# XXXII.—*Description of parts of the Skeleton and Teeth of five species of the Genus* Labyrinthodon (Lab. leptognathus, Lab. pachygnathus, *and* Lab. ventricosus, *from the Coton-end and Cubbington Quarries of the Lower Warwick Sandstone*; Lab. Jægeri, *from Guy's Cliff, Warwick; and* Lab. scutulatus, *from Leamington); with remarks on the probable identity of the* Cheirotherium *with this genus of extinct Batrachians.*

By RICHARD OWEN, Esq., F.G.S., F.R.S., Instit. Reg. Sc. Paris. Corresp.

[Read February 24, 1841.]

PLATES XLIII. to XLVII.

AT a preceding meeting I communicated the results of a microscopic examination of the teeth of the so-called *Mastodonsaurus Jægeri* of the German Keuper, and of the similarly-formed teeth of a reptile from the New Red Sandstone of Warwick, by which it was shown that they differed only in a slight or specific modification of a very peculiar generic structure, which distinguishes them from the teeth of all other reptiles, and apparently from those of all other animals; and as the terms *Salamandroïdes* and *Mastodonsaurus* were objectionable, I proposed that of *Labyrinthodon*, as expressive of this peculiar dental structure, for the genus of reptiles thus characterizing the British and Continental New Red Sandstones.

There remained then, as a subject of interesting research, to determine from the fossils of the British strata referable to the genus *Labyrinthodon*, whether these would be confirmatory or subversive of its Batrachian nature, and whether, if essentially a Batrachian, its remains would manifest any or how great an affinity to the Saurian or any other order of cold-blooded animals. The means of contributing some facts towards the solution of these questions have been obligingly afforded me by Dr. Lloyd of Leamington since the transmission of my former paper to the Society.

Having communicated to Dr. Lloyd the results of the microscopic examination

of the tooth of the *Labyrinthodon laniarius* from the Coton-end quarry, he was so good as to bring up to London the whole of the collection of reptilian fossils from the New Red Sandstone formation of Warwick and Leamington, which are deposited in the museums of those towns, and obtained for me the same liberal permission as on the former occasion, to apply to any of the teeth which these fossils might contain the microscopic test.

Amongst these fossils, two distinct species of the genus *Labyrinthodon* were at once evident, and were represented by portions of upper and lower jaws, an anterior frontal bone, two vertebræ, one of which is nearly entire, a sternum, a fractured humerus, an iliac bone with a great part of the acetabulum, the head of the femur, and two ungueal phalanges. The maxillary fragments containing teeth, besides the agreement in dental structure, as I have ascertained by microscopic examination of sections from each fossil, likewise correspond with the German *Labyrinthodon* in the relative size, mode of implantation, and arrangement of the teeth: the maxillary teeth, *e. g.*, are almost all of moderate and equal size, and these are closely arranged in a single straight row, each tooth being implanted by a broad base in a distinct but not deep socket; whilst the remaining teeth, two or three in number on each side of the upper and lower jaws, are of much larger size, and are situated less regularly at the anterior part of the dental series.

### Labyrinthodon Leptognathus.

I shall commence with the description of the fossils from the Coton-end sandstone quarries, near Warwick, which indicate the smaller species of *Labyrinthodon*, to which the name of *leptognathus* is here given, in reference to the slender character of its long lower jaw.

*Upper Jaw.*—The first of these fossils (Pl. XLIII. fig. 1, 2, 3.) is the anterior part of the left side of the upper jaw, including the nasal bones. It shows that the maxillary or facial division of the skull was broad, much depressed, and flattened, resembling the skull of the gigantic Salamander, and also that of the Alligator, and having the outer surface of the bones strongly sculptured by depressions and furrows as in the Crocodilian family. The portion of jaw here described contains the alveoli of the anterior moiety of the single row of small teeth and the base of one of the great anterior tusks, which ranges in the same line with the small serial teeth, but is directed obliquely backwards, the smaller serial teeth projecting more vertically from the alveolar margin of the jaw, and being slightly inclined outwards. In a few places the contiguous teeth are in place, but throughout the greater part of the series only those of alternate sockets. The base of the tooth projects directly from the outer wall of the socket, there being no alveolar ridge external to it. The alveolar series in this specimen contains in an extent of two inches three lines, thirty-one sockets including the large anterior tooth. The base of the smaller tooth is subcompressed

antero-posteriorly. The large anterior tooth (Pl. XLIII. fig. 2, *a*) is three times the size of the first of the serial teeth which succeeds it, and the size of the serial teeth gradually diminishes as they are placed further back, so that the eighth tooth, counting the sockets from the first, is little more than half a line in diameter at its base; beyond this the teeth are of equal size, slender in proportion to their length, and gradually diminishing from the middle of the crown to the apex, which is not very acute where entire; a linear pulp cavity is continued along the centre of the tooth, nearly to this part. The transverse section of the apical two-thirds of the tooth is cylindrical, its outer surface smooth; the basal third is fluted, as in the teeth of the lower jaw; the outer wall of the socket is anchylosed to this fluted base, and slightly excavated in the interspaces of the teeth that are in place. From the flatness and thinness of the maxillary bones the sockets of the teeth are necessarily shallow. The length of the common-sized serial teeth is about two lines, their greatest diameter one-third of a line; the diameter of the base of the large internal anterior tusk is two lines and a half.

The outer surface of the maxillary bone begins to bend from the perpendicular almost immediately above the alveolar process, and is continued through the rest of its extent in a nearly horizontal plane. The whole breadth of the left upper jaw appears to be included in the fossil for the antero-posterior extent of an inch opposite the middle of the dental series. The breadth of this part from the median longitudinal suture to the external alveolar process is one inch three lines; two inches and a half is therefore the breadth of the skull at this part. The upper jaw gradually expands to the posterior part of the fragment, where it is one inch and a half in breadth on the left side; the anterior part of the fragment, which contains the large tusks, slightly expands or inclines outwards. Where the upper jaw is entire, a portion next the median suture, four lines in breadth, is separated from the maxillary bone by a longitudinal harmonia running nearly parallel with the median one; the bone so defined corresponds with the position of the nasal bone in the Crocodile. The whole of the outer surface of the bones here described is sculptured with large irregular grooves and sinuses. One of the largest grooves, which is an angular and not a rounded furrow, runs nearly parallel with the alveolar process, between two and three lines above it, defining it, as it were, from the upper and flat surface of the jaw; a second principal furrow, as wide but less angular than the outer one, commencing at the posterior part of the fragment, a line and a half distant from the outer one, inclines inwards as it advances forwards with a slightly irregular course, and terminates in the fragment preserved at the naso-maxillary suture. The above two principal grooves are separated by a longitudinal row of elliptical pits, which increase in size as the grooves diverge, and the wider anterior interspace is occupied by additional smaller pits. The portion of the upper maxillary bone included between the oblique groove and the nasal suture is marked with

longitudinal impressions or smaller grooves, which converge anteriorly. The upper surface of the nasal bone is impressed by elliptical and oblong pits, the intervening ridges of which form an irregular open network. The preceding sculpturing of the nasal and maxillary bones resembles that of the corresponding bones in the Crocodiles, but presents a relatively larger and coarser pattern; and when it is remembered that analogous sculpturing characterizes the crania and other bones of certain species of fishes, the ribs and sternum of the *Trionyx* and the jugal bones of the Spotted Cavy among Mammalia, much importance need not be attached to this indication of the Saurian affinities of the present extinct reptiles.

The affinity of the *Labyrinthodon* to the Crocodile is more essentially shown by the broad and entire upper jaw, which deviates widely from the Batrachian condition of the same part.

In both the caducibranchiate and perennibranchiate species the upper maxillary bones present the form of slender elongated styles, attached only by a slightly expanded anterior extremity, from which they project backwards and generally terminate in a free and disengaged point: the external surface rises nearly vertically above the alveolar margin, and is not extended horizontally over the upper surface of the skull, but a very wide interval is left between the maxillary and nasal bones; and while the maxillary bones thus form so small a proportion of the upper wall of the nasal cavity, their palatal processes contribute as little to the formation of the floor of the same cavity. In the Crocodiles, on the contrary, the palatal processes of the maxillary bones extend horizontally inwards and meet at the middle line of the roof of the mouth, and thus form an unbroken floor to the nasal cavity. In the present fossil we have already seen that the superior maxillary extends inwards to the nasal bone, forming with it a continuous strong bony roof over the nasal cavities. The whole of the under surface of the fossil was covered with the sandstone matrix, but the fractured margin, opposite the alveolar border, exhibited the edge of a thin plate of bone, uninterrupted in the longitudinal extent, and forming the floor of a wide and shallow nasal cavity; thus affording a strong indication that the Labyrinthodon breathed air like the higher reptiles. That the bony palate extended as far in the transverse as in the longitudinal extent was indicated by the projecting base of a fractured conical tooth, twice the size of the large anterior fang of the maxillary series, and situated internal to the anterior small serial teeth. Although the *Labyrinthodon* resembles the Crocodile in the character of the bones forming the upper surface of the maxillary part of the cranium, and in the interception of a wide and shallow nasal cavity between two horizontal plates of bone, yet the main evidence of its affinity to the higher Saurian was to be derived from the condition of the bony palate, first in regard to the bones composing it, and, secondly in their relation to the dental system.

In Crocodiles, the floor of the nasal cavity is chiefly formed by the maxillary

bones; in Batrachia, by the palatines and vomer: in all Crocodiles the bones of the palate are edentulous, in all Batrachia they support teeth. There was evidence in the fossil in question of a large laniary tooth projecting from the palatal surface of the mouth, internal to the series of maxillary teeth. I had first to determine whether this was supported, like the great laniary teeth of the lower jaw, upon the same bone, viz. the superior maxillary, which supported the serial teeth, or whether it was a true palatal tooth. I am indebted to the skilful sculpturing of Mr. Scharf, spontaneously undertaken by him with a view to render his drawings of the present fossil more clear and instructive, for the means of determining this question, and for bringing into view some most interesting parts of the cranial anatomy of the *Labyrinthodon*. The palatal processes of the maxillary bones, instead of extending to the middle line, as in the Crocodiles, are very narrow, as in the Batrachia. The osseous roof of the mouth is principally constituted by a pair of broad and flat bones (Pl. XLIII. fig. 2, *b*), analogous to those which Cuvier describes as a divided vomer in the Batrachia. These bones are, however, of much greater relative extent than in any known Batrachia; they defend the mouth with a more extensive roof of bone than exists in any lacertine reptile; physiologically the *Labyrinthodon* in this part of its structure comes nearest to the Crocodile, but the structure itself, morphologically, is essentially Batrachian; that is to say, the bony roof of the mouth is formed by a greater development of the vomerine bones, situated, as in the Batrachians, at a part of the skull which is occupied solely by the maxillary bones in the Crocodiles.

