XIII. *On the Structure of the Jaws and Teeth of the Iguanodon.*

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IN the deltas and estuaries of rivers that are of great extent, and which flow through countries of varied geological structure, we naturally expect to find the remains of terrestrial vertebrated animals that have been transported by the currents from far-distant lands, in a more or less mutilated state; the skeletons broken up—the bones dissevered, fractured, and waterworn—the teeth detached from the jaws and dispersed—and all these separated parts promiscuously imbedded in the mud, silt, and sand of the delta, and intermingled with the debris of the flora of the country, and the durable remains of fishes, mollusks, and crustaceans, that inhabited the freshwater, or were denizens of the adjacent sea. Such is the condition in which the bones and teeth of oviparous quadrupeds are found in the Wealden formation of the south-east of England; and hence the difficulty of obtaining satisfactory evidence of the form and structure of the extinct reptiles whose relics are so abundant in some of these deposits.

To this cause may be ascribed the remarkable fact, that although several hundred teeth, belonging to seven or eight genera of Saurians, have been collected from these fluviatile strata, scarcely a portion of the cranium, and but a few fragments of the jaws, have been discovered. Every relic of this kind is consequently in the highest degree interesting, and it is therefore most gratifying to me to have it in my power to lay before the Royal Society a considerable portion of the lower jaw, with teeth, of an Iguanodon, recently obtained from a quarry near Cuckfield in Sussex; the locality in which, nearly thirty years since, I first discovered the teeth of this colossal herbivorous Lizard.

In the communication which I had the honour to address to this Society in 1841 *, a fragment of the lower jaw of a Saurian was described as that of a young Iguanodon, and the anatomical considerations which led me to offer that interpretation were fully detailed. But although from the form and mode of implantation of the fangs of the mature teeth, and the position of the germs of the successional ones, this inference appeared to be highly probable, yet as none of the crowns of the teeth remained, the peculiar dental characters of the Iguanodon were absent, and the presumed generic identity could not be unequivocally established; since it was possible

* Philosophical Transactions, Part II. p. 131.

that the fossil might belong to the Hylæosaurus, or to some other genus of reptiles whose bones occur in the Wealden deposits.

The specimen to which I now solicit attention consists of nearly the entire dentary and coronoid bones of the right side of the lower jaw of an adult animal, retaining two successional teeth in place, and the germ of a third, with the alveoli or sockets of seventeen or eighteen mature molars. This fossil is the first indisputable portion of a jaw of the Iguanodon hitherto brought to light; although nearly a quarter of a century has elapsed since the publication in the Philosophical Transactions* of my first memoir on the teeth of this extinct reptile.

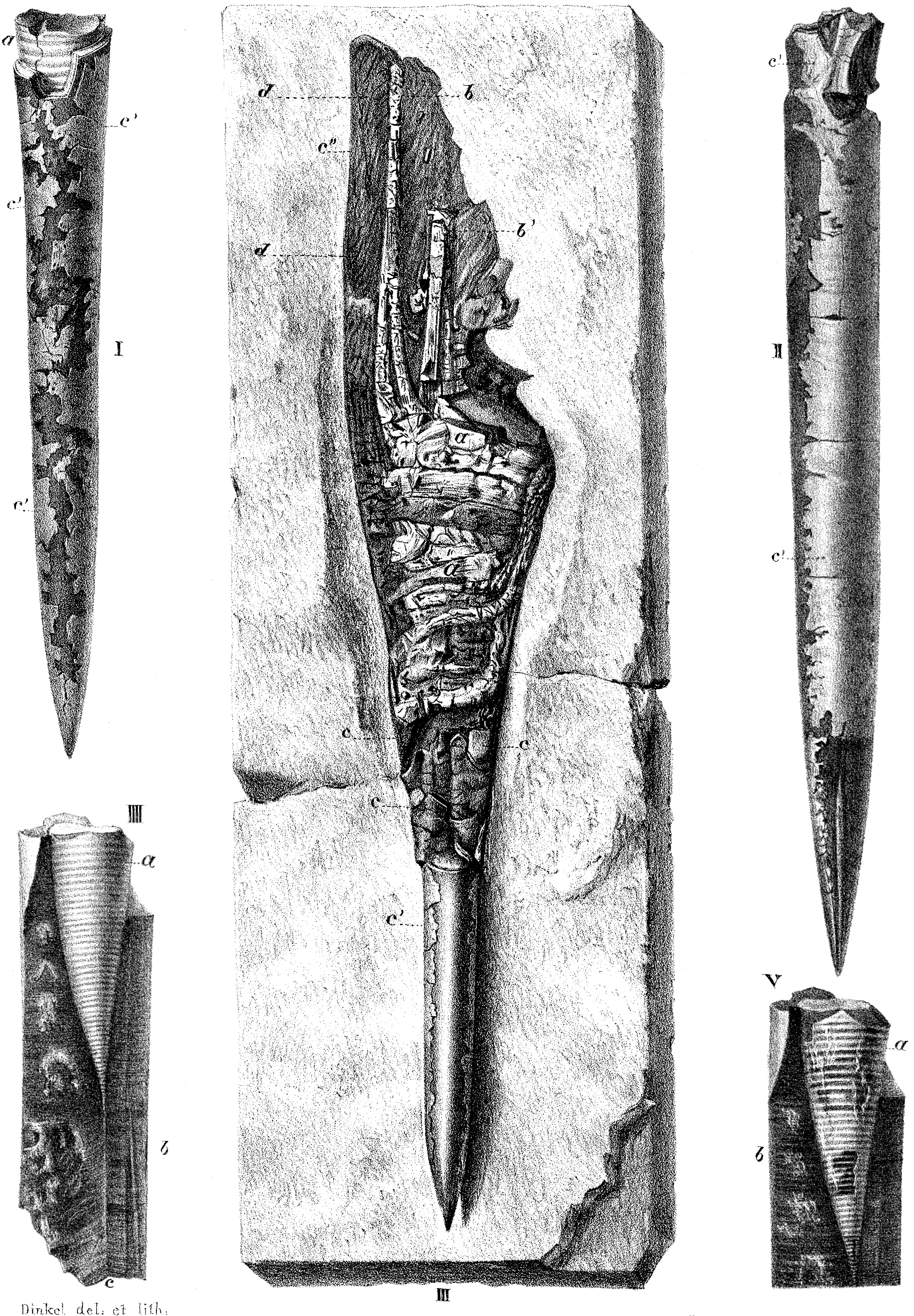
From the striking analogy presented by the worn teeth of the Iguanodon to the condition of the abraded molars in some of the large herbivorous Mammalia, the discovery of the maxillary organs of this reptile was an object of the highest palæontological interest, in order to determine in what manner the mastication of vegetables was effected by an animal belonging to a class, in which no living species is provided with jaws so constructed as to be capable of a triturating or grinding motion; nor with cheeks to retain the food while such a process is performed†. And though from the absence of mature teeth in the sockets, and of the articular portion of the jaw, the proximal end being destroyed, the specimen before us does not afford a complete solution of the problem, yet it possesses characters sufficiently definite and intelligible to throw important light on the structure and functions of the dental organs of the Iguanodon; and it has also enabled me to ascertain the form of the upper jaw, from a portion of the left maxillary bone, collected many years since, and now in the British Museum, but whose peculiar characters I was previously unable satisfactorily to interpret.

