-frontal bones; moreover, the nasal bones do not usually extend in *Ichthyosaurus* nearly to the extremity of the snout. If, however, the Ichthyosaurian nasals had extended no further backward than in *Protorosaurus*, they would have come as far forward anteriorly, and if the frontal bones had grown to fill the space thus left vacant the post-frontal bones would have been pushed outward and backward; though there can be little probability that the post-orbital part of the Protorosaurian skull could have been Ichthyosaurian. On the palate the resemblance is greater than among Plesiosaurs, because the palate is open in the middle line in *Ichthyosaurus* and the bones are elongated and taper to their

extremities. The form of the pterygoid bone is quite as much like *Ichthyosaurus* as *Plesiosaurus*. But, though the superficial resemblance is more obvious with *Ichthyosaurus*, I believe the resemblances with *Plesiosaurus* are the more important.

A certain resemblance may be considered to be shown by the Triassic Crocodile Belodon; but that type, which has the orbits placed far back, has large ant-orbital vacuities, above which the external nares are situate; the nasal bones are exceedingly small and short; and the pterygoid bones which meet in the median line do not extend so far back as in *Protorosaurus*.

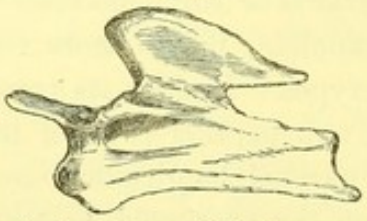
In none of the types with which comparison has been made are teeth ever present on the bones of the palate. The existing groups of Reptiles in which this character is seen are Ophidia, Lacertilia, and Rhynchocephalia, in all of which orders the external nares are terminal or sub-terminal. The same relation characterises the extinct Reptiles which have teeth on the bones of the palate, such as *Hyperodapedon* and *Rhynchosaurus;* and therefore, if as close a general resemblance should exist between such types and *Protorosaurus*, as the Nothosaurs have shown, the probabilities will incline to the anterior nares having been terminal. *Rhynchosaurus* apparently has teeth on both the palatine and pterygoid bones; the pterygoid is firmly united to the quadrate, the palate is open in the median line, but there is seemingly no very close resemblance to *Protorosaurus* in the forms of the bones. The upper surface of the skull is fairly comparable in contour, in the relative positions of the vacuities, in the broad, flat, frontal region, and in the existence of a parieto-frontal crest formed by the temporal muscles. The brain-case, however, in *Rhynchosaurus* appears to be distinct from the roof bones of the head, as in *Procolophon* and some Lizards; and this condition has no parallel in *Protorosaurus*. No existing Reptile, so far as I am aware, has teeth on the vomer; and this toothed condition of all the bones of the palate prevents detailed comparison being made with Lizards or Rhynchocephalia. The character, so common among Fishes and extinct Amphibia, is the more remarkable as a comparatively isolated resemblance to lower types. Besides its terminal pair of tusk-like incisors, *Rhynchosaurus* has apparently two parallel rows of teeth upon the palatal plate of the maxillary, and two short parallel longitudinal rows in the hinder part of the palate, which appear to be upon the pterygoid, or pterygoid and vomerine bones, for no separation can be made out with certainty between the bones of the palate. In *Rhynchosaurus* the malar bones are produced downward and backward so as partly to overlap the lower jaw, as in *Parieasaurus*, a character of which *Protorosaurus* gives no indication. *Rhynchosaurus* has the post-fronto-squamosal arch strongly developed, of which no trace is preserved in the *Protorosaurus*.