The vomerine bones vary much in their form in the Batrachia; those of the Menopome come nearest in this respect to the *Labyrinthodon*, especially in the expanded anterior extremity of the bone, and it is upon the outer side of this expansion that the large tooth just alluded to is situated in the present species of *Labyrinthodon*. The corresponding part of the palatal bone in the Menopome and gigantic Salamander supports a transverse row of small teeth; and the large tooth of the *Labyrinthodon* is the outermost of a similar transverse row of teeth extending, five in number, across the anterior expansion of each palatine bone, the three median ones being small and equal, the two outermost much larger. In the present fossil these teeth appear to be alternately shed and reproduced; that is, the first, third and fifth, counting outwards from the middle line, were in place, the second and fourth being indicated by their empty sockets: this is analogous to the condition of the maxillary series of teeth, and it is an order of shedding and renewal which is common in many fishes where these processes succeed each other frequently and quickly, and by which the dental series is always kept in an efficient state. The outermost or fifth tooth is placed behind, as well as to the outer side of the socket of the fourth displaced tooth; and, while it terminates the trans-

verse row of palatal teeth, it forms the commencement of a longitudinal row of small and equal-sized teeth, which is continued backward from the large exterior tooth of the transverse row along the outer margin of the vomerine bone: the whole of the series of palatal teeth thus describe an arch nearly concentric and parallel with the external maxillary series of teeth, and the large tusks occupy the corresponding situations in each row. In the lacertian reptiles the examples of such an inner or palatal row of teeth are very few, and the series, when it does exist, is very short, and is situated towards the back of the palate upon the pterygoid bones, as in the *Iguana* and *Mosasaur*. With the Ophidians the comparison of the present reptile is out of the question; and their palatine teeth are never arranged transversely to the axis of the mouth. In the Batrachians this is the most common disposition of the palatal teeth; they form a short transverse series at the anterior part of the divided vomer in the Frog, and at the posterior part of the divided vomer in certain Toads, as *Hyladactylus*; the palatal teeth form an extensive transverse row along the anterior margin of the vomer in the *Menopome* and gigantic Salamander, but are not extended longitudinally. In the *Amphiume*, on the contrary, the palatal teeth form a nearly longitudinal series along each outer margin of the long and narrow vomerine bone: the extinct *Labyrinthodon* combines both these dispositions of the palatal teeth. In the Menopome and most other Batrachians the posterior extremities of the maxillary bones are free, and the wide posterior palatal spaces, which are covered by membrane only in the recent animal, are uninclosed externally. In the genus *Rana* the pterygoid bones extend outwards and forwards so as to touch the palatine and maxillary bones, and circumscribe this aperture, which, however, is of great extent. In the *Labyrinthodon* the aperture (Pl. XLIII. fig. 2, *c*) is much more completely circumscribed by bone, and, from the greater development of the vomerine bones, its extent is much diminished. In the present specimen the posterior palatal aperture forms a longitudinal ellipse, ten lines in the long and five lines in the short or transverse diameter: it occupies apparently the same relative position as in the *Iguana*, but a much smaller proportion, if any, of its posterior contour must be completed by the pterygoid bone in the *Labyrinthodon*. The anterior transversely produced plate of the vomerine bone has its external margin expanded in the longitudinal direction, and abuts by an extensive slightly convex surface against the narrow palatal process of the upper maxillary bone. The anterior and posterior margins of this process of the vomerine bone are concave, the former (Pl. XLIII. fig. 2, *d*) being the posterior boundary of the anterior palatal opening, and the latter the anterior boundary of the posterior palatal opening. What the extent of the anterior palatal orifice may have been, and how far the superior maxillary and intermaxillary bones extended beyond the part of the upper jaw at which the present fossil terminates, is indicated by the length of the lower jaw of

the same species next to be described, and by the fragment of the upper jaw of the second and larger species of *Labyrinthodon*. The broad palatal plate of the palatine bones in the present fossil extends two inches behind the transverse row of teeth, and probably much further in the entire skull; it is nine lines in breadth anteriorly and six lines in breadth on the inside of the posterior palatal foramen; the surface next the mouth, which does not support teeth, is smooth and slightly convex. From the curve of the remaining part of the contour of the anterior palatal foramen (*d*, fig. 2. Pl. XLIII.), it may be concluded that it was not confluent with its fellow, as in the Crocodiles, or as in the Frog and Menopome, but that the two were distinct as in the *Iguana*. From the structure of the portion of the nasal cavity preserved in the present fossil, it may be inferred that the *Labyrinthodon* differed from the Batrachians, and resembled the Saurians in having distinct posterior nasal apertures surrounded by bone, and that its mode of inspiring air was the same as in the higher organized reptiles; other physiological inductions consequent upon this will be noticed in the description of the portion of skull of the larger species of *Labyrinthodon*; and I shall conclude the description of the present fossil by again calling attention to the satisfactory proof of its essentially Batrachian affinities, which the structure of the palate and palatal teeth have yielded.

*Lower Jaw.*—The next fossil which I proceed to describe, and which, like the preceding one, is from the sandstone in the neighbourhood of Warwick, consists of six inches of the anterior part of the left ramus of the lower jaw (Pl. XLIV. figg. 8 and 9); this ramus is slender, straight, and with its symphysial extremity abruptly bent inwards; the inner line of the symphysis here forming a regular and deep curve. Its breadth, at the posterior fractured part, is ten lines; at the anterior part, behind the inflected symphysis, seven lines; the breadth of the anterior fractured portion is one inch. The structure of this long and straight ramus of the jaw presents almost as striking a Batrachian character as any of those derived from the foregoing fossil; that is to say, the angular piece is of great breadth, extends on both sides of the jaw, and is continued forwards to near the symphysis, forming the whole of the inferior part of the ramus of the jaw, and extending upon the inner as far as upon the outer side of the ramus, the inner plate performing the function of the detached 'os operculare' in the Crocodile's jaw. The dentary piece is supported upon a deep and wide groove along the upper surface of the angular piece, which groove looks obliquely outwards; the angular piece also projects beyond the outer edge of the groove, so as to form a strong convex ridge on the external side of the jaw below the dentary piece; this character, which in the large Bull-frog (*Rana pipiens*) is confined to the posterior part of the maxillary ramus, is here continued to near the anterior extremity. The teeth in this fragment are long and slender, and so closely correspond in size and shape with those in the upper

jaw last described, that they must be regarded as belonging to the same species. There are not less than fifty sockets in a single linear series, and at the anterior inflected part of the jaw is the base of the socket of a large tooth six lines in diameter; the serial teeth gradually diminish in size toward the anterior portion of the jaw; the posterior teeth, which are slightly compressed at their base, in the antero-posterior direction, present here about a line and a half in diameter; the anterior ones half a line across the same part; the length of some of these small anterior teeth above the sockets is three lines, they are terminated by subacute extremities; the sockets do not lie between parallel lines; the alternate ones are placed a little more internally. The teeth were present chiefly in the more external sockets; but where they remained in both, the row of teeth presented the same slightly zigzag disposition. Owing to the circumstance of the anterior part of the jaw having been broken, it cannot be determined whether any of the smaller or serial teeth were continued external to the large anterior tusks,—a remarkable ichthyic character which I shall have to notice in a subsequent fossil. The sockets of the teeth are as shallow in the present as in the preceding fossil; the outer wall is more developed than the inner, and the anchylosed bases of the teeth more nearly resemble in their oblique position those of the existing Batrachia. The teeth are directed slightly inwards, and are probably received within the series of the upper jaw when the mouth is closed. The striation and fluting is confined to the basal third of the tooth, as is also the labyrinthic inflections of the external cement. Above this part the dentine consists of fine calcigerous tubes, radiating from the linear remains of the pulp-cavity at right angles to the surface of the tooth; being parallel with the axis of the tooth where they form its apex, and gradually inclining outwards until they become transverse to that axis, which is their disposition in the body of the tooth, between the apex and the commencement of the inflected vertical folds of the cement. Beyond this part, therefore, the tooth of the *Labyrinthodon* resembles, in the simplicity of its intimate structure, that of the entire tooth of the ordinary Batrachia and of most reptiles. The vertical inflected processes of the cement are at first short and straight, occurring at pretty regular distances around the circumference of the tooth; so that here the tooth partakes of the structure which I have before described as characterizing the base of the tooth of the *Ichthyosaurus*. Soon, however, the primitive inflected folds of cement sink deeper into the dentine and commence their undulating course; other processes, at first simple like the preceding, begin to penetrate the dentine at the interspaces of the primary folds; these begin to take on a sinuous course a little nearer the base of the tooth; and a transverse section at this part exhibits the modification of the labyrinthic structure exhibited in the woodcut, fig. 2, p. 511.

The long and slender character of the maxillary ramus, suggesting the name of

the species of *Labyrinthodon* to which it belonged, will give an idea of the proportion of the skull included in the first-described fossil; the length of the head as compared with the breadth approximates more nearly to the proportions of that of the Crocodile and *Nothosaurus* than to those of the ordinary Batrachian skulls: among existing Batrachia, the Amphiuma, in this respect, seems to have most closely resembled the present species of *Labyrinthodon.*

*Vertebra.*—The vertebra here described (Pl. XLV. figg. 5–8.) was discovered in the same sandstone quarry at Coton-end as the portion of the skull and upper jaw of the *Labyrinthodon leptognathus*, and it bears the same proportionate size to those parts as exists between the vertebræ and skull of the Menopome, and between a larger vertebra from the Warwick sandstone and the jaws of the larger species of *Labyrinthodon* next to be noticed. In the larger vertebra alluded to there is evidence of a condition of the articular extremities characteristic of the lower or perennibranchiate division of Batrachia among existing reptiles. From the essential resemblance which will be pointed out between the jaws of the two species of *Labyrinthodon*, it could not be anticipated that their vertebræ would present two types of structure so different as the bi-concave and concavo-convex articulations. From the figure given of the smaller vertebra now under consideration*, it appeared nevertheless that one of the articular surfaces of this vertebra was convex, and from the form of the articular processes (for this figure is unaccompanied by any detailed description), this surface seemed to be the posterior one; I therefore wrote to Dr. Lloyd, requesting permission to have the vertebra transmitted to me. It was imbedded, with the exception of the surface figured in the plate quoted, in the sandstone matrix. Part of the anterior articular surface of the body of the vertebra was uncovered, the opposite end of the vertebra was broken off, and a mass of the sandstone projected from the broken surface. With the assistance of Mr. Clift, sufficient of this matrix was cleared away to expose the centre and bottom of a concave surface (Pl. XLV. fig. 8.), to all appearance similar in depth and form with that on the anterior end of the bone (Pl. XLV. fig. 7.); thus proving its correspondence in this important character with the vertebra of the larger species of *Labyrinthodon.* The body of the vertebra is subelongate and subcompressed, with a smooth exterior surface terminating below in a slightly produced longitudinal median ridge. Its length is nine lines, its breadth at the middle four lines; at the articular extremity nearly six lines. The articular concavity appears, as in the larger vertebra, not to have begun immediately from the margin, but to have been surrounded by a flattened circular surface; this part, however, is much broken. The depth of the articular concavity is not very great; at least four lines of the osseous tissue must have intervened at the middle of the body of the vertebra between the anterior and posterior concavities; these are much deeper and more conical in the perennibran-

* Geol. Trans., Second Series, vol. v. Pl. XXVIII. fig. 10.

chiate reptiles. The smooth lateral surface of the vertebral body is not continued in a regular curve to the lower margin of the vertebra, but bends toward that ridge somewhat abruptly at two lines distance from it, as shown in figures 5. and 7. Pl. XLV. The present vertebra exhibits the same exceptional condition in the Reptilian class as do the vertebræ of existing Batrachians, in having the superior arch or neurapophyses anchylosed with the centrum. The vertebra belongs to the dorsal series, and from each side of the base of the neural arch there extends obliquely, outwards and upwards, a thick and strong transverse process, the fractured condition of which, on both sides, prevents, however, its length from being ascertained. A very slight ridge ascends from the centrum along each side of the under part of the transverse process; the two ridges slightly converging and bounding a shallow concavity beneath the transverse process. The upper part of the base of the transverse process is continued in an uninterrupted curve into the posterior oblique processes, but it is separated from the anterior ones by a deep oblique and slightly curved fissure. The anterior oblique articular surfaces commence three lines behind the articular surface of the body of the vertebra; they diverge as they pass forward, and thus leave that part of the medullary canal exposed; the aspect of the articular surface is obliquely upward and inward. The spinous process commences at their angle of union, and its base is extended to the corresponding angle of union of the posterior oblique processes, gradually increasing in thickness as it proceeds backwards; the spinous process was broken off close to its base. The posterior articular processes extend beyond the posterior articular surface of the body of the vertebra as far as the anterior articular surfaces fall short of it; and they must have covered in the succeeding vertebræ that portion of the spinal canal so left unprotected by its own arch. The spinal canal is slightly expanded at its two extremities, and appears, so far as I have been able to fairly excavate it, to sink in its progress into the substance of the centrum, approaching, as it were, to that peculiar structure which prevails in the still more ancient reptiles of the magnesian conglomerate. The strength and direction of the transverse processes indicate an expanded respiratory cavity protected by ribs.