Before entering upon the description of the highly interesting fossil which forms the principal subject of this memoir, I beg to express my most grateful acknowledgments to Captain Lambart Brickenden, of Warminglid, Sussex, by whom it was discovered, and skilfully extricated from the sandstone in which it was imbedded; and who, although I was personally unknown to him, in the true spirit of an ardent and liberal promoter of science, placed it at my disposal, as the original investigator of the fossil Saurians of the Wealden; a tribute of respect that I regard as a high reward for my humble efforts to advance those branches of natural knowledge, to which I have devoted the leisure moments of a life of professional toil.

The specimen when discovered was imbedded in a block of the fawn-coloured sandstone which occurs interstratified with beds of clay and limestone, throughout a considerable part of the Wealden districts of the south-east of England; fortunately this stone is not very compact, so that organic remains can be extricated from it by a skilful manipulator, with but little difficulty. This fossil, like most of the bones and teeth

* "Notice on the Iguanodon, a newly discovered Fossil Reptile, from the Sandstone of Tilgate Forest, in Sussex."—Philosophical Transactions for 1825.

† See Cuvier, Oss. Foss. tome v. p. 351.



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found in the sandstone, is heavy, and of a rich umber colour, from impregnation with oxides of iron. It consists of the dentary, and part of the coronoid or complementary bone, of the right side, and is entire at the anterior part, but the posterior or opposite extremity is imperfect, probably to the extent of several inches. Its original relative position in the jaw will be understood by referring to my former communication*, in which the peculiar construction of the lower jaw in Saurian reptiles is described. In this place it may, however, be proper to remark, that of the six pieces on each side of which the inferior maxilla consists, that containing the teeth, and forming the anterior portion or symphysis, is termed the *dentary*; and the posterior part of this bone is united on the outside by suture to the *complementary* or *coronoid*, *angular*, and *surangular*; while on the mesial or inner side, it is covered below and behind the teeth by an expansion of the *opercular* bone.

The specimen is represented of the natural size in Plate XVI.; its dimensions are as follow:—

	inches.
Length from the front of the symphysis to the posterior extremity of the bone	21
Greatest width of the outer surface measured over the convexity, from the lower margin to the upper alveolar edge	$6\frac{3}{4}$
Greatest thickness at the posterior part	$2\frac{3}{4}$
Length of the alveolar parapet for twenty teeth	15
Breadth from the anterior termination of the alveolar space across to the inner margin	$4\frac{1}{4}$
Height of the alveolar parapet at the posterior part	2
Width of the alveolar space at the posterior part	$1\frac{1}{4}$
Width of the alveolar space at the anterior part	$\frac{3}{4}$
Length from the first anterior tooth to the symphysial extremity	5
Height of the successional tooth (Plate XVI. fig. 1, *b*) $1\frac{1}{2}$ inch; greatest width $\frac{7}{8}$.	

The mesial or inner aspect of the fossil (Plate XVI. fig. 1) is flattened and smooth, and shows the successional teeth which remain in their original places (*a*, *b*), and the sockets (*f*, *f*, *f*,) for nineteen or twenty teeth; the inner alveolar plate having been destroyed, and the mature molars dislodged, before the bone was imbedded in the rock. The deep conical groove or furrow, so constantly present on the inner side of the dentary bone in reptiles, and which from its being covered by the splenial or opercular piece, it may be convenient to designate the *opercular furrow*, is here entirely exposed (fig. 1, *d*, *d*) in consequence of the removal and destruction of that maxillary element. It is very large, and prolonged anteriorly (*d*) to within six inches of the symphysis; the opercular piece must therefore have more nearly corresponded with that of the Varanians or Monitors than with the Iguanas, in which it is of a rhomboidal figure, and relatively of limited extent. The lower margin of the jaw is thick and convex at the posterior part, and gradually becomes thinner towards the front, where it expands horizontally into a broad scoop-like process, which is terminated anteriorly by an obtuse projection or tubercle (Plate XVI. fig. 1, *e*); it thins out mesially to form the symphysial suture (*s*) that connects it with the opposite ramus.

The upper margin is formed by the alveolar process, which has a thick external

* See Philosophical Transactions for 1841, Plate V. figs. 3. 7.

parapet, deeply furrowed on the inner side, as seen in this view, by the sockets for the mature teeth (*f*, *f*). Strongly-defined ridges occupy the interspaces, and rising above the sockets produce a sharp crenated upper border. The alveolar space is protected on the inner side by a moderately strong plate or wall, which must originally have nearly equalled the outer parapet in height, but is now in a great measure broken away: within this process the germs of the successional teeth were developed.

The mode of implantation of the teeth appears to have been intermediate between the pleurodont and thecodont types; for the teeth were not anchylosed to the alveolar wall as in the Iguanas, but free as in the Crocodiles; yet as the ridges that separate the dental sockets are smooth and rounded, it may be inferred that these were not rendered complete alveoli by transverse plates extending from the outer to the inner parapet, as is the case in the Megalosaurus*.

The dental sockets diminish in size, but somewhat irregularly, from the posterior to the anterior termination of the alveolar process; and the latter suffers a corresponding diminution in breadth, and terminates suddenly at the distance of five inches from the front. At this point the upper margin becomes attenuated and contracted in a vertical direction, and descending with a gentle curve, expands horizontally and mesially to unite at the symphysial suture (*s*) with the opposite ramus, the anterior part of the jaw being edentulous.

From the fortunate preservation of two successional teeth in their original position, the mode of dental development in the Iguanodon is clearly demonstrated. The coronal portion of the tooth was first formed, as seen in the germ, Plate XVI. fig. 1, *a*; and the entire crown was completed (fig. 1, *b*) before the secretion of the shank or fang commenced, as in the existing Saurians. The formative pulp was situated in a distinct depression or cavity, on the inner side of the root of the tooth it was destined to supplant: this is obvious by the positions of the teeth above described; and also by the remains of a third germ towards the posterior part (fig. 1, *c*).