The condition of the teeth, anchylosed to the palate, with corresponding cavities in the positions where fangs would usually be, is a remarkable peculiarity, which needs further elucidation. The teeth are anchylosed to the jaw in Labyrinthodonts; but I know of no such union or such sub-dental loculi among Reptiles as are here seen. The cavities may have remained after the teeth emerged from them by absorption of

the base of the fang when the tooth became anchylosed. I am inclined to regard the attachment of the teeth as having more in common with Serpents and certain Lizards than any other group of existing animals; but the resemblance cannot be accounted one of affinity. And the question arises whether the sub-dental cavities are not to be interpreted as a stage in the history of the formation of the socket for alveolar teeth, which became developed in a later period of time. If there had been sufficient evidence to establish this interpretation, it would have tended to make *Protorosaurus* comparable with some Ornithosaurs from Solenhofen, to which resemblances may be seen in the general structure of the skull and conformation of the palatal bones, though no Ornithosaur has teeth on the bones of the palate.

The vertebral column.—The atlas is very short and not anchylosed to the axis. There are about 7 cervical vertebræ: 16 dorsal; two or three sacral; and an unknown, but large, number in the tail. These numbers throw no light on the affinities of the fossil. The elongation of the cervical vertebræ, as VON MEYER pointed out, is better paralleled among Ornithosaurs than any other group. The strongly developed neural spine is not found in all members of this group, but is sufficiently characteristic. VON MEYER's figures appear to show that the vertebræ have the articular ends of the centrum slightly concave; and therefore it is probable that if the opisthocœlous condition which the type appears to show is not delusive the form of the articulation is not constant. I do not know of any Ornithosaur which has a like antero-posterior elongation of the neural spine. The cervical ribs are Ornithosaurian. The dorsal vertebræ are remarkable for the rounded base and depth of the centrum, which supports a large neural arch with vertical truncated neural spine. This form of vertebra approximates rather to the Crocodilian than the Lacertilian type, but is

Fig. 3.



Fourth cervical vertebra of *Protorosaurus Speneri*.

better matched among existing Birds with amphicœlous vertebræ, Pterodactyles, Dinosaurs, and Nothosaurs, though it never has anything like a neural platform; and there is no certain evidence of any ribs having more than one articular head, though the articulation of the rib was quite as high in lateral position as among Crocodiles. On the whole, the Ornithosaur comes closest, though *Rhynchosaurus*, in the form of the centrum, is not dissimilar. There is no approximation to the massive neural arch of *Nothosaurus*, and the centrum is more elongated than in that genus.

The sacrum presents no peculiarities; and, although only two pairs of strong sacral ribs were developed to support the ilium, that bone appears to have been sufficiently

extended to have articulated with more. The tail is equally devoid of characters which suggest affinities. In depth the centrum has more in common with the Crocodilian and Dinosaurian types than with Nothosaurs, which have the centrum shorter, or with Lacertilians or Ornithosaurs, which have it more depressed. The divided condition seen in the neural spine of the later caudal vertebræ probably indicates a complete development of the neural arch upon each of the protovertebral elements which go to make up the centrum; though the vertebra must still be regarded as highly differentiated, since the caudal ribs are given off from its anterior moiety as processes directed transversely, while the chevron bones, which represent them on the posterior moiety, have already descended to the inferior visceral margin. The theory of the double-headed articulation of dorsal and cervical ribs is not unconnected in some animals with the hypothesis that the transverse process and chevron bone blend in the anterior part of the body to form one rib with two articulations, and sometimes with a pair of sternal ribs to each distal extremity. The attachment of the ribs being high up, as well as the length of the ribs, would indicate that the respiratory and vital organs in *Protorosaurus* were well developed; and the mode of attachment of the ribs in most Reptiles and higher Vertebrates appears to depend partly on the way in which they are elevated by the lungs, and partly on the muscles which come into play in connecting the ribs with the vertebræ. So that the double-headed attachment of the dorsal ribs in modern Crocodiles is fundamentally different from the attachment in Birds, only because the transverse processes have become so much elongated as to remove the rib from the side of the centrum. But the Mammalian and Avian ribs are typically single-headed, and the second head or tubercle is obviously only a consequence of the rib being brought into contact with the neural arch; so that, if no transverse platform is developed, the rib cannot have a second articulation. And it is on this condition that I account for the single-headed ribs of *Protorosaurus*, since nothing is needed to make the rib double-headed but a transverse development of the neural arch, such as I shall subsequently describe as partially developed in the genus *Mesosaurus*.