*Episternum.*—A symmetrical bone, most resembling the episternum of the *Ichthyosaurus*, but with the median piece broader, flatter and thinner, so nearly corresponds in its proportions with the preceding vertebra that I here describe it, as belonging very probably to the *Labyrinthodon leptognathus* (Pl. XLV. figg. 9 and 10). The stem, or middle piece of this bone diminishes to a mere plate or film below, and thickens towards the upper end where the cross-pieces are given off, and these pass outwardly at right angles to the median stem and support, each, a pretty deep and wide groove, contracting to a point at the upper part of the median stem: these grooves indicate strongly the presence of clavicles, which are wanting in the Crocodiles, where the sternum or episternum presents only its median piece, with

broad lateral cartilages for the attachment of the coracoids. In the Lacertians it would seem that these lateral cartilages were ossified, and the sternum thus converted into a large rhomboidal plate.

In the anourous Batrachia there are clavicles as well as coracoids; and in the Toad the mesial extremities of the clavicles rest upon the transversely expanded anterior extremity of an episternal bone, which among recent reptiles bears the nearest resemblance to that of the *Labyrinthodon*, to which genus the present bone most probably belonged. It is represented of the natural size, at Plate XLV. figg. 9. and 10.

The fossils above described, consisting of a part of the skull and dental system, a dorsal vertebra, and an episternum, prove the *Labyrinthodon* to have been essentially Batrachian, with striking and peculiar affinities to the higher Saurians; these affinities lead, in the form of the skull and the sculpturing of the cranial bones, to the Crocodilian group; and in one part of the dental structure, in the form of the episternum and the biconcave vertebra, to the extinct Ichthyosaur; while in the condition of the bony palate the deviation from its essentially Batrachian character produces a resemblance to the Lacertian type.

The anchylosis of the base of the teeth to distinct and shallow sockets is a point in which the *Labyrinthodon* resembles certain fishes, as the *Sphyræna*: I am disposed also to believe, from the absence of any trace of alveoli of reserve for the successional teeth, that these were reproduced, as in many fishes, especially the higher *Chondropterygii*, which, it may be remembered, formed the *Amphibiæ natantes* of Linnæus, in the soft mucous membrane or gum which covered the alveolar margin, and subsequently became fixed to the bone by anchylosis, as in the Pike and Lophius among osseous fishes. Nor is it extraordinary that the present extinct Batrachian genus should have its relations of affinity thus radiating in different directions, since we find in the extinct reptilian forms of a later epoch, the combination of Saurian characters with Ichthyic vertebræ and extremities. We possess, as yet, no indication from fossils of the structure or form of the locomotive organs of the *Labyrinthodon leptognathus*. But it is by no means improbable that the impressions figured by Messrs. Murchison and Strickland, found on a slab of sandstone from Shrewley Common, Warwick, are the foot-marks of this very species.

The learned authors of the paper quoted, state their belief that these footsteps "were formed by an animal probably allied to the Batrachia." (*l. c.* p. 318.) They differ from the feet of Frogs in having the outer toe of both the hind- and fore-feet the longest, while in Frogs the second toe is longest: it is moreover evident that the animal possessed a tail. In both these deviations from the Batrachia a corresponding approach is made to that family of reptiles to which the modifications of the Batrachian characters of the fossils in question have tended.

LABYRINTHODON PACHYGNATHUS.

*Lower Jaw.*—I now proceed to describe the fossils on which I have founded a second species of *Labyrinthodon*, and shall commence with a well-preserved portion of the right ramus of the lower jaw (Pl. XLIV. figs. 1, 2, 3.). This fossil measures nine inches and a half in length; the bone is thick and rounded, one inch and a half deep and one inch broad at the posterior fractured part, thirteen lines broad and seven lines deep at the anterior expanded and subdepressed end, which is curved inwards towards the symphysis of the jaw, and which supports two of the great cuspidate or laniary teeth, and the socket of a third. The structure of this lower jaw, which was broken across into two nearly equal portions, was the first object of attention. On the inner side of the anterior moiety it appeared to be strengthened by an opercular piece, in the form of a thin plate, gradually narrowing to a point, and terminating at the beginning of the inward curvature of the ramus (fig. 2.). This was obviously a more complicated structure than exists in the jaws of fishes; whilst in reptiles the inner side of the ramus of the jaw is supported by a distinct plate of bone in both Batrachians and Saurians. This complication, however, is due to a different structure in the Batrachia from that which obtains in the Sauria. In the lower jaw of the Frog, for example, it is produced by a continuation of the angular element upon the inner side, as high as upon the outer side of the jaw; whilst in Saurians the inner splint-like plate exists as a distinct piece, to which Cuvier has given the name of 'os operculare.' The question then to be determined was, to which of those structures was due the appearance above mentioned, of an opercular piece on the inner side of the maxillary ramus in the Keuper reptile? I may first observe, that the outer side of this ramus presents a structure not to be found in any Saurian jaws, viz. a well-marked longitudinal impression running parallel with the lower border of the jaw, about half-way between that and the alveolar border, towards which it gradually inclines, and then abruptly bends downwards and backwards. This impression evidently leads to a harmonia or toothless suture (like those which join together the different elements of a compound jaw), into which the sandy matrix has insinuated itself. The lower piece corresponds in depth and forward production with the large angular element of the jaw of the Frog, in which the angular piece is continued nearer to the symphysis than in any known Saurian; but in the fossil it swells out as it were beyond the level of the upper or dentary piece, and forms a bold and broad convex ridge along the lower part of the outer side of the ramus, which subsides at only a short distance from the symphysial bend. The angular piece forms a similar projection on the outer side of the posterior half of the jaw in the Frog.

Two transverse fractures of the present fossil display the relations of the external plate of the angular piece with the thin internal bony laminæ; the two pieces are

uninterruptedly confluent, and form a single broad and strong piece of bone, supporting the dentary piece upon a groove along its upper surface (fig. 2, *b.*), and terminating anteriorly at the bend of the expanded dentary element, which there receives the extremity of the angular element in a notch.

The fossil fragment exhibiting the above structure is five inches and a half in length, and probably forms little more than the anterior third of the ramus of the jaw; there is sufficient, however, to demonstrate that its structure is essentially Batrachian. A similar portion of the lower jaw of a Saurian would have exhibited either the dentary element simply, or inclosed at the posterior fractured end, between the extremities only of the separate angular and opercular elements. The continuation of the angular element alone, forming the lower half of the ramus, to near the symphysis, and supporting the dentary piece in a groove on its upper surface, is as striking a Batrachian character in the fossil of the British sandstone as that observed by Prof. Jaeger in the occipital bone of the great *Salamandroïdes* of the German Keuper.

The smaller serial teeth in the present portion of jaw are about forty in number, and their sockets are in close contact with each other; they very gradually diminish in size as they approach both ends of the series, but chiefly so towards the anterior part of the jaw. One of the smallest teeth at this end of the jaw is recumbent in front of the great laniaries; I think it very probable that it was an incompletely developed tooth of replacement, not yet erected and anchylosed to the bone,—a circumstance in accordance with the view which I have entertained of the place of development of the successional teeth. The alternate sockets are empty in a considerable portion of the posterior part of the series, agreeably with the law of shedding and replacement illustrated in the *Lab. leptognathus*, so that the teeth thus appear to be separated by wider intervals than their sockets prove them to be. The form of the teeth is conical, with the base slightly compressed in the direction of the axis of the jaw; the largest transverse diameter of one of the posterior of these serial teeth, where it emerges from the socket, is three lines; the same diameter of the anterior serial tooth is one line and a half, its length four lines and a half. The great laniary teeth appear to be three in number in each symphysis, and the one nearest the symphysis is somewhat larger than the other; but they are probably not in place and use at the same time. The greatest diameter of the base of the largest of these tusks, which is subcompressed, is five lines; its length, judging from an entire tooth of the same species, must have been at least one inch and a half. The lines of the inflected cæmentum form well-marked longitudinal striæ all around the basal half of the tooth, and the interspaces of the striæ form convex ridges, as in the large tooth of which I described the labyrinthic structure in my previous paper, and which is most probably a laniary tooth of the present species. These ridges are fewest near the termination of the striæ, being divided and multiplied by new longitudinal striæ,

caused by new inflected folds of the cement near the basis of the tooth; the apical half of the tooth has a smooth and polished external surface; the pulp-cavity is continued of small size into the centre of this part of the tooth. In the smaller serial teeth, which in other respects, except their less gradual diminution of size, correspond with the preceding description of the anterior larger tusks, the central pulp-cavity is more quickly obliterated: the texture of the teeth is dense and brittle; the alveoli, as already described, are large, moderately deep, but complete. The outer wall of the alveolar processes in the present fossil is not higher than the inner wall, as is the case in Frogs and Toads, the Salamanders and the Menopome, in all which Batrachians the base of the teeth is soldered to the inner side of an external alveolar plate, as in the Lacertians. It may be said, therefore, that in the more complete structure of the socket the *Labyrinthodon* manifests an affinity to the Crocodilian and Plesiosaurian reptiles; but, on the other hand, a similarly complete dental socket is present in certain Scomberoid and Sauroid fishes. The base of the teeth, moreover, in the *Labyrinthodon pachygnathus*, as in the *Lab. leptognathus*, is anchylosed to the bottom of the socket, as is likewise the case in the fishes cited. We have a still more striking ichthyic character in the *Labyrinthodon*, in the continuation of the row of small teeth anterior and external to the two larger teeth. For a double series of teeth, thus occasioned, does not exist in the maxillary bones, either superior or inferior, of any Saurian reptile; but in the Batrachian order it is found in the lower jaw of the *Cæcilia*, and it is not an uncommon structure in fishes. We cannot notice without interest the manifestation of another ichthyic character in the primæval Batrachia whose remains we are attempting to interpret*.

*Upper Jaw.*—The second fossil of the *Labyrinthodon pachygnathus* which I have to notice is a *fragment* of the superior maxillary bone of the left side (Pl. XLIII. fig. 4.), three inches and a half in length, including twenty-four of the serial teeth; these teeth resemble those of the lower jaw, being moderately short, with a thick antero-posteriorly subcompressed, finely-striated base, and a sharp, subincurved apex. The outer alveolar plate is rather deeper than the inner one, but the teeth are implanted in distinct, though wide and shallow, elliptical sockets. The labyrinthic structure is confined to the striated base: in the upper half of the crown it is as simple as in the *Ichthyosaurus* or Crocodile, but there is no true enamel: the outer coat consists of a thin layer of cement. The relation of the cement to the dentine, as exhibited by a transverse section of the tooth, one line above the socket, is well calculated, from its greater simplicity, to illustrate the principle of the more complicated modifications of the labyrinthine dental structure first discovered. The processes which radiate from the pulp-cavity, twelve in number at the line of section, proceed straight to about midway between the

* The successional teeth in *Plesiosaurus* and *Nothosaurus* are sometimes so far developed before they displace their predecessors, as to cause the appearance of a double row.

centre and the circumference of the tooth, where each terminates in a slight dilatation. In like manner, the inflected folds, converging from the circumference of the section, proceed inwards in a straight line to within one-fourth of the distance to the central pulp-cavity. The inflected substance consists of the thinnest layer of cement. The calcigerous tubes radiate according to the usual laws, and resemble in diameter, in the width of their interspaces, in their secondary undulations, their dichotomous bifurcations and small lateral branches, the same tubes in the large tusk with the more complex labyrinthine structure.