Although the peculiar characters of the molars of the Iguanodon were described somewhat in detail in my former communications, and the present fossil confirms in every essential particular the inferences suggested by the detached teeth, as stated in my memoir of 1825, yet several new and important points relating to the development and functions of the dental organs, are elucidated by the new acquisition which Capt. BRICKENDEN's researches have brought to light. The second tooth (Plate XVI. fig. 1, *b*) which occupies its natural position in the alveolar space, consists of the entire crown, having the serrated margin as perfect as in the recent state; and this is the first evidence I have obtained as to the mode in which the teeth were implanted. The flat enamelled front, characterized by its longitudinal ridges, is placed mesially, and parallel to, and within the inner alveolar wall; the smooth convex face filling up a depression in the outer parapet, in the interspace of two sockets of the mature molars. This position is the reverse of that in which the successional teeth in the Iguana are developed; for in that reptile the coronal germ occupies the same relative place as

* See Dr. BUCKLAND's Bridgewater Essay, Plate 23.

in the mature state; namely, with the ridged face outwards, and the smooth side inwards, or towards the cavity of the mouth.

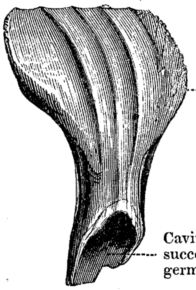
As the coronal portion of the tooth in the Iguanodon is not symmetrical, one lateral margin presenting a gentle curvature (Plate XVIII. fig. 4, *a*), and the other forming a broad angle at the base of the serrated border (Plate XVIII. fig. 4, *b*), the teeth belonging to one side of the lower jaw may readily be distinguished from those of the other; the lateral marginal angle (*b*) being always situated posteriorly. Guided by this character, Dr. Melville and myself examined the numerous teeth in the British Museum and in my own collection, and were enabled readily to determine to which ramus any tooth belonged. Thus, for example, the specimen represented, Plate XVIII. fig. 4, which is the very counterpart of that implanted in the jaw (Plate XVI. fig. 1, *b*), is a perfect successional tooth, consisting of the crown before the formation of the fang, and belonging to the right side (*a* denotes the anterior, and *b* the posterior angle). The specimen, Plate XVIII. fig. 5, appertained to the opposite or left lower side, as is shown by the situation of the posterior marginal angle (*b*).

The position of the lower teeth in relation to the alveolar process, appears to have been somewhat changed during the upward growth of the coronal portion consequent on the progressive development of the fang; and it seems probable that the face of the crown became inclined rather obliquely forwards and outwards, and that the mature teeth were arranged in an imbricated manner. This opinion is supported by the form of the alveoli in the outer parapet, and the corresponding oblique curvature in the fangs of the mature molars, as shown in Plate XVIII. fig. 5; but this inference does not admit of that absolute proof which the perfect adaptation of a full-grown tooth to one of the sockets would afford; for the alveoli are irregular, and none of the detached teeth in my possession will fit either of the sockets in the recently discovered dentary bone.

The situation of the germ in relation to the tooth it was destined to supplant, is invariably on the inside of the mouth; in the lower molars the excavation in the mature tooth occasioned by the upward growth of the germ, is consequently on the enamelled mesial face, as is shown in my original memoir*: in the upper tooth the germ was lodged in an excavation on the smooth convex aspect, as will subsequently be demonstrated (see Plate XVIII. fig. 2^a, *f*).

In the fossil represented in the annexed sketch, the cavity produced by the pressure of the germ is situated in the fang of the tooth in place; in other examples, however, the successional dental excavation is on the base of the enamelled crown; for in the Iguanodon the old teeth were retained till nearly the entire coronal portion was worn away, and the crown of the tooth, from the abrasion by use above, and the removal of the fang by absorption below, was reduced to a mere disk, before it was finally shed; as in the specimen (figured in Xylograph, No. 2, p. 188).

Xylograph, No. 1.

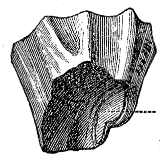


Lower tooth of the right side.

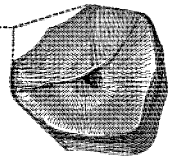
* Philosophical Transactions, 1825, Plate XIV. fig. 7 *a*.

Xylograph, No. 2.

Lower tooth reduced by abrasion of the crown and absorption of the shank.



Cavity formed by the pressure of a new tooth.



As the surface of the crown when abraded by mastication invariably possesses two distinct facets (Xylograph, No. 4, and Plate XVIII. figs. 1^b and 2^b), it is obvious that the arrangement of the lower teeth in relation to the upper was intermediate, or subalternate, as is the case in the ruminants ; the further consideration of the dental characters of the Iguanodon will be resumed in a subsequent part of this memoir.

The *external aspect* of the specimen (Plate XVI. fig. 2, and Plate XVII. fig. 4) presents in its transverse diameter a gentle convexity, traversed by a slightly elevated longitudinal ridge, which lies parallel to, and immediately beneath, the row of vascular foramina, commonly met with in this part of the lower jaw in reptiles ; and towards the posterior extremity the side of the bone is somewhat compressed below the longitudinal eminence; according in this respect with the portion of a lower jaw of a much smaller reptile, described in a previous memoir*. The upper edge of the bone is formed by the outer alveolar parapet, which is deeply scalloped or crenated by the terminations of the sockets of the teeth ; the angular eminences indicate the intra-alveolar ridges. A reference to the figures (Plates XVI. and XVII.) will impart a more correct idea of the configuration of this part of the fossil than any verbal description. The whole surface of the bone is covered with minute punctuations and striæ.

The relative thickness and proportions of the different parts of the specimen, and its external contour, are shown in the reduced figure of the section exposed by the fractured posterior extremity, Plate XVII. fig. 3 ; and in this view is seen the dental canal (3) which contained the large blood-vessels and nerves that supplied the teeth and integuments of the lower jaw ; its longest diameter at this part is six-tenths of an inch.

The numerous and large vascular foramina which afforded passage to the vessels and nerves from the dental canal to the external integuments, form a striking character in this aspect : they open obliquely forwards ; nine are distributed at regular intervals in a line with the alveolar margin, from the posterior end of the bone to nearly opposite the successional tooth in place. A fracture in the middle of the outer surface (Plate XVII. fig. 4, *h*) at the distance of $4\frac{1}{2}$ inches from the posterior end, exposes the dental canal filled with sandstone : its diameter is here two-fifths of an inch.