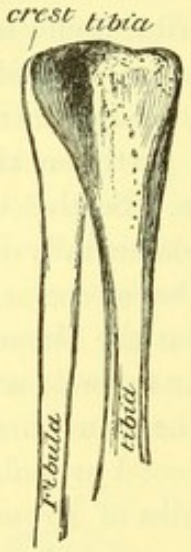
The sternal ribs are imperfectly known. Von Meyer represents them as rods, of which two, or possibly three in some cases, are attached to the enlarged sternal end of each costal rib. The sternal ribs, however, were probably composite; and I am disposed to believe that each consisted of two lateral pieces on each side, united by squamous overlap with a median piece in the middle line of the abdomen. Sternal ribs are seen in *Lariosaurus*, in *Mesosaurus*, in *Stereosternum*, in *Rhynchosaurus*, and other Triassic and Permian types, as well as in *Plesiosaurus*. Their structure is in every case substantially the same when it can be observed; though the number of sternal ribs to each costal rib varies. The nearest approximation to this condition among existing Reptiles is seen in *Hatteria*. I have no doubt *Rhynchosaurus* is a Rhynchocephalian; but *Lariosaurus*, *Mesosaurus*, &c., are Nothosaurians.

The pelvis and hind-limb.—The pelvis is not complete in any specimen. But the ilium appears from the sum of the evidence to have an antero-posterior elongation

and a distinctive form, but was more nearly comparable with the bone in Solenhofen Pterodactyles than in any other kind of animal, living or extinct.*

It is probable that the bone was supported as an arch, of which the extremities met the bodies of vertebræ, and the middle was attached to sacral ribs. In this matter we are not entitled to reason from the Hanover and Dresden specimens, because they have already been regarded as referable to another, though allied, genus; but the ilium is always broken and more or less displaced, and this favours the view that it was arched as in those types. The acetabulum is unknown. The ischium and pubis are altogether Pterodactylian, being expanded bones essentially comparable in contours and mode of union, with an obturator foramen between them; the pubis smaller than the ischium, with the ilium extending anteriorly and posteriorly beyond both bones. Something of the same type of pelvis is seen among Anomodonts, and

Fig. 4.



Nothosaurians and Plesiosaurians show a similarity in the ischium and pubis. It is also paralleled among the Cetiosaurian Dinosaurs, and after the Ornithosaurs these Dinosaurs would approximate most closely to *Protorosaurus* in pelvic structure. This pelvis is more comparable to the Crocodilian than to the Lacertilian type. So far as the ilium is concerned, an approach to this type is made by the Jurassic *Scaphæosaurus*.

The femur, as already remarked, is Dinosaurian in its straight strong build, truncated proximal end, and distal condyles. If it has not the lateral trochanter or the proximal trochanter usual in Dinosaurs, the latter is absent from the femur of so typical a Dinosaur as *Hadrosaurus*, and the former is absent in *Stegosaurus* and some other American genera.

An approximation to this form of femur is found among Nothosaurians, but those animals never exhibit the perfect ossification of the extremities here seen, or distal

* Seeley, 'The Ornithosauria,' p. 60, 1870.

condyles. The second segment of the limb is more like that of a Dinosaur than any other animal. Very few Dinosaurs have the tibia and fibula as long as the femur, but Professor MARSH has figured this condition in *Laosaurus;* and in *Compsognathus* the relative elongation of the second segment of the limb is greater than in *Protorosaurus.* Ornithosaurs also have this segment of the limb the longer, but then the fibula is only developed proximally, as among Birds. The proximal expansion of the tibia in *Protorosaurus* and its cnemial crest, well seen in the type specimen, are typically Dinosaurian (fig. 4). The sigmoid flexure seen in the fibula in some examples of *Protorosaurus* suggests that the bone terminated distally in front of the tibia, as in *Archæopteryx* and certain Dinosaurs.