The external wall of this portion of the jaw is straight, and nearly flat; and slopes upwards and slightly inwards from the narrow ridge which runs along the outside of the alveoli. The inner or palatal process of the jaw is as narrow as that of the *Labyrinthodon leptognathus*, and terminates internally by a smooth, regularly rounded, convex margin, which describes a slight concavity in the antero-posterior direction, and most probably formed the external boundary of the posterior palatal opening: the breadth of the palatal plate of the maxillary bone at the middle of this fragment is four lines, but at each extremity of the fragment it is six lines. At the posterior part of the fragment the palatal surface is flat, and impressed with a few small pits: anteriorly it is traversed by a shallow longitudinal groove.

This condition of the palatal process of the maxillary corresponds more closely with that in the Frog than in any other existing reptile. In all the Batrachia the palatal process of the maxillary bone is very narrow, and is not extended inwards at any part to join the palatine bone, so as to complete the bony roof of the mouth; but the inner boundary of the palatal process in the Frog is more parallel with the alveolar ridge; and a portion, corresponding in extent with the present fragment, would not give that concavity of the inner border of the palatal process which the present fragment presents.

I suppose, therefore, that the palatal process here must have extended inwards at the anterior part of the maxillary, and probably so as to join the palatal bone, as in the *Lab. leptognathus*, and agreeably with the traces of an extended bony floor of the nasal cavities exhibited in the portion of the upper jaw which comes next to be considered.

This characteristic fossil, which is from the quarry at Coton End, includes a considerable portion of the left maxillary and intermaxillary bone, and shows the lateral contour of the anterior palatal foramen (Pl. XLIII. figg. 9 and 10). The superior or external plate of the intermaxillary bone is broken away, but the external plate of the maxillary bone remains, together with the internal or palatal plate, in the portion of that bone which is here preserved. The outer margin of the present fossil is impressed with a portion of a wide groove, having the same sinuous contour as the long oblique groove in the fragment of the upper jaw of the smaller species of *Labyrinthodon*. The inner border of the fragment is obliquely

thinned off, apparently for supporting the corresponding margin of the nasal bone: two or three wide, deep, subangular longitudinal grooves run nearly parallel with this border, external to which other shorter and similar grooves radiate towards the outer margin of the fragment. In no species of Crocodile is the external surface of the cranial bones sculptured by such deep and wide incisions, or excavations, relatively to the size of the bones. The ridges between these grooves in the *Labyrinthodon* have their edges rounded off. The depth of these inflections of the external surface of the bone brought to mind the corresponding inflections of the external surface of the teeth which form so striking a characteristic of the present extinct Batrachian family. The interspace between the sculptured maxillary bone and the co-extensive palatine plate here preserved, is nowhere more than two lines and a half in depth; but the two plates may have been unnaturally approximated by pressure. The wide and shallow nasal cavity is occupied by the matrix (Pl. XLIII. fig. 10, *e*).

The chief deviation from the Crocodilian type of structure which the present fossil presents, is the continuation of the palatal plate (*b*) of the intermaxillary bone for some distance, about an inch, to the outer side of the base of the external plate or process.

In the Crocodiles the external wall of the intermaxillary bone rises from the outer border of the palatal process, and is united by the whole of its posterior margin with the maxillary bone. A different structure of the intermaxillary bone prevails in the Batrachia: here the external is not co-extensive with the internal or palatal plate, but it rises from a longitudinal tract traversing the middle of the palatal plate, in the form of a compressed process, leaving an interspace between its outer margin and the maxillary bone: in the Frogs there is likewise an interspace between the external plates of the two intermaxillary bones, which does not exist in the Menopome, among the perennibranchiate Batrachia. Now, in the *Labyrinthodon*, the intermaxillary bone presents the same peculiar modification of the Batrachian condition of this bone as in the higher organized Batrachia. The palatal process of the intermaxillary, for example, is extended beyond the outer plate, both externally (Pl. XLIII. fig. 9, *b*), and, but in a less degree, internally, where it forms part of the boundary of the anterior palatal foramen (fig. 9, *c*), whence the outer plate rises in the form of a compressed process from a longitudinal tract (fig. 9, *a*), on the upper part of the palatal process. The outer plate in the specimen is broken off near its origin, and the fractured surface gives the breadth of its base, stamping the fossil with a Batrachian character conspicuous above all the Saurian modifications by which the essential nature of the *Labyrinthodon* appears at first sight to be masked.

*Anterior frontal.* (Pl. XLIII. fig. 11.)—With the indications of Crocodilian affinities in the maxillary portion of the cranium just described, we cannot feel sur-

prised to find other bones of the cranium in the present Batrachian family modified after the same type; such appears to be the case in the fossil now under consideration, which I regard as an anterior frontal bone, similar in form to that of the Crocodile. It presents a superior, horizontal, expanded and slightly convex surface, pitted with large irregular impressions, thinning off to a fine edge at the inner side, and sending downwards from its posterior and outer part a broad and slightly concave process, the smooth surface of which strikingly contrasts with the irregularly sculptured one of the horizontal plate. This smooth surface, if I am correct in my idea of the nature of the bone, must form a part of the anterior boundary of the orbit, which it indicates to have been of large size. The posterior margin of the horizontal plate does not extend so far back, or overhang so abruptly the smooth orbital plate, as in the Crocodile.

The orbital plate is also characterized in the present fossil by a deep pit, from which a groove is continued forwards; there is a smaller foramen in the corresponding part of the smooth orbital plate in the anterior frontal of the Crocodile. The present fragment is two inches and a half in length, and the same in breadth; the depth of the orbital plate is one inch three lines; the thickness of the fractured angle of the bone, which would have joined the lachrymal, is three lines.

Hitherto I have not received any other portions of the cranium of the *Labyrinthodon pachygnathus* than those which have been described. They demonstrate that the facial or maxillary part of the skull was formed in the main after the Crocodilian type, but with well-marked Batrachian modifications in the intermaxillary and inferior maxillary bones. The most important fact which they make known is, that this Sauroid Batrachian had subterminal nostrils leading to a wide and shallow nasal cavity, extending horizontally backwards, and separated by a broad and almost continuous palatal flooring from the cavity of the mouth; which plainly indicates that their posterior apertures were placed far behind the anterior or external nostrils; whereas, in the air-breathing Batrachia, the nasal meatus is short and vertical, and the internal apertures pierce the anterior part of the palate, where they are readily closed and opened by the tongue in the act of swallowing the air.

But breathing by deglutition must have been as difficult, if not as impossible, in the *Labyrinthodons* as in the Crocodiles; and we may infer, therefore, that the apparatus for breathing by inspiration must have existed in the one as in the other. The inability to supply air to the lungs by deglutition is compensated for in the Crocodile by the power of dilating the cavity containing the lungs; which power is given by an apparatus of ribs encompassing the thorax and of their appropriate muscles. It may be reasonably anticipated, therefore, that the skeleton of the *Labyrinthodon* will be found to be provided with well-developed ribs, which,

if present at all in the existing Batrachia, exist only as straight and short rudimentary styles. Now the cause, or the essential condition of this defective state of the costal apparatus in the existing Batrachia is well known to be their fish-like mode of generation; viz. the simultaneous development of their numerous ova, which demands a capacity and produces a distention and dilatation of the abdomen incompatible with the presence of the bony hoops which encompass that cavity in the reptiles that develope fewer ova, and mature them at successive intervals. Hence, if the structure of the nasal cavity of the *Labyrinthodon*, as displayed in two of the fossils here described, forbids the supposition that they breathed air after the manner of Batrachians, we may infer a Saurian condition of a part of their skeleton which has not yet been seen, and even gain considerable insight into the generative economy of a race of reptiles peculiar to one of the most ancient periods at which this order of vertebrate animals was called into existence.

*Vertebra.*—Of the bones of the trunk there exists in the present collection only a fragment of a vertebra referable to the *Labyrinthodon pachygnathus* (Pl. XLV. figs. 1–4.). The fragment in question consists of the upper part of the body of a vertebra, with the anchylosed neurapophyses, from which the transverse, the spinous and the posterior oblique processes have been broken away. The length of this fragment is two inches; the breadth of the articular end of the body of the vertebra one inch three lines; the upper half of this surface is preserved at the posterior part of the vertebra, showing that it is slightly concave, in which it deviates from the vertebral system of existing Saurians and anourous Batrachians, but corresponds with the vertebra of the *Labyrinthodon leptognathus* before described.

The fractured surfaces for the transverse processes show them to have been broad and thick at their origin; they measure nine lines in antero-posterior diameter and four lines in vertical extent. Below the transverse processes the body of the vertebra is compressed and concave; there is a small excavation at the anterior part of the base of each transverse process. The spinal canal is five lines broad and four lines high. The base of the spinous process is much contracted at the middle of the neurapophysial arch, from which point it has been based upon two distinct ridges, which thence diverge to the outer side of each of the anterior oblique processes. The articular surface on each of these processes is flat, and looks upwards and slightly inwards.

The concavity of the posterior articular surface of the centrum is demonstrated, and a like configuration of the anterior end may be safely inferred: thus, in the biconcave character of the vertebra, its lateral compression and smooth surface, the thickness of the transverse processes, and the size, shape and direction of the oblique processes, a close generic resemblance is manifested between the present vertebral fragment and the more perfect one of the *Labyrinthodon leptognathus*; and the fissure at

the anterior part of the transverse process must be regarded as a corresponding structure with that more extensive fissure which separates the anterior part of the transverse process from the base of the oblique process in the smaller vertebra. It is, therefore, a modification to which attention should be paid in examining vertebræ or portions of vertebræ from the New Red Sandstone.

*Bones of the Extremities.*—The fossils to be noticed under this head are few, but significant.

I am disposed to refer to the anterior extremities the proximal end of a long bone (Pl. XLV. figg. 11–15.), which presents all the characteristics of the corresponding part of the humerus of a Toad or Frog; viz. the convex, somewhat transversely extended articular end, the internal longitudinal depression, and the well-developed deltoid ridge. This fragment, which includes perhaps the upper half of the bone, is two inches in length and thirteen lines in breadth; it diminishes, chiefly by the subsidence of the deltoid crest, to a subtrihedral shaft with the angles rounded off; it presents moderately thick compact walls, with a central medullary cavity. In this structure, as well as in its general form, the present bone agrees with the Batrachian and differs from the Crocodilian type.

*Right Ilium.*—The most complete bone in the present collection, not belonging to the cranial series, is the right ilium (Pl. XLV. figg. 16. and 17.), which presents, like many of the previously described bones, a combination of Crocodilian and Batrachian characters. It is nearly six inches in length, and is therefore most probably referable to the same species as the jaws last described. It supports on its anterior and outer surface the same proportion of the acetabular cavity as in the Crocodiles. This cavity is bounded on its upper part by a produced and sharp ridge, as in the Frog; which ridge is not emarginate at its anterior part, as in the Crocodile, but it subsides at the posterior part of the cavity, the surface of which is here continuous with the outer surface of the produced posterior part of the bone.