At the anterior termination of the alveolar space, a slight protuberance (Plate XVII. fig. 4, *i*) marks the commencement of the upper margin of the symphysial region, which is defined by a sharp smooth ridge, that sweeps downwards and inwards to form the front of the jaw. A deep groove, beset with foramina (Plate XVII. fig. 4, *k*),

* Philosophical Transactions, 1841, Plate V. figs. 1, 8, 9.

constitutes a strong line of demarcation between the inner and outer boundary of this area; the latter is thick and convex, and terminates anteriorly, as already mentioned, in a mammillary protuberance or tubercle (Plate XVI. *e*, and Plate XVII. fig. 4, *e*). A series of foramina, eight in number, extends along the outer and inferior surface of the symphysis; the terminal one, which is three-fourths of an inch in its transverse diameter, is situated immediately under the mental tubercle (*e*) above described. The mesial or inner edge of the symphysis, which in connection with the ramus of the left side formed the median suture of the lower jaw, is thin and expanded; the articulating surfaces of the two dentary bones appearing to have overlapped each other (Plate XVI. fig. 1, *s*, and Plate XVII. fig. 1, *s*, *s*); but as the edge of the bone is somewhat broken, the line of junction is not quite determinable; but the two rami do not seem to have been united by anchylosis.

On the under surface of the symphysis there is a depressed oval area, bounded laterally and posteriorly by a slightly elevated ridge (Plate XVII. fig. 2, *l*, *l*); probably for the insertion of the protractor muscles of the tongue.

The coronoid bone (Plate XVI. fig. 1, *m*, and Plate XVII. fig. 4, *m*), of which only a portion remains, is much more expanded outwardly than in any recent Saurian.

With respect to the length of the jaw to which this specimen belonged, an approximative estimate only can be offered, since we have no means at present of determining the relative size of all the different pieces that entered into the construction of the maxillary organs of the Iguanodon. From the appearance of the fractured end, it seems probable that the dentary bone was prolonged backwards five or six inches before it united with the surangular and angular: upon this supposition its entire length must have been two feet, and the number of teeth about twenty. In the Iguana and most Lizards the dentary element is half the length of the jaw; and if this proportion be taken as the standard of comparison—and it appears to be the most probable one—the length of the jaw of this individual was four feet. An eminent palæontologist* has estimated the length of the head of the largest Iguanodon at only thirty inches; having taken as the basis of his calculation, the length of six dorsal vertebræ, which in the Iguana is equal to that of the lower jaw. But the specimen before us proves either that the same scale of proportions is not applicable to this colossal Saurian, or that much larger dorsal vertebræ than those from which the measurement was taken, are yet to be discovered; for several teeth in my possession exceed in magnitude the largest sockets of this dentary bone. Even if we take the

* Reports of the British Association for 1841. Article 'British Fossil Reptiles,' p. 143. "If there be any part of the skeleton of the Iguana which may with greater probability than the rest be supposed to have the proportions of the corresponding part of the Iguanodon, it is the lower jaw, by virtue of the analogy of the teeth and the substances they are adapted to prepare for digestion. Now the lower jaw gives the length of the head in the Iguana, and this equals the length of six dorsal vertebræ; so that as five inches rather exceeds the length of the largest Iguanodon vertebra yet obtained, with the intervertebral space superadded, on this calculation *the length of the head of the largest Iguanodon must have been two feet six inches.*"

abbreviated proportions of the short blunt-headed lizards as the scale—as for example the Chameleons—the length of the jaw of this Iguanodon must have exceeded three feet.

I will now describe the portion of a left upper maxilla in the British Museum, which corresponds so perfectly in its general characters with the lower jaw, as to leave not the slightest doubt of its having belonged to the Iguanodon, although no teeth remain to establish the identity.

Portion of the Upper Jaw, Plate XIX. figs. 1, 2*.—This specimen consists of the anterior part of the left maxillary bone, having on the under surface (fig. 1) the alveolar furrow with the bases of the sockets of ten teeth; and on the upper (fig. 2), the deep channels of the infra-orbital vessels and nerves that supplied the teeth and integuments of the front of the jaw and face on the left side: this fossil is represented of the natural size. Dr. MELVILLE, who has most kindly aided me by his profound anatomical knowledge throughout this investigation, and liberally devoted much time and attention in instituting the necessary comparisons between my specimens and those formerly collected by me, and now in the British Museum, with the jaws and teeth of recent reptiles, has favoured me with the following observations on this subject.

"This fragment of the left maxilla, which is eight inches five lines long, and two inches seven lines broad, formed the lower boundary of the nasal surface; it is broken off where the vertical parapet rises to enclose the olfactory fossa. The corresponding part in the skull of an Iguana (*I. tuberculata*), measuring four inches two lines in length, is six lines long, or nearly one-eighth that of the cranium; this ratio gives five feet four inches as the length of the skull of the Iguanodon to which the fossil belonged; but as the brain and the organs of sense would have a less proportion to the whole bulk in these gigantic Saurians than in the small species of existing Lizards, we may infer a diminution in the absolute size of the head, corresponding with the abbreviation and contraction of the cranium; and the length in the adult would probably average about four feet.

"The breadth of the fragment continues uniform; in front it is rounded off externally (x), and exhibits the oblong terminal irregular surface for articulation with the intermaxillary bone by which it was overlapt. The large infra-orbital canal (fig. 2, a, a) opens at the junction of the posterior and middle third, and midway between its margins; passing into a broad and deep sigmoid groove which curves inwards as it advances so as nearly to reach the inner edge in the centre of its course, where it gives off a retrograde furrow extending over the internal margin (fig. 2, b). In front it is deflected outwards, extending along the posterior border of the intermaxillary

* I discovered this fossil in 1838, in a quarry near Cuckfield, and it was labelled in my Catalogue "*fragment of the upper jaw of an Iguanodon.*" By the kind permission of Mr. KÖNIG, the specimen has recently been cleared of the sandstone with which it was partially invested, so as to expose its peculiar characters as represented in Plate XIX.

surface; and rising to a higher level, becomes faint, and terminates one inch behind the anterior extremity; several small vascular foramina open where it ceases. A rough, irregularly triangular, and excavated tract, separates it from the outer edge of the bone; its apex is behind, about $1\frac{1}{2}$ inch from the infra-orbital orifice; its base corresponds to the rounded anterior and external angle, where it passes into the low external border.

"The roof of the infra-orbital canal presents a deep concavity behind (fig. 2, *c*), with the smooth lateral surface of the groove rising into it externally; this is evidently part of the floor of an upwardly emergent canal about an inch in diameter; the thin partition continued backwards between it and the canal below is destroyed, and the posterior segment of the circumference removed; a comparison of the fossil with the skull of an Iguana will confirm this statement.