The tarsus differs from that seen in Dinosaurs in some important particulars. First there is a large astragalus which appears in the SWEDENBORG specimen to have an ascending talon; then there is a compressed calcaneum, which in the Waldenburg specimen articulates with the cuboid bone. Between this proximal row and the distal row of three cuneiform bones are the cuboid and naviculare. This remarkably well developed tarsus is distinctive of *Protorosaurus,* and Mammalian in its elements.

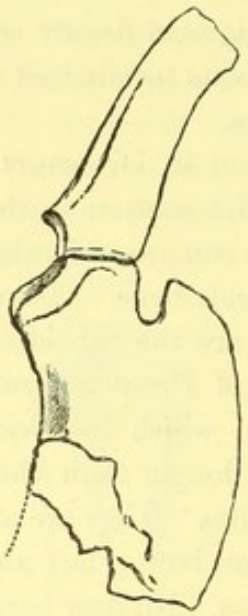
There are five stout metatarsals, which increase in length from the first to the fourth, while the fifth is but little longer than the first. They do not decrease in stoutness, as is the case with Crocodiles. They are more elongated than among Lizards, though *Scaphæosaurus* * has similar bones, but shorter than in *Compsognathus* and some Ornithosaurs, like *Dimorphodon.* No near parallelism is possible with Dinosaurs, because the bones of the digits are so greatly elongated in *Protorosaurus,* for this condition gives a Lacertilian character to the hind-limb, though the stoutness of the phalanges and metatarsals is more Dinosaurian. From the shortness of the first and fifth digits, and especially of the metatarsals of those digits, the foot has a suggestive aspect of degeneration, which, when the metatarsals came to be carried in an elevated position, might result in the development of such a foot as is seen in *Allosaurus,* though the fact that the fourth metatarsal is the longest seems to offer some difficulty in the simplification of the Protorosaurian foot. The digital bones are ossified on the Dinosaurian type.

The shoulder-girdle and fore-limb.—The shoulder-girdle is less perfectly preserved than the pelvis. Bones which I regard as the coracoid and scapula are preserved in the Munich specimen. If these are traced off and articulated, they show that the coracoid was relatively large, but, like the scapula, is suggestive of Dinosaurian or Ichthyosaurian form, though the coracoid is not without some resemblance to the bone in Plesiosaurs, and Plesiosaurs always want the narrow anterior notch. Only a trace of these bones is seen in the Vienna specimen, where the very imperfect coracoid and scapula appear to have had similar forms; but there is no evidence whether the coracoids met in the median line, or whether other bones

* VON MEYER, 'Fauna der Vorwelt,' "Reptilien aus dem Lithographischen Schiefer des Jura," t. xiii.

extended between them. Much more complete remains of the shoulder-girdle are preserved in the Freiberg specimen, but the bones figured by VON MEYER are not easily understood, and are very different from the bones in the Munich fossil. They are probably displaced, and till I have examined the original can offer no decisive opinion on structures which appear to unite the characters of Plesiosaurs and

Fig. 5.



Dinosaurs with distinctive ordinal characters. The scapula is formed on the Nothosaurian type, while the coracoid is unlike that of any Nothosaur, and might be Lacertilian or Dinosaurian. And the arch appears to include other elements, which are probably the interclavicle and clavicles; so that the resemblance to Dinosaurs which appears to be indicated by the bones in the Munich slab may have to be modified in favour of a more generalised interpretation of affinity.