Above the acetabulum, in the Frog, the ilium gives off a broad and depressed process, the lower extremity of which is separated from the acetabulum by a smooth concave groove; there is no such process or groove in the Crocodile, but only a slight rising of the upper border of the acetabulum, against which the sacral ribs abut. In the present ilium there is a well-marked process in the analogous situation to that in the Frog, and separated also by a smooth concave surface from the upper edge of the acetabulum, but this process, instead of being depressed, is compressed and curved forwards; its internal extremity is pointed and bent, representing, as it seems, the rudiment of the long anterior process of the ilium in the anourous Batrachia. This process, in the *Labyrinthodon*, does not attain the parallel of the anterior margin of the acetabulum; and the bone terminates in a thick

truncated extremity a few lines anterior to the acetabulum, as in the ilium of the Crocodiles. The most marked character in which the present fossil deviates from the corresponding bone in the Crocodiles, is its extent posterior to the acetabulum: this part of the bone is compressed with a thick and rounded external and inferior margin; it becomes thinner and terminates in a fine edge internally and above; is slightly convex externally and concave on the opposite side, where it is also excavated by the articular surface for the sacrum.

In the Frog, as in the other tailless Batrachia, the ilium, besides being remarkable for its extreme length and slenderness anterior to the acetabulum, is also characterized by its mode of articulation to the vertebral column,—a transverse process of a single vertebra abutting against the anterior extremity of the produced ilium. In the Crocodile, on the contrary, the transverse processes of two vertebræ which are thickened and expanded, are joined to a rough concave articular surface occupying the inner side of the ilium opposite and a little posterior to the acetabular cavity. In some species the two articular surfaces are separated by a slight interspace; in others they are confluent, their respective proportions being indicated by an entering angle of the non-articulating surface of the bone.

In the fossil we find, as in the ilium of the Crocodiles, a well-marked, rough, elongated, concave articular surface divided by a corresponding but less produced angle of the non-articular surface of the bone, and unquestionably destined for the reception of the external extremities of at least two broad and strong transversely extended sacral ribs. It is continued from the process above the acetabulum upon one-half of the long posterior process: the length of this articular surface is four inches; its greatest breadth one inch three lines; the antero-posterior diameter of the acetabulum is two inches; its vertical diameter one inch and a half. In the Batrachia a broad and thin process is continued downwards and inwards below the acetabular cavity, representing the pubis, and this is separated from the acetabulum by a well-developed ridge and the concavity below it.

In the Crocodile, where the lower part of the acetabular cavity is always completed by the upper extremity of the pubis, the anterior and inferior part of the ilium offers an obtuse process at the posterior part of the lower boundary of the acetabular cavity: the *Labyrinthodon* agrees with the Crocodile in this structure. As the iliac bone here described was discovered in the same quarry with the two fragments of the cranium and the portion of the lower jaw of the *Labyrinthodon pachygnathus*; and as it presents a similar combination of Batrachian and Crocodilian characters, it may be concluded to have belonged to the same species and possibly to the same individual. The cranial fragments correspond in size with those in the head of a Crocodile between six and seven feet in length, but the ilium supports an articular cavity for the reception of the head of a femur, somewhat

greater than that exhibited by the same bone of a Crocodile twenty-five feet in length. If both belonged to the same individual, we should have an example of a reptile with hinder extremities of disproportionate magnitude as compared with those of existing Saurians, but which would approximate in this respect, as in many other particulars already pointed out, to some of the existing anourous Batrachians.

That such a reptile of a size equal and in some species far superior to that of the *Labyrinthodon*, to which the present fossils are here referred, formerly existed at the period of the formation of the New Red Sandstone, is abundantly manifested by the remains of those singular impressions of footsteps to which the term *Cheirotherium* has been applied.

*Femur.*—In the same quarry which yielded the above-described iliac bone, was found the hemispherical head of a femur, of a size corresponding with the articular cavity or acetabulum of that bone (it is figured, below the acetabulum, in Pl. XLV. fig. 18.). On the not improbable supposition that this is part of the skeleton of the same species of *Labyrinthodon* as that to which the humerus belonged, the relative size of these bones more nearly resembles that which must have characterized the so-called *Cheirotherium* than obtains in any recent Batrachian.

*Phalanges.*—The fossil from the Warwick sandstone figured as a tooth, in the memoir of Messrs. Murchison and Strickland (*loc. cit.* fig. 9. Pl. XXVIII.), differs from every known Saurian or Batrachian tooth in presenting a semi-elliptical transverse section, being flattened on one side and convex on the other, and being unusually curved. The unsymmetrical character of this fossil is so extremely rare a form in the simple conical teeth of reptiles, that I applied for and obtained permission to examine its intimate structure. The base of the fossil was fractured, but exhibited no trace of pulp-cavity. A transverse section taken from its middle, and viewed by transmitted light under a power of 200 linear dimensions, presented numerous parallel close-set Haversian canals, with concentric lamellæ surrounding each, and minute and simple radiated cells in the interspaces; there could be no doubt, therefore, that it was a true bone, and I conceive it to be most probably a terminal phalanx of a toe. It measures ten lines in length, is curved, and gradually diminishes in size from one end to the other. There is likewise in the collection a second terminal phalanx in the form of an elongated cone, with the articular surface slightly concave at the base; one side flattened, the opposite side convex; the apical extremity in both these phalanges is simply attenuated, but presents no trace of nail; they are strictly Batrachian in this respect, and from their size are referable to the hind-foot of the *Lab. pachygnathus*.

Thus then the fossils of the lower sandstones of Warwick and Leamington, though few, bear good testimony to the affinities of the reptiles of that ancient stratum. They all agree with each other and with the *Mastodonsaurus Jægeri*

of the German Keuper in their essentially Batrachian nature; for the well-marked and peculiarly complicated character of the dental structure admits of no doubt that the gigantic species of the Keuper-schiefer, with its Batrachian double condyle, is at least generically related to the *Labyrinthodons* of our own sandstones. With the deviations from the ordinary Batrachia manifested in the dental structure, and in the Crocodilian modifications and sculpturing of the cranium, it might reasonably have been anticipated that corresponding peculiarities should exist in the locomotive extremities, and fortunately we obtain a clue to this part of the organization of lost species by data independent of the osseous remains and more copious in the particulars which they reveal.

The New Red Sandstone has of late years contributed to the ichnological department of the history of extinct animals one of its most remarkable and problematical examples, in the footsteps of the so-called *Cheirotherium*. Without recapitulating the various conjectures to which these impressions have given rise, I may observe, that, adopting the opinion of Dr. Buckland and other distinguished geologists, that they were the foot-prints of an animal and not vegetable impressions, I have long entertained the opinion, and have expressed it in my lectures, that they were the foot-prints of a reptile and not of a marsupial or other mammal, and that this reptile most probably belonged to that family of the class which includes the Frog and other anourous Batrachia which offer a similar disproportion between the fore- and hind-legs. But, on the supposition of the Cheirothere being a Batrachian, it was not less evident that it was quite peculiar and distinct from any known Batrachian or other reptile in the form of its feet. The analogy of the Crocodilian reptiles would indicate the short and freely-projecting digit to be the outer or fifth toe, whilst the closer correspondence of the Batrachian feet would prove it to be the inner or first toe; but the thickness, relative size and position of the remaining toes are peculiarities of the Cheirotherian footsteps.

In the *Labyrinthodon*, however, we have a Batrachian reptile, and one that differs very remarkably from all known Batrachia and every other reptile in the structure of its teeth: it is also a Batrachian, which, with strong affinities to the Sauria, appears to have presented the same inequality of size between the fore and hind extremities as does the so-called Cheirothere: and both the footsteps and the fossils are peculiar to certain members of the triassic formations. May we not then be justified, upon this evidence, in adding the name *Cheirotherium* to *Mastodonsaurus* and *Phytosaurus* among the synonyms of the genus Labyrinthodon?

I have already alluded to footsteps of a different but somewhat allied form, as being probably those of the *Lab. leptognathus*. These footsteps actually occur associated with those of the *Cheirotherium* on the same slab, in the sandstone quarries at Storeton, but are more Crocodilian in their character.

If it should be proved that the *Lab. pachygnathus*, the larger and stronger-awed species, really had bones of the extremities corresponding with those that left the so-termed Cheirotherian impressions, while the impressions of the less anomalous form more closely agreed with the proportions of the osseous remains of the smaller and weaker species, the difference of the impressions will probably lead to a subgeneric separation. Be that as it may, the evidence that the fossils belong to one and the same natural Batrachian family is not thereby weakened. The progress of palæontological research may expand the application of the term *Labyrinthodon* to the family of Sauroid Batrachians; but at present, to avoid an unnecessary multiplication of names, I shall retain it as the generic appellative of the two British species and of the gigantic German *Salamandroïdes*, whose huge feet might well have fitted the impressions of the '*Cheirotherium Hercules.*'

### Labyrinthodon Jægeri.

*Lower Jaw.*—Two considerable portions of the posterior half of the lower jaw of a large reptile, obtained by Dr. Buckland from the new red sandstone at Guy's Cliff, Warwick, have been referred to in his memoir and in that of Messrs. Murchison and Strickland, on the Warwickshire Sandstones. Both specimens are represented of the natural size in Plate XLVII.; one (figg. 1, 1*) includes portions of the angular and dentary pieces; the other (figg. 2 and 3.) is a considerable portion of the angular piece. This specimen exhibits on its outer surface (fig. 2.) the same bold sculpturing and radiated disposition of the grooves and ridges which characterize the bones of the cranium and upper jaw of the *Labyrinthodon*, figured in Pl. XLIII. figs. 1 and 9, and Pl. XLVI. fig. 6. But a more important evidence of the affinity of the Guy's Cliff fossil to the previously determined *Labyrinthodons* is given by the canal on the inner and upper part of the angular piece (Pl. XLVII. fig. 3.) for the reception of the dentary element. The specimen which includes part of the dentary piece still more satisfactorily establishes the generic identity of the large reptile of Guy's Cliff with the *Labyrinthodon* or *Mastodonsaurus*, by the size, mode of implantation, juxtaposition and alternate displacement of the serial teeth (Pl. XLVII. fig. 1*). From the analogy of the *Labyrinthodon pachygnathus*, the laniariform tusks at the anterior part of the jaw must have equalled in size those of the *Labyrinthodon Jægeri*, with which gigantic species of Sauroid Batrachian the British species represented by the Guy's Cliff fossils is, in my opinion, identical.

The description and figures of these most interesting fossils in the present memoir have been taken from plaster casts, which Dr. Buckland had, fortunately, caused to be made: the originals have been mislaid, and have, hitherto, been sought for in vain. Should they be recovered and the structure of the teeth be then examined by microscopic sections, I venture to predict, from the more obvious

characters in the casts, that those sections will confirm my deductions by presenting the peculiar labyrinthine structure. Between the *Labyrinthodon Jægeri* and the foot-prints of *Cheirotherium Hercules*, Egerton, the same correspondence of size exists as between *Lab. pachygnathus* and *Cheirotherium Kaupii*.

### Labyrinthodon (Anisopus) scutulatus.

But though the evidence of more than one species of a distinct and peculiar genus of large Batrachians in the sandstones yielding the impressions of the *Cheirotherium* and other Reptilian footsteps be admitted to be valid, and the fossil remains be allowed to correspond in size with the animals which have left those footsteps, yet the opinion which I have formed from a comparison of the texture and markings of the bones, that the fragment of humerus and femur, and the iliac bone before described, belong to the same species, may not be received with the same implicitness; since they were not discovered in such juxtaposition as would indicate them to have formed part of the same skeleton. Other evidence may therefore be demanded in proof of the proposition that the Labyrinthodont Batrachians likewise corresponded with the Cheirotherian footsteps in the small size of the anterior as compared with the posterior extremities.