"The infra-orbital canal, which is eight lines wide behind and four lines high, bends inwards as it retrogrades from its anterior opening. The inner surface is only four lines from the nasal aspect of the fragment behind, so that after a course of a few inches, it would have emerged on the floor of the nasal cavity. The roof is incised obliquely outwards, and the inner portion of it extends forwards to the retrograde groove. The portion of the external surface of the alveolar process that remains, slopes inwards, and exhibits no traces of vascular foramina."

From the almost entire destruction of the alveolar walls of the furrow, deep transverse excavations (Plate XIX. fig. 1, *f*, *f*, *f*) are the only remains of the dental sockets. As the fangs of the teeth of the upper jaw, as will be shown in the sequel, were more curved than in the lower series, and their implantation presented a corresponding modification, as is the case in the dental organs of certain existing Monitors, the width of the alveolar space is greater than in the lower jaw.

Dental characters.—Although the peculiar form and structure by which the teeth of the Iguanodon are distinguished from those of all other animals have been described in my former communications, yet as the mode in which the teeth were implanted in the jaws was then unknown from actual observation, no attempt was made to ascertain the dextral or sinistral position of the detached specimens; nor to separate the lower from the upper series, and thus determine the dental arrangement by which the jaws of this colossal reptile were invested with the functions of those of the existing herbivorous Mammalia. To solve this highly interesting problem, it became necessary to institute a rigorous and minute comparison and examination of all the teeth of the Iguanodon to which we could obtain access; the results of the investigation are detailed by Dr. Melville in the following statement.

"*Teeth of the Lower Jaw*, Plate XVIII. figs. 4, 5, 6.—The lower tooth is curved, with the concavity outwards, or towards the external alveolar parapet; the upper and lower limbs, corresponding respectively to the wedge-shaped crown, and elongated taper fang, are not separated by a constriction or neck, but are flattened in opposite directions. In the upper moiety of the coronal segment, it is compressed transversely with a convex outer, and a flat inner aspect, and gradually increases downwards in width and thickness, from the broadly-rounded excentric apex to its greatest longitudinal diameter. It continues to expand transversely while decreasing in breadth; subconcave planes also replace the serrated edges at which the surfaces meet above; it obtains its greatest thickness where the tooth is bent on itself to form the fang; the latter diminishes rapidly in both diameters, and the lateral facets are brought in contact below, and obliterate the inner surface; in fully-formed teeth the fang tapers to a point*.

"The inner coronal aspect has a rhomboidal outline, and is covered with a thin layer of enamel extending on the margins; it is flat in the antero-posterior diameter, and only slightly convex vertically. The upper serrated edges ascend converging; the anterior is the longest and most curved; it sweeps rapidly backwards above to the excentric apex, which thus presents a broad front shoulder. The inferior margins are striated or granulated, but destitute of serrations; the posterior is bent forward below to meet the straight lower front edge. The angle to which the hinder margin inclines is more prominent and acute than that formed by the anterior edge; and by this character the teeth belonging to the respective rami of the lower jaw may be distinguished.

"The enamelled surface is divided into two unequal channelled areas by a primary longitudinal ridge (Plate XVIII. fig. 4, *n*, and fig. 5, *n*); commencing at the apex, it intersects the long diagonal, and terminates behind the lower angle, from which a broad secondary elevated tract ascends along the floor of the wide anterior groove, nearly obliterating it in front. A slight convexity, rapidly subsiding, passes upwards in front of the superior posterior edge.

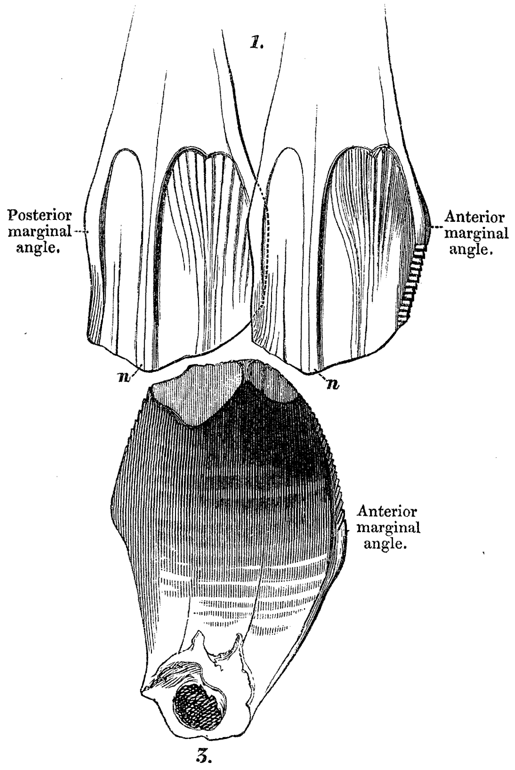
"The relative width and depth of the longitudinal grooves, and the prominence of the intervening ridges, vary in different specimens; and the edges of the ridges are more or less replaced by planes; the ratio of the upper to the lower margins also differs. The serrations are produced by small convex mammillated ridges separated by slight intervals; the inner edges of the anterior apical ones are prolonged downwards; those on the posterior margin are abraded, apparently by absorption, during the upward growth of the germ. The inner convex surface of the fang is variously grooved and flattened, becoming ridge-like below; it is in apposition with the outer alveolar parapet. The lateral planes converge inwards, and are grooved longitudinally: the posterior plane presses forwards the inferior hinder coronal margin; they extend as high as the obtuse angle of the crown, and leave between them, as they diverge in their ascent, an unenamelled triangular space on the inner aspect. Expansions of the alveolar septa on each side are adapted to the lateral planes of the fang, and the inner parapet is deficient opposite the triangular tract above-mentioned, but is closed below, separating the alveolus from the cavity of reserve in the secondary dental groove.

* Philosophical Transactions, 1841, Plate VII. figs. 1, 2.

"The teeth never become anchylosed to the sockets; the great transverse diameter of the dentary element of the jaw above appears to have allowed of the outward curvature of the elongating fang, while the inner surface was maintained nearly vertical. By the same provision the germ attained a considerable size before it pressed upon and excavated the root of the tooth, which it was destined ultimately to displace. The wedge-shaped crown and the anterior serrated recurved trenchant edge, must have rendered the teeth in this early stage very efficient instruments, in the absence of incisors, for cutting vegetable food.

Xylograph, No. 3.

Outer aspect.