The fore-limb is much smaller than the hind-limb. The form of the humerus with its expanded ends might be Rhynchocephalian, Lacertilian, or Dinosaurian. One large humerus figured by VON MEYER as the Fulda specimen is quite Dinosaurian and has a large radial crest, but there is no proof that this can be referred to the same genus as SPENER'S fossil, though the small specimens appear to have a similar form and to possess a radial crest; but this might be Lacertilian as well as Dinosaurian. The smaller limb bones are equally remarkable for wanting characters suggestive of definite affinity with existing Reptiles. They are not Crocodilian, not like any Lizard known to me, and not typically Dinosaurian, but only to be described as of generalised type. The carpus consists of rounded bones, of which five form a distal row corresponding to the five metatarsals, and three the proximal row, which lies on the radial side, so that the ulna appears to articulate directly with the fifth distal carpal. If in form of the bones the carpus appears Plesiosaurian, it is as much Cetacean in that respect, and in structure makes as near an approach to Mammalian type as to Reptiles.

The metacarpus has the bones more nearly equal in length than the metatarsus ; three are fasciculated in the middle, and the inner and outer bones are shorter and more spread out laterally.

From this discussion I conclude that *Protorosaurus* has no predominant affinity with any existing order of animals. Its cranial characters appear to separate it widely from other ordinal groups. If the strongest resemblance of the upper surface of the skull is with certain Nothosaurs, the dental characters separate it. The second strongest resemblance is probably with certain Jurassic Ornithosaurs. The vertebral column as a whole has much in common with Pterodactyles, more perhaps than with any other group, but the differences in the articulation of the ribs and the sacrum separate it. The pelvis is intermediate between that of Pterodactyles and Plesiosaurians or Nothosaurs. The hind-limb is in its proximal segments suggestive of Dinosaurs, and in its distal segments approximates to Lizards. The scapular arch is too imperfectly known to yield marked evidence of affinity. The fore-limb shows no striking differentiation. The animal is therefore of an ancient stock, and may have been derived from the group from which Ornithosaurs were developed. Hence I conclude that VON MEYER was fully justified in regarding *Protorosaurus* as the type of a distinct order of Reptiles, for which the name Protorosauria may be conveniently used.

DESCRIPTION OF THE PLATES.

PLATE 14.

Figure of specimen in College of Surgeons (No. 308, natural size).

Figs. 2–7. Cervical vertebræ : *sa*, transverse process of sacral vertebra ; *f*, femur ; *fi*, fibula ; *t*, tibia ; *a*, dermal armour.

PLATE 15.

Enlargement of skull and details of the teeth.

Fig. 1. *n*, nasal ; *f*, frontal ; *p*, parietal ; *so*, supra-occipital ; *pf*, prefrontal ; *pm*, premaxillary ; *s*, ? sclerotic armature ; *q*, quadrate bone ; *pt*, pterygoid bone ; *pl*, palatine bone ; *v*, vomer ; *d*, dentary bone ; *a*, articular bone ; *an*, angular ; *s.an*, surangular ; *sp*, spleniate.

Figs. 2, 3. Teeth in skull.

Figs. 4, 5. Teeth on the pterygoid bone.