A valuable contribution towards the required demonstration is afforded by the specimen, with the description of which the present paper terminates: this specimen (Pl. XLVI. fig. 1.) consists of a closely and irregularly aggregated group of bones, manifestly belonging to the same skeleton, and including four vertebræ more or less complete, portions of ribs, four long bones of the extremities, one end of a large flat bone, and several small dermal osseous scuta, all cemented together by a mass of soft sandstone. This highly valuable and unique fossil was discovered in the new red sandstone at Leamington, and was transmitted to me for examination in the course of last summer by Dr. Lloyd. Being at that time unacquainted with any other than the dental characters of the *Labyrinthodon*, I had no evidence of the relationship between that genus and the present fossil, for this presented no trace of teeth. I shall first give the notes which I originally took of this fossil, and afterwards enter upon the comparisons which prove it to belong to the same family, if not to the same genus, as the Warwickshire Batrachians.

The group of bones from the new red sandstone at Leamington belong to a small reptile with the biconcave system of vertebræ, but which, from the length, structure, and form of the long bones of the extremities, must have been of terrestrial rather than marine habits, and which had the skin defended by numerous small rhomboidal bony scutes, with a smooth central surface, and with the outer surface sculptured by three or four longitudinal ridges (fig. 5.). This reptile has had four legs, and the hind-legs have been at least twice as long and as

strong as the fore. Of the bones of these extremities there may be recognised a humerus, a femur, and the two tibiæ. The humerus (fig. 1, *h.*) is one inch in length, regularly convex at the proximal extremity, expanded both at this and the distal extremities, and contracted in the middle. There is a portion of a somewhat shorter and flatter bone, bent at a subacute angle with the distal extremity of the humerus, and which presents the nearest resemblance to the anchylosed radius and ulna of the Frog. Both the extremities are wanting in the femur (fig. 1, *f.*), the shaft of which is slightly bent, and is subtrihedral; its walls are thin and compact, and include a large medullary cavity. The tibia (fig. 1, *t.*) is as long, but thicker and stronger than the femur; both tibiæ have lost their articular extremities, but both exhibit that remarkable compression of their distal portion which characterizes the corresponding bone in the anourous Batrachia, and both likewise exhibit the longitudinal impression along the middle of the flattened surface; the length of the most perfect of these shafts of the tibia is two inches one line.

Associated with these bones is the extremity of a broad and compressed bone, which bears most resemblance to a portion of lower jaw, but does not afford the requisite characters for precise determination. The breadth of the entire end is one inch three lines; this is terminated by a gently convex outline; the fragment slightly contracts towards its broken end, which is one inch broad; one surface of the fragment is slightly convex; the opposite surface rises into a broad, obtuse, longitudinal ridge; the fractured surface exhibits a central medullary cavity, surrounded by a close cancellous structure, varying from one to two lines in thickness. If, as appears at first sight, it formed any part of the lower jaw, the proportions of the head of this Batrachian reptile must have been enormous; and the same disproportion opposes itself to the comparison of this bone with the expanded sacrum of the Toad, or with the scapula, coracoid, ischium or pubis, at least, if we take these bones in any known reptile as the standard of comparison. Nevertheless the deviations from ordinary proportions which extinct species occasionally present in parts of their skeleton, as *e. g.* the cervical vertebræ in the *Plesiosaurus*, the fingers of the Pterodactyle, &c., forbid the rejection of the idea, that the bone in question may have actually formed part of the same skeleton with the contiguous bones of the extremities and vertebræ.

The most perfect of these vertebræ is four lines in length; the vertical diameter of the articular extremity two lines, its transverse diameter one line and a half. Each terminal articular surface is pretty deeply and regularly concave, with the periphery convex: in two of the vertebræ these surfaces slope in a parallel direction obliquely from the axis of the body, as in the dorsal vertebræ of the Frog, and are not, as usual in Saurians, at right angles with that axis; so that they indicate an habitual inflection of the portion of the spine formed by them, analogous to that

which we observe in the humped or bent back of the Frog. But the vertebræ of existing caducibranchiate Batrachians have their posterior auricular surface convex, and are articulated, as is well known, by ball- and socket-joints: the biconcave vertebræ, therefore, of the extinct reptile under consideration would indicate its affinity with the more fish-like forms of the Batrachian order. The neurapophyses are anchylosed completely, without trace of suture, with the vertebral body, which is also a Batrachian character among existing reptiles:* they rise in the present fossil vertically and parallel with each other, are nearly coequal in length with the centrum, and are joined above by a broad and flat basis of the spinous process, from each angle of which the oblique or articular processes are continued; the surfaces of these processes are flat; the plane of the anterior ones looks upwards, that of the posterior ones downwards. A long and strong transverse process is sent off from each side of the base of the neurapophysial arch. The spinous process arises from the whole length of the middle line of the neurapophysial arch; it is not very high (about half a line); its chief peculiarity is the expansion of its elongated summit into a horizontally flattened plate, the sides of which slightly overhang the base of the spine; the upper surface of this plate is sculptured by irregular pits, and this character strongly indicates a similar structure of the flat bones of the cranium. The large atlas of the Toad presents a similar flattening of the summit of its elongated spine. The sides of the body of the vertebræ are smooth, concave in the longitudinal direction, owing to the lateral compression of the part below the transverse processes; the lower part of the body slopes inwards on each side to a median, inferior, slightly marked ridge.

In comparing these vertebræ with those of other reptiles, extinct and recent, although the biconcave structure is most prevalent in the species from strata below the chalk, yet the anchylosis of the vertebral arch, the obliquity of the centrum, the terminal expansion of the spine, and the depth of the articular depressions, indicate the Batrachian character of the present vertebræ. The aquatic Salamanders, including the gigantic species from Japan, and the great extinct Salamander of Scheuchzer, with all the Perennibranchiate Batrachia, have both extremities of the vertebra concave; but these concavities are generally conical, not hemispherical, as in the fossil: the neurapophyses in the fossil are higher, the spinal canal is deeper and wider, and the spinous process stronger and more expanded superiorly, than in the lower Batrachians.

The portions of ribs in the present fossil are few and small, but sufficient to indicate that the extinct reptile in question possessed them longer and more curved than in any existing species. Here then is demonstrated an important Saurian

* This structure prevails in the vertebræ of certain extinct Saurians.

modification of the thorax, which could only be inferred from the structure of the nasal cavity in the larger Labyrinthodons. And the light which the small reptile from the Leamington sandstone thus throws upon the organization of the larger Warwickshire Sauroid Batrachia is the more valuable on account of the correspondence of their vertebral characters, and of the proportions of their locomotive extremities. But the decisive evidence of dental structure is still wanting; nay, more, it may be objected that the Leamington fossil exhibits a character, in the small, bony, dermal sculptured plates, not yet found in the Warwick or Wirtemberg Labyrinthodons, which seems to remove it from all Batrachia—the naked reptiles, as they are emphatically termed,—and to approximate it to the Loricated order. Unquestionably these scuta form a striking instance of the Crocodilian affinities of the Leamington Batrachian; but we have already seen the same affinities manifested in other parts of their organization, by the Warwick and Wirtemberg Labyrinthodons. As these detached superficial bones are the most liable to be separated from the fragmentary skeleton of the individual they once clothed, the mere negative fact of their absence, when so small a proportion of the bones of the trunk of any *Labyrinthodon* has yet been found, is insufficient to prove a difference of dermal structure between the Leamington and Warwickshire species.

No anatomist, indeed, can contemplate the extensive development and bold sculpturing of the dermal surface of the cranial bones in the *Labyrinthodontes pachygnathus* and *leptognathus*, without a suspicion that the same character may have been manifested in bony plates of the skin in other parts of the body. And granting that this structure existed, to what extent, it may be asked, does it affect the claims of the *Labyrinthodon* to be admitted into the order of Batrachia, in which every known species is covered with a soft, lubricous and naked integument? To this question it may be replied, that the skin is the seat of the most variable characters in all animals; and, if considered apart from the modifications of the osseous and dental systems, is apt to mislead the naturalist who is in quest of the real affinities of a species. Suppose, for example, that the existing Chelonian reptiles were exclusively mud-tortoises, or with a soft and naked skin, as in the species of *Trionyx* and *Sphargis*, would the discovery of the osseous carapace of a true Testudo, in a fossil state, in connexion with a skeleton in other respects essentially corresponding with the modifications exhibited by a Trionyx, prohibit the association of the fossil in the same order of reptiles with the Trionyx, because of the indication of the scutes? It unquestionably ought not to affect such a determination. And so with respect to the Labyrinthodont Batrachia; if all the species have pushed their affinities to the Crocodilians so far as to have had their trunk defended by bony dermal plates, yet their double occipital condyle, their comparatively simple lower jaw, their large

palatal vomerine bones and teeth, and the other osteological characters already detailed, must still be deemed decisive of their essentially Batrachian nature.

If the evidence which I have been enabled to adduce in the present paper be compared with that previously recorded relative to fossils of the Batrachian family, the additions to this department of Palæontology will be found as follows :—

With the exception of the posterior fragment of the skull, on which Professor Jaeger's *Salamandroïdes giganteus* is founded, no Batrachian fossil had been detected anterior to the miocene tertiary period. The characters of Prof. Jaeger's fossil induced him to regard it as closely allied to the gigantic Newt or Salamander,—the *Homo diluvii testis* of Scheuchzer. It is placed between that fossil, which is the *Salamandra gigantea* of Herm. V. Meyer, and the *Triton Noachichus* of Goldfuss, in the 'Palæologica' of the former author. But the double condyle of the *Salamandroïdes* is a character also presented by the *Cæciliæ*, which some naturalists still class with the Ophidian reptiles. In the Catalogue of Fossil Batrachians* published by Dr. Tschudi, the *Salamandroïdes* of Jaeger is omitted: he commences his list by the statement, that, in epochs anterior to the Molasse, there is not, with certainty, known to be any trace of the fossil remains of Batrachia†. M. Tschudi, with many other continental palæontologists, although admitting the identity of the *Salamandroïdes* and *Mastodonsaurus*, place both fossils in the Saurian group.

The present researches afford additional evidence of the Batrachian character of the *Salamandroïdes* of the Alaunschiefer of the German Keuper; and they show that it is not merely a Batrachian, like the Salamander, but is a member of a peculiar family of Sauroid Batrachia, the more important characters of which were before unknown. It has now been demonstrated that this family, the species of which characterize and are peculiar to the new red sandstones, had a dental system differing from all other Batrachia in the inequality of size of the front and back teeth, the former being developed into great laniariform tusks; and that the teeth differ from those of all other animals in their peculiarly complex labyrinthine structure, whence the name of the family; which, at present, I use generically. The extinct Labyrinthodonts deviated from the Salamanders and other Batrachia in the Crocodilian development and sculpturing of the external and superior bones of the cranium, and in the structure of the pelvis, in which also they approximated to the Crocodiles: and one species certainly, and the others probably, receded from the Batrachia, in the same direction, in having dermal osseous plates.