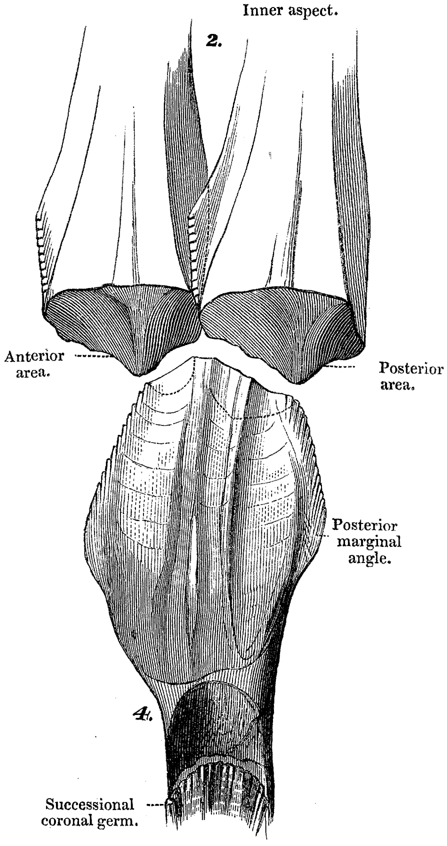
Outer aspect.

Upper molars of the right side of the jaw.

Lower tooth of the right side.

Xylograph, No. 4.

Inner aspect.

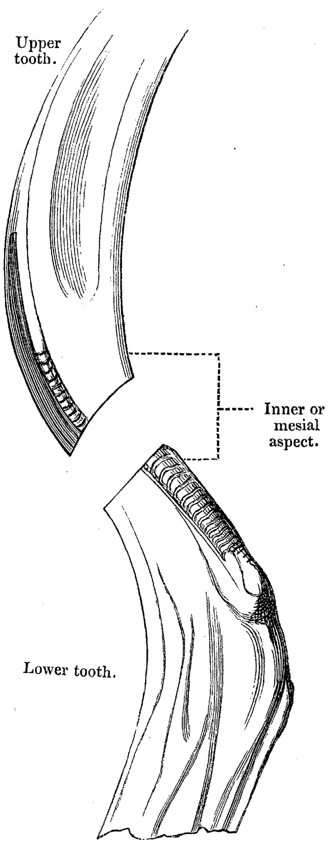


Inner aspect.

The arrangement of the upper and lower molars, and the situation of a lower successional germ, are shown in the above figures. In the wood-cut No. 3, two upper molars of the right side are represented on their external or enamelled aspect, and a corresponding lower molar beneath them; in No. 4, are seen the opposite or internal aspect, and the position of the successional germ in the fang of the lower tooth.

"*Teeth of the Upper Jaw*, Plate XVIII. figs. 1, 2.—After the determination of the form and position of the teeth of the lower jaw, yielded by the instructive specimen previously described, the next question to be determined was, whether the teeth in the upper maxilla had the same shape and curvature as those of the lower. Upon examining the extensive series in the British Museum, several teeth were found differing in shape from the now-ascertained type of the lower molars of the Iguanodon. These are, however, in all essential respects so analogous to the inferior teeth, that no reasonable doubt can exist of their having belonged to the upper jaw of this reptile. From the mutual adaptation of the grinding surfaces, and the situation of the excavation produced by the replacing germ—which in all analogous cases is in the mesial aspect of the fang—the inference was obvious that these teeth not only did belong to the upper series, but that they were curved in an opposite direction to those of the lower; namely, with the convexity external, and the concavity internal; the hollow for the successional germ being situated in the latter (Plate XVIII. fig. 3^a, *f*). Thus the upper and lower molars were related to each other nearly as in the Ruminants; the outer aspect below corresponding to the inner above; the triturating facet inclining from above downwards and outwards in the inferior series, and from below upwards and inwards in the superior; in the lower teeth the enamelled edge is within and the most elevated, while in the upper it is external and inferior. The annexed diagram (Xylograph, No. 5) of an upper and lower tooth, seen in profile, explains this arrangement.

Xylograph, No. 5.



View in profile of an upper and lower molar, of the left side.

"By this adjustment the hard unvascular dentine with its coating of enamel, played on the softer vaso-dentinal tract of the tooth opposed to it below; and a bevelled or chisel-like surface was maintained for triturating the food when drawn into the mouth by the large prehensile tongue, which is indicated by the procumbent and inferiorly excavated symphysis. The upper molar is also distinguished by the smaller antero-posterior diameter of the crown—by the great prominence of the primary ridge (*n*)—by the breadth of the vertically convex surface of the fang—by the width of the lateral facets—and by the contraction of the internal or vertically concave surface which becomes ridge-like below.

"The anterior and inferior serrated edge is rapidly recurved towards the blunt excentric apex, and forms above an obtuse prominent angle with the upper segment of that border, which is striated, and everted as it were by the encroachment of the anterior deeply concave lanceolate facet impressing the lower portion of the crown and fang. The broad area between it and the primary ridge, exhibits numerous striæ of enamel converging as they descend to a secondary ridge; on the crest of which, one is prolonged before the outer edge of an anterior apical serration. The posterior coronal margin is nearly straight, plain above, and serrated below. The primary ridge forms a strong convex buttress subsiding towards each extremity; it is slightly inclined to the hinder edge, and nearly obliterates the smaller posterior area.

"From the inversion of the teeth in the upper jaw, we naturally expect to find some alteration in the configuration of the molars; while the position of the apex, of the primary ridge, and of the areas into which it subdivides the crown, will remain as in the lower series. On these grounds I am led to conclude that the smaller area always indicates the posterior part of the tooth, whether of the upper or lower jaw; but the marginal angle and the reflected edge are anterior in the upper molars, and posterior in the lower, these characters having relation to the manner in which the series of teeth are arranged. In the lower jaw the posterior margin of the molar overlaps, or rather projects internally beyond the anterior edge of the tooth behind, but in the upper it is situated externally to it (Xylographs, No. 3 and 4, page 193.); a similar arrangement takes place in the Ruminants. The mechanical advantages resulting from the opposite curvature of the teeth in the upper and lower jaw, are too obvious to require comment."

As it is very rarely that a specimen occurs in which the absorption of the fang, from the upward growth and pressure of a new tooth, has not taken place in a greater or lesser degree, it is probable that the formation of successional teeth was in constant progress at all periods of the animal's existence, as is the case in most of the Saurian reptiles.