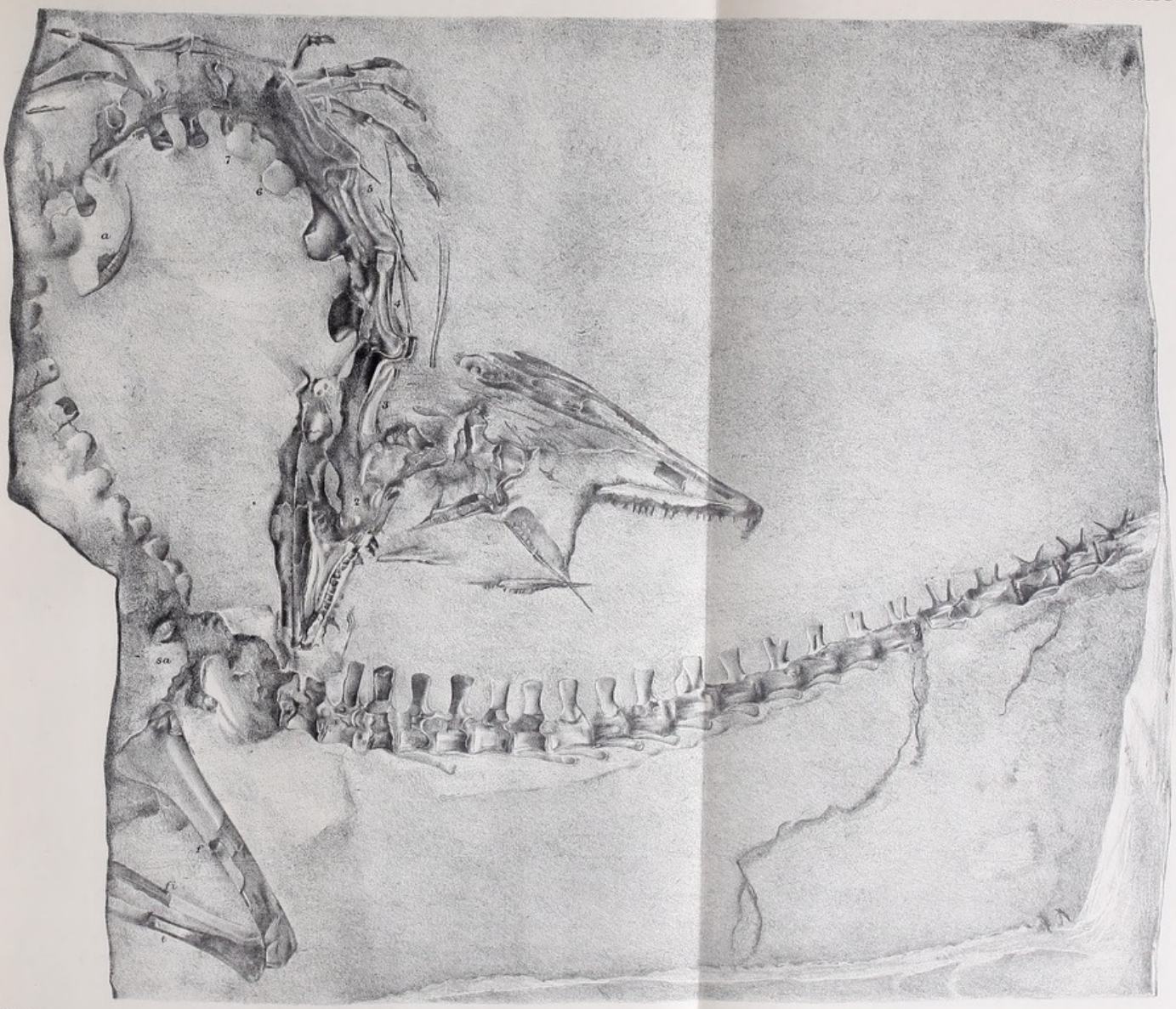
Figs. 6, 7. Teeth on the vomerine bones.

Figs. 8, 9, 10. Teeth in the lower jaw. The appearance of a fang in fig. 9 may result from the alveolar border rising above the base of the tooth.

Fig. 11. Dermal armour.

PLATE 16.