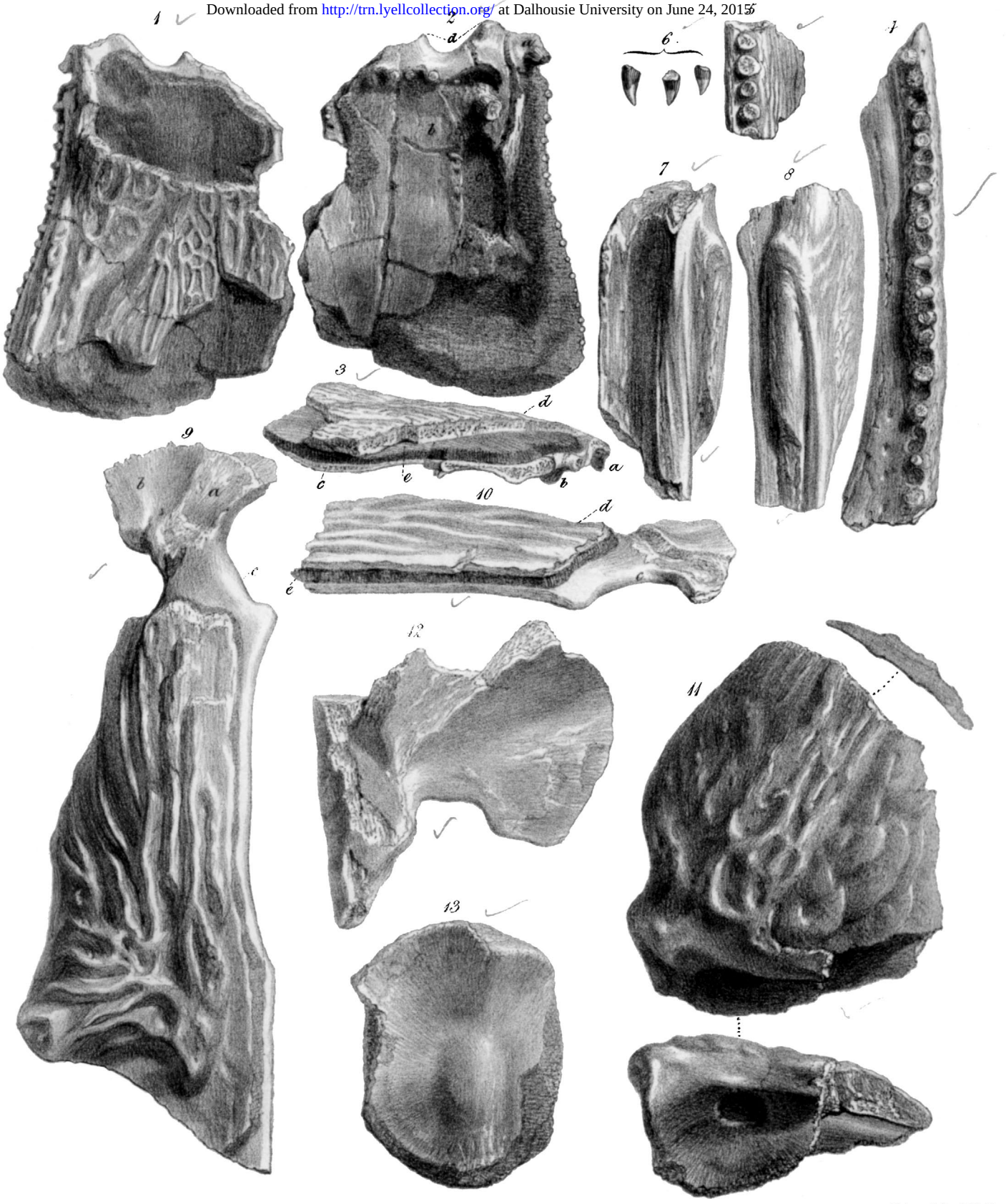
* In the Mémoires de la Société des Sciences Naturelles de Neuchâtel, tom. ii. 4to. 1839.

† "Aus den der Molasse vorausgehenden Epochen, lassen sie mit Gewissheit keine spuren fossiler Ueberreste von Batrachiern nachweisen."—p. 19.

The minor differences in the vertebræ and other parts noticed in the foregoing descriptions need not here be repeated, but sufficient has been recapitulated to show that the extinct Batrachians that characterize the new red sandstones once constituted a family of that order, hardly less remarkable or better defined in its characters than the equally extinct family of Enaliosaurs in the highest order of reptiles. It is not, perhaps, too sanguine an expectation to anticipate that subsequent researches may show that the Labyrinthodont family is not less rich in species, manifesting subgeneric modifications of the typical structure.

The following are those which at present are known :—

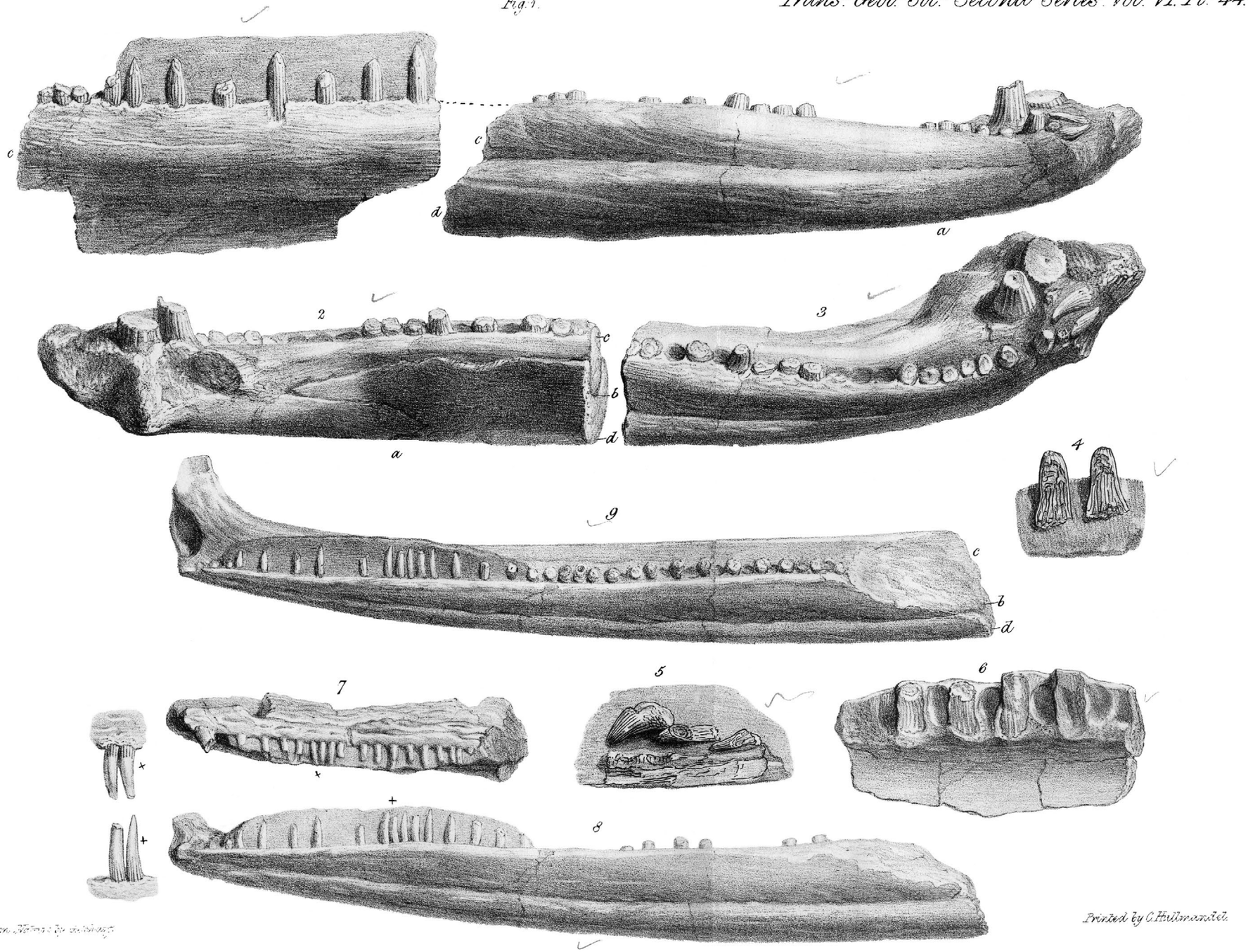
*Labyrinthodon Jægeri.*
——————— *pachygnathus.*
——————— *leptognathus.*
——————— *ventricosus.*
——————— *scutulatus.*




...g from Nat. by G. Schaaf.

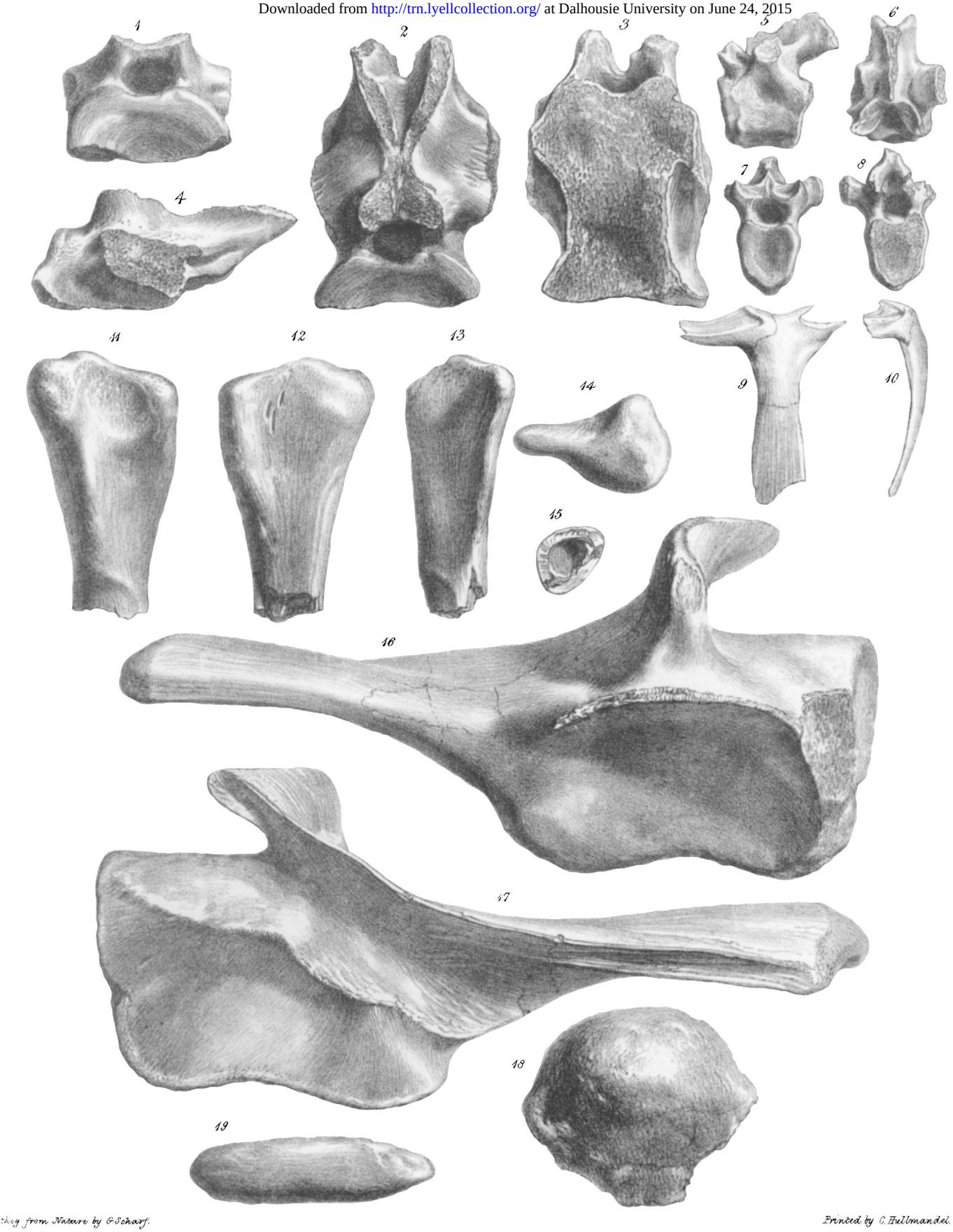
Printed by C. Hullmandel.

Fig. 1, 2, 3. Labyrinthodon leptognathus. Fig. 4—11. Labyrinthodon pachygnathus.




Printed by C. Hullmandel.