The internal structure of the teeth is in striking accordance with the external form and mechanical arrangement of the dental organs; for the central body of dentine or tooth ivory is of a softer and coarser texture than in any other known Saurian, and closely resembles that observable in the colossal vegetable feeders of the Sloth tribe—the Mylodon and Megatherium*. But towards the periphery of the anterior part of the tooth the dentine is finer and harder; and not only the front of the crown, but also the inserted base, is covered by a thick layer of enamel; and from this peculiar arrangement of substances of different degrees of hardness, the tooth, in every stage, must have been admirably adapted for the trituration and comminution of vegetable food. A vertical slice of a tooth, showing the pulp-cavity, with the dentine traversed by vascular canals radiating from the centre, and running parallel with the calcigerous tubes, is represented as seen by transmitted light, and magnified eight diameters, in Plate XVIII. fig. 3.

The dental pulp becomes ossified in the old teeth, so that whatever the degree of abrasion, the exposed masticating coronal surface is solid; this is seen even in the

* "The intimate structure of the vascular dentine of the Bradypus resembles that of the inner half of the dentine of the Iguanodon."—*Odontography*, p. 329.

last stage, when the crown is reduced to a mere plate of dentine, as in the specimen previously figured (Xylograph, No. 2, *ante*, p. 188)*.

As the articular piece which contains the socket of the lower jaw for receiving the inferior head of the *os quadratum* is unfortunately wanting, the mechanism of the articulation can only be conjectured; for although several examples of the tympanic bone —which in reptiles as in birds connects the lower with the upper maxilla—are preserved in my former collection, neither of the specimens is sufficiently perfect to indicate the precise mechanism of the joint. One of the tympanic bones found in the same quarry with teeth and bones of the Iguanodon, and which I am led to consider as having belonged to that reptile, is 6 inches high and $5\frac{1}{2}$ inches wide; it consists of a thick pillar, which is contracted at the sides in its vertical direction, and has two thin expanded lateral processes; it terminates both above and below in an elliptical and nearly flat surface; it is very cavernous from the large size of the tympanic cells. This bone differs considerably from the corresponding element in the Iguana, the peculiarity, doubtless, having relation to some modification in the mechanism of the lower jaw, by which the more complete comminution of vegetable substances was effected, than by maxillary organs constructed after the usual Saurian type.

Physiological inferences.—In instituting a comparison between the maxillary organs above-described, and those of the existing herbivorous lizards, with a view of obtaining some physiological deductions from the peculiar osteological characters of the fossil remains, we are at once struck with their remarkable deviation from all known types in the class of reptiles. In the *Amblyrhynchi*, the most exclusively vegetable feeders of the Saurian order, the alveolar process beset with teeth is continued round the front of the mouth; the junction of the two rami of the lower jaw at the symphysis presenting no edentulous interval whatever, and the lips are not more developed than in other reptiles: in the Iguanas, as shown in my former memoir, the same character exists. In the carnivorous Saurians the teeth are also continued to the symphysial suture on each side. The extinct colossal lizards offer no exception to this rule; in the acrodont Mosasaurus of the Chalk, and in the thecodont Megalosaurus of the Oolite and Wealden, the jaws are armed with teeth to the anterior extremity. In short, the edentulous, expanded, scoop-shaped, procumbent symphysis of the lower jaw of the Iguanodon has no parallel among either existing or fossil reptiles; and we seek in vain for maxillary organs at all analogous, except among the herbivorous Mammalia. The nearest approach is to be found in certain *Edentata* —as for example in the *Cholœpus didactylus* or Two-toed Sloth, in which the anterior part of the lower jaw is edentulous and much-prolonged: the correspondence is still closer in the gigantic extinct *Mylodons*; in which the symphysis resembles the blade of a spade used by turf-diggers, and has no traces of incisive sockets; and were not this part of the jaw elevated vertically in front, and the rami confluent, it would pre-

* For a detailed account of the microscopical structure of the teeth of the Iguanodon, see "Odontography, or a Treatise on the Comparative Anatomy of the Teeth," by Professor OWEN, p. 246–253.

sent the very counterpart of that of the Iguanodon. This striking resemblance will be obvious to any one who will compare the illustrations subjoined to this memoir, with the magnificent specimen of the *Mylodon robustus* in the Hunterian Museum*.

The great size and number of the vascular foramina distributed along the outer side of the dentary bone and beneath the border of the symphysis (Plate XVI. fig. 2, and Plate XVII. fig. 4), and the magnitude of the anterior outlets which gave exit to the vessels and nerves that supplied the front of the mouth, indicate the great development of the integuments and soft parts with which the lower jaw was invested†.

The sharp ridge bordering the deep groove of the symphysis, in which there are also several foramina, evidently gave attachment to the muscles and integuments of the under lip; and there are strong reasons for supposing that the latter was greatly produced, and capable of being protruded and retracted, so as to constitute in conjunction with a large fleshy prehensile tongue, a powerful instrument for seizing and cropping the leaves and branches, which, from the construction of the teeth, we may infer constituted the chief food of the Iguanodon.

Thus we find the mechanism of the maxillary organs of the Wealden herbivorous Saurian, as elucidated by recent discoveries, in perfect harmony with the remarkable dental characters which rendered the first known teeth so enigmatical to the palæontologist, and another interesting proof is obtained of the constancy of those laws by which the correlation of organic structures is governed.

In the Iguanodon we have a solution of the problem how the integrity of the type of organization peculiar to the class of cold-blooded Vertebrata was maintained, and yet adapted, by slight and simple modifications, to fulfil the conditions required by the economy of a gigantic terrestrial reptile, destined to obtain support exclusively from vegetable substances; in like manner as the extinct colossal herbivorous Edentata which flourished in South America, ages after the Country of the Iguanodon and its inhabitants had been swept from the face of the earth.

Thus in the unlimited production of successional teeth at every period of the animal's existence, in the mode of implantation of the teeth, and in the composite structure of the lower jaw—each ramus consisting of six distinct elements—the Saurian type of organization is unequivocally manifest; while the intimate structure of the dental organs corresponds with that of the Sloths, and the subalternate arrangement and reversed position of the upper and lower series of teeth, with that of the Ruminants. And again, the edentulous and prolonged symphysis, and the great develop-

* In the *Mylodon Darwinii* the rami of the lower jaw anterior to the teeth are contracted vertically, and converge to a longer and narrower symphysis, which is inclined forwards at a more open angle with the horizontal ramus, than in the *Mylodon robustus*; and therefore still more nearly approaches that of the Iguanodon. See Professor Owen on the Mylodon.