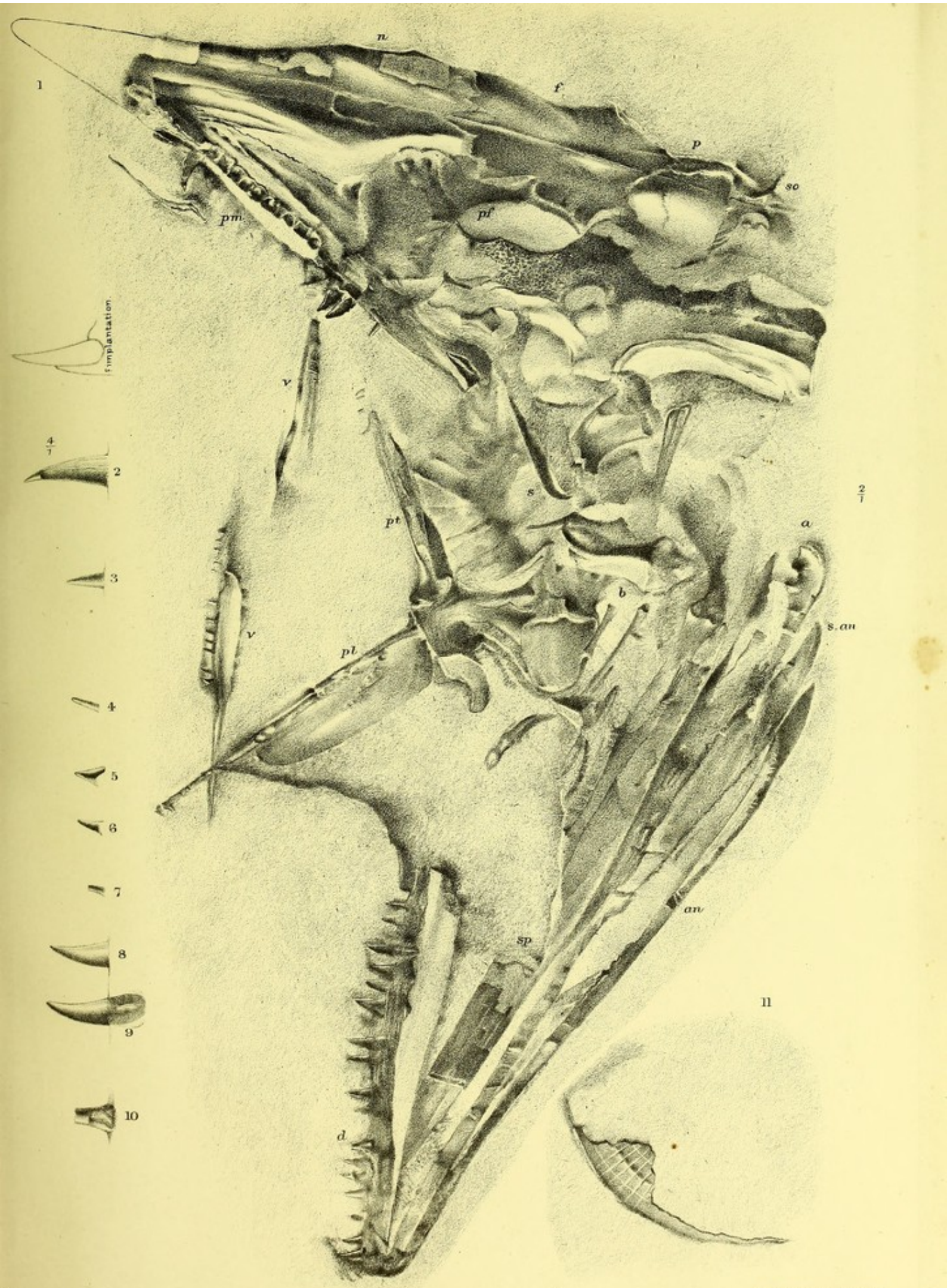
Outline restoration of the skeleton of *Protorosaurus* reduced. The shoulder girdle is omitted. The restoration is based chiefly upon the Vienna specimen.



G. M. Woodward del. et lith.

Protorosaurus Speneri.