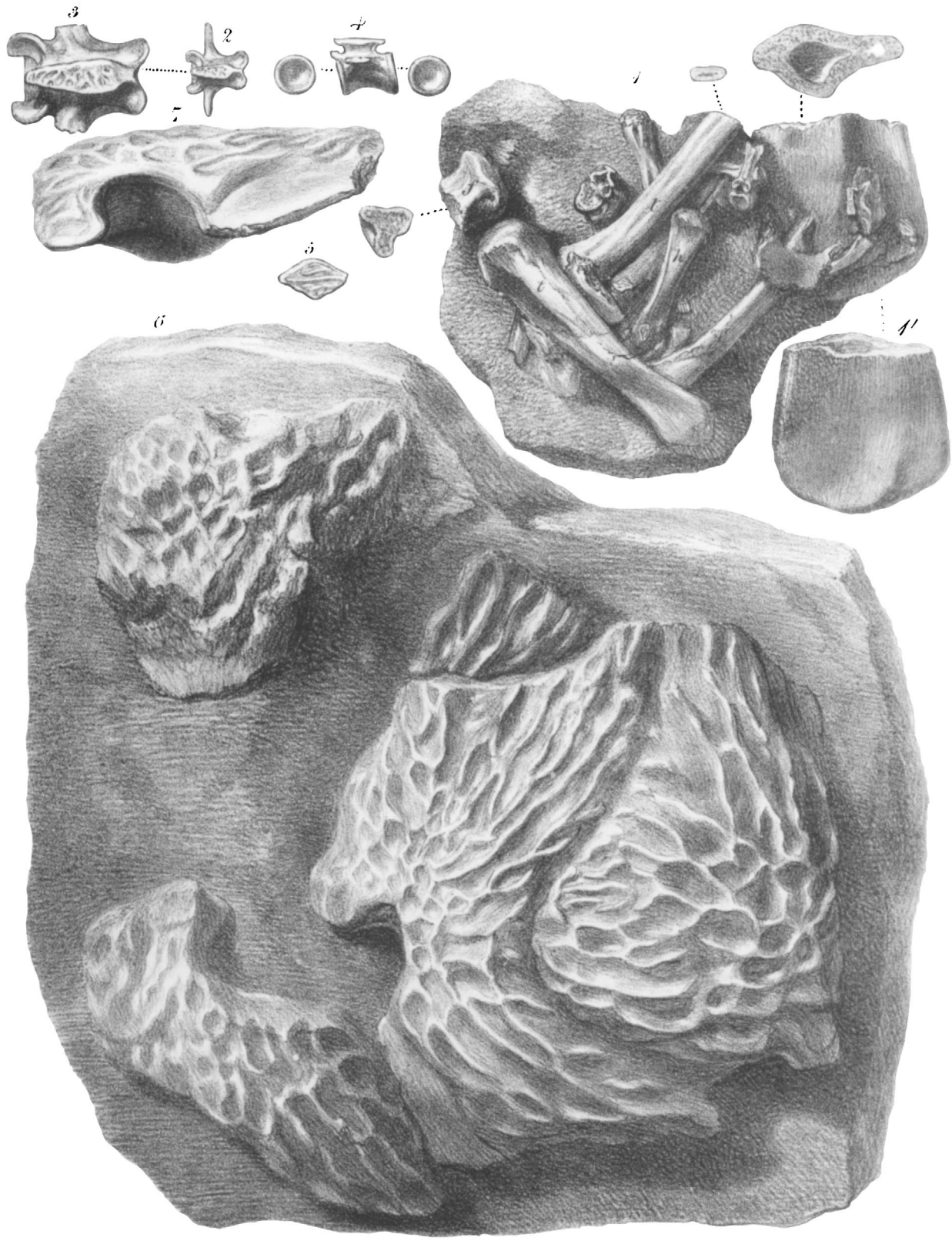
Fig. 1–3. Labyrinthodon pachygnathus. Fig. 7–9. Lab. leptognathus.
Fig. 4–6. Lab. Jaegeri.




Drawn from Nature by G. Scharf.

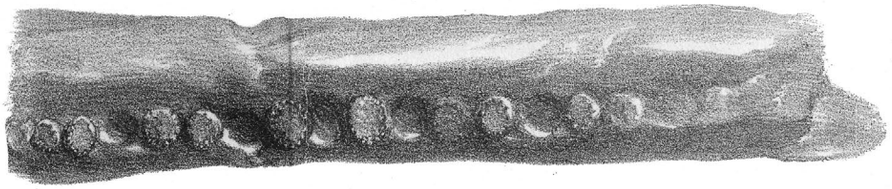
Printed by C. Hullmandel.

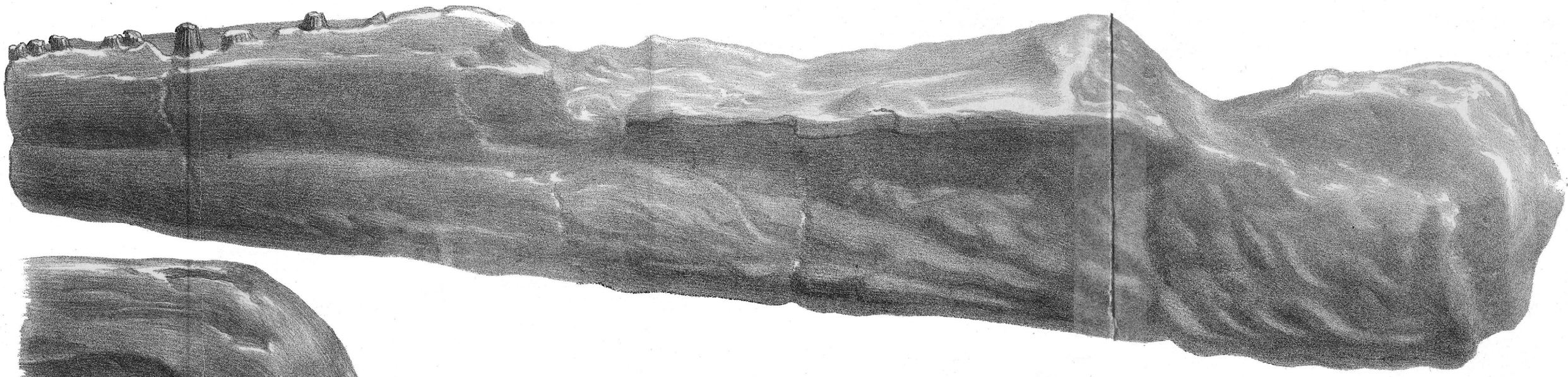
Fig. 1_4, 11_18 Labyrinthodon pachygnathus. 5_8 Lab. leptognathus.
Fig. 9 10. Lab.:..... Fig. 19. Coprolite.



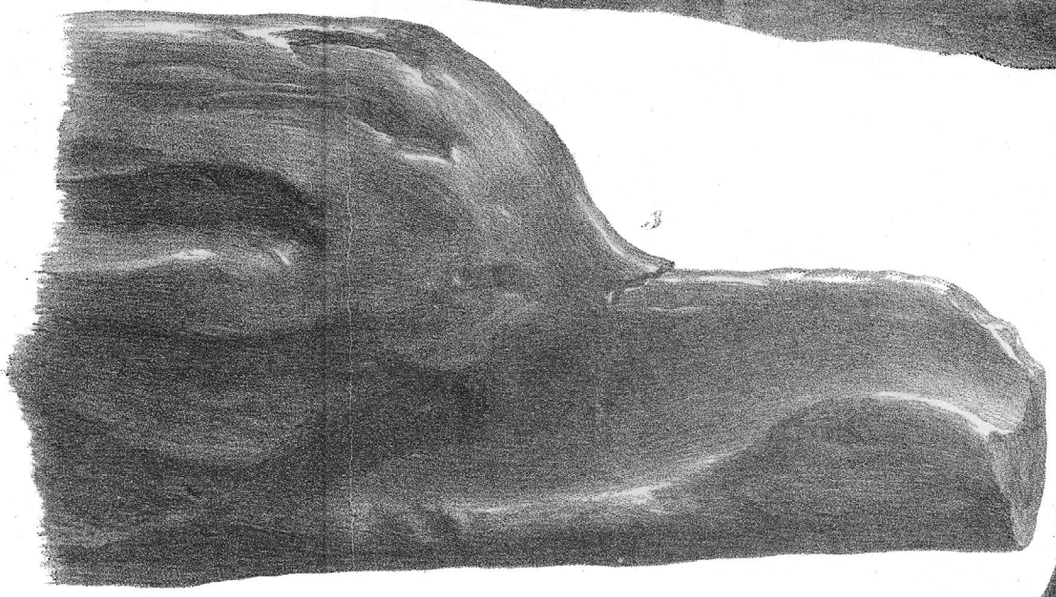

1–5. Labyrinthodon scutulatus. 6, 7. Labyrinthodon pachygnathus.

1*

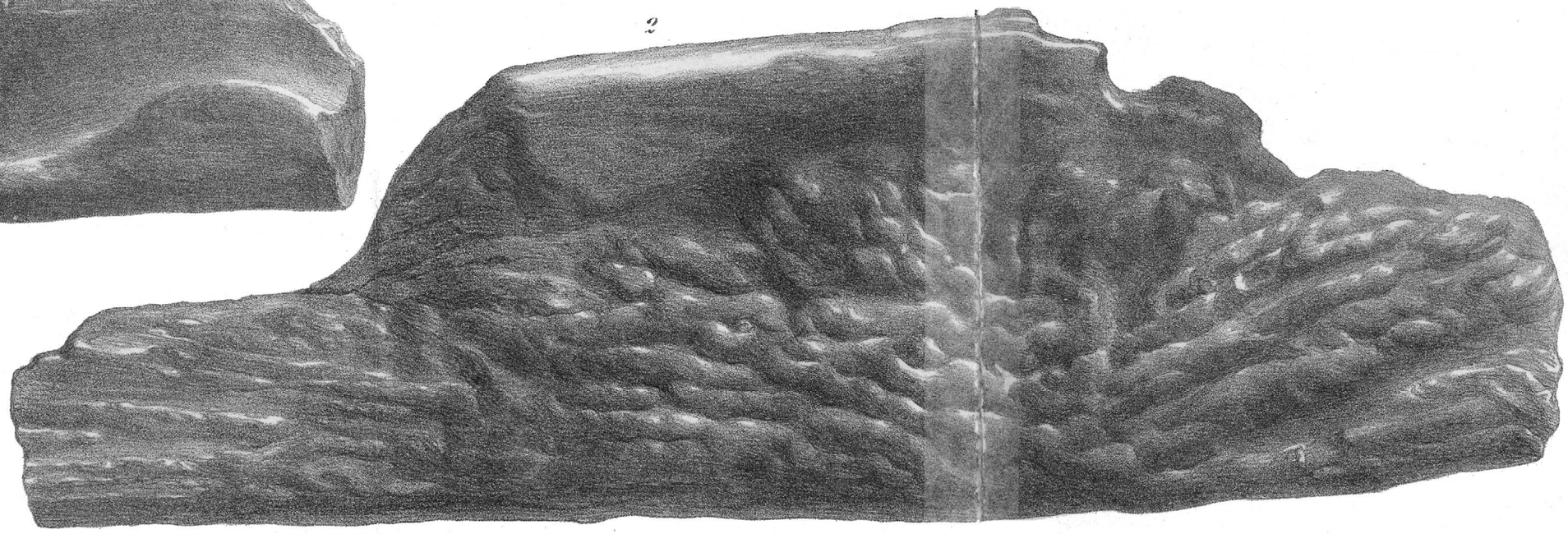




3



2



Lithog. from Nature by G. Scharff.

Printed by C. Hullmandel.

Labyrinthodon Jaegeri.