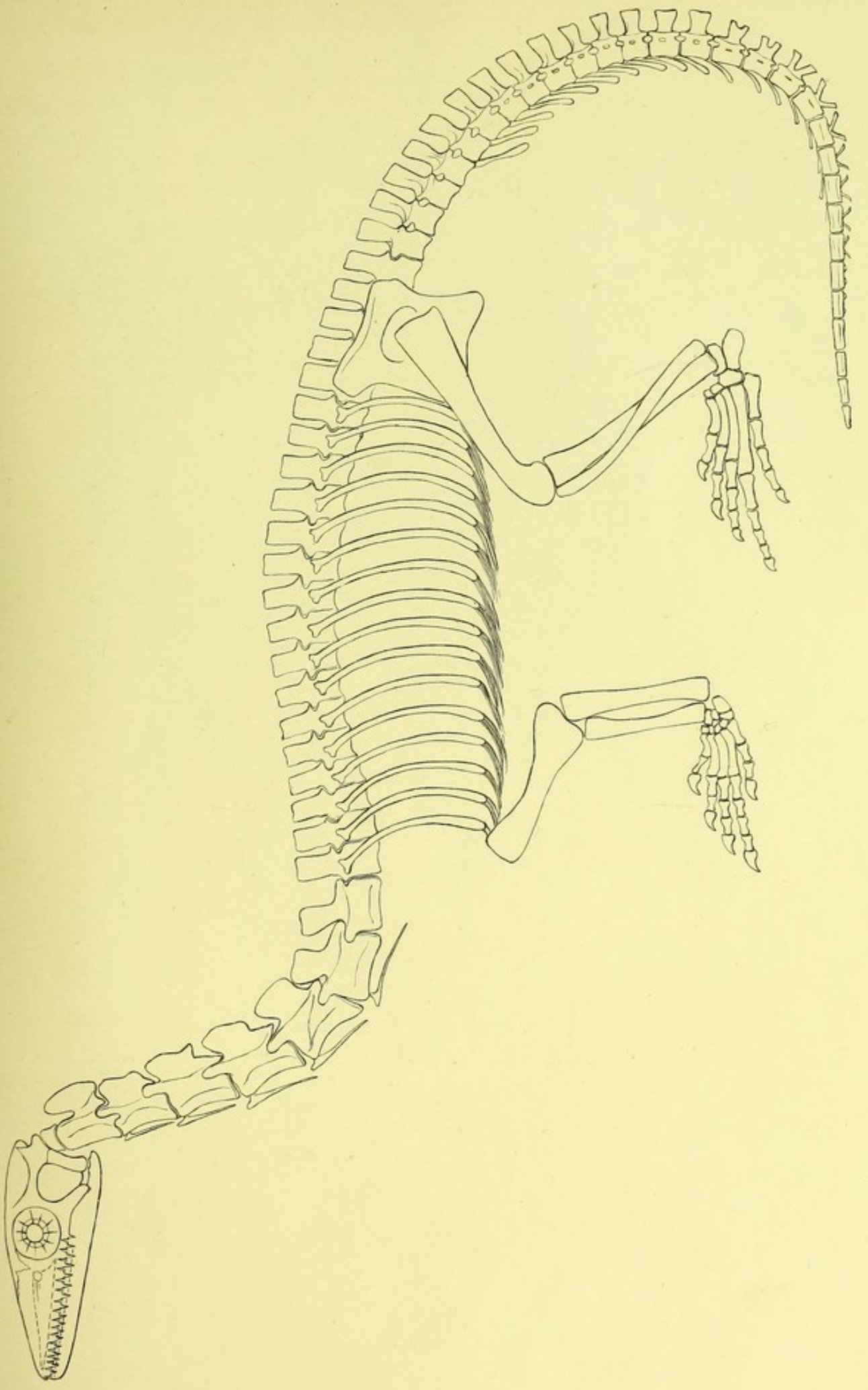
West, Newman & Co. imp.



M. Woodward del. et lith.

West, Newman & Co. imp.

Skull of Protorosaurus Speneri.



Restoration of the Skeleton of Protorosaurus.

G.M.Woodward del. et lith. West, Newman & Co. imp.