† The external vascular foramina are remarkably augmented in the dentary bone of the Iguanodon as compared with other reptiles. In the colossal Mosasaurus, the dentary piece of a jaw $4\frac{1}{2}$ feet long, has but ten or twelve relatively small foramina; in the Iguana but five or six; in the Monitors six; in the Crocodiles they are numerous, but small and irregular. In the Megalosaurus there are four foramina, and several small ones.

ment of the lower lip and the integuments of the jaws, as indicated by the size and number of the vascular foramina, present a striking analogy to the Edentata, with which indeed other parts of the osteology of the Iguanodon bear a remarkable resemblance; as for example, the sacrum formed by the anchylosis of five vertebræ, the expanded vertebral portion of the ribs, &c.; while the massive femur with its medullary cavity, well-marked trochanters and condyles, and the short and strong metatarsal and phalangeal bones, remind us of the gigantic recent pachyderms.

In fine, we have in the Iguanodon the type of the terrestrial herbivora, which in that remote epoch of the earth's physical history, termed by geologists "*The Age of Reptiles*," occupied the same relative station in the scale of being, and fulfilled the same general purposes in the economy of nature, as the Mastodons, Mammoths, and Mylodons of the tertiary periods, and the large pachyderms of modern times.

Although many important characters of the osteology of the Iguanodon are still unknown, we may, I conceive, from the data hitherto obtained, safely infer that this gigantic herbivorous reptile was equal in bulk to the Elephant, and as massive in its proportions; for living exclusively on vegetables there must have been a large development of the abdominal region. Its limbs must have been of proportionate size to sustain and move so enormous a carcass. The hinder extremities in all probability presented the unwieldy contour of those of the Hippopotamus and Rhinoceros, and were supported by strong short feet, protected by broad horny ungual phalanges. The fore-legs appear to have been less bulky, and adapted for seizing and pulling down plants and branches of trees. The teeth and jaws demonstrate its power of mastication and the nature of its food; and the remains of coniferous trees, arborescent ferns and cycadeous plants, with which its relics are commonly associated, indicate the character of the flora adapted for its sustenance.

I forbear entering at this time upon other considerations relating to the fossil reptiles of the Wealden, in the hope of being able to lay before the Royal Society, on some future occasion, an account of several other interesting Saurian remains from the strata of Tilgate Forest; but I beg to subjoin the following supplementary remarks on my last memoir.

Regnosaurus Northamptoni, Phil. Trans. 1841, Plate V. figs. 1, 8.—The portion of the lower jaw of a Saurian formerly described as that of a young Iguanodon*, is proved by the specimen discovered by Captain BRICKENDEN, to be generically or subgenerically distinct from the *I. Mantelli*, although unquestionably belonging to the same remarkable family of herbivorous reptiles; and the internal structure of the teeth in this specimen, so far as I can judge from a microscopical examination of a very small fragment from the upper part of the fang, corresponds more nearly with that of the Iguanodon than with the very fine and dense tooth-ivory of the teeth of

* Philosophical Transactions, 1841, p. 131.

the Hylæosaurus. I therefore propose to distinguish this fossil Saurian by a name indicative of the district from which, in common with so many relics of the same class, it was obtained—*Regnosaurus** ; with the specific appellation of *Northamptoni*, as a tribute of respect to the eminent nobleman whose approaching retirement from the Presidency of the Royal Society is so much to be regretted.

19 *Chester Square, Pimlico*,
May 24, 1848.

Description of the Plates.

PLATE XVI.

A considerable portion of the right ramus of the lower jaw of an adult Iguanodon from the Wealden sandstone of Tilgate Forest, discovered by Capt. Lambart Brickenden, F.G.S. The figures are of the size of the original.

Fig. I. The inner or mesial aspect.

a. The coronal germ of the first anterior tooth, in its alveolus.

b. The crown of a successional tooth in its natural situation.

c. Portion of the base of a successional tooth. The above are visible in consequence of the removal of the inner parapet of the alveolar process.

d, d. The deep elongated *opercular furrow*, originally covered by the splenial or opercular bone.

e. An obtuse tubercle or projection forming the anterior termination of the symphysial portion of the jaw.

f, f, f. Denote some of the alveoli or sockets of the mature molar teeth.

m. The coronoid or complementary bone.

s. The articulating surface forming the symphysial suture.

Fig. II. An oblique external view of the same specimen. In this figure the coronoid process (*m* of fig. 1) is not delineated, and the fractured posterior end of the fossil is represented to show the situation of the great dental canal (*g*), and the thickness of the parietes of the bone ; the internal course of this canal is exposed by the fracture (*h*).

PLATE XVII.

Fig. I. Outline of the anterior part of the lower jaw of the Iguanodon, seen from above ; reduced one-half the natural size in linear dimensions.

s, s. The symphysial suture.

e, e. The mental tubercle.

* *Sussex Saurian*; the County of Sussex was anciently inhabited by the *Regni*.

Fig. II. Outline of the under or inferior aspect of the same.

l. l. Area for the attachment of the protractor muscles of the tongue.

e, e. The mental tubercle.

Fig. III. Section presented by the posterior fractured end of the specimen (see Plate XVI. fig. 2); reduced half linear.

1, 1. The outer wall or parapet of the alveolar process.

2. Remains of the inner or mesial alveolar parapet.

3. Posterior section of the great dental canal; the lesser foramen indicates the channel for the vessels sent off from the main trunk to supply the dental germs.

4. The *opercular furrow*.

Fig. IV. The external aspect of the specimen represented in Plate XVI., reduced one-half in linear dimensions. In this view the numerous vascular foramina leading from the dental canal are distinctly shown; they extend in a line parallel with the alveolar margin, and are continued to the anterior extremity of the symphysis; one large foramen being situated immediately under the mental tubercle (*e*).

e. The mental tubercle forming the anterior extremity of the symphysis.

h. A fracture on the side of the bone, by which the course of the great dental canal is exposed to view.

i. An eminence at the commencement of the anterior edentulous portion of the jaw.

k. A deep groove beneath the margin of the symphysis.

m. The coronoid process.

PLATE XVIII.

Teeth of the Iguanodon.

Fig. 1. A molar tooth belonging to the left side of the upper jaw, having the crown worn by use: from Tilgate Forest.

1. The outer or external aspect, showing the ridged and enamelled surface of the crown.

1^a. Lateral view of the tooth.

1^b. Surface of the crown worn smooth by mastication, and presenting two distinct facets (1 and 2), produced by the attrition of the corresponding lower molars.

f. The fang.

n. Marks the primary ridge.

Fig. 2. Upper molar of the left side, in which the crown of the tooth is much abraded

and the fang in a great measure absorbed, from the downward growth of a successional tooth.

2. The enamelled and ridged external aspect of the crown.

2ª. The smooth convex inner aspect of the same.

2ᵇ. The abraded coronal surface with its double facets (1 and 2).

a. Anterior margin.

b. Posterior marginal angle.

f. Remains of the fang, showing the cavity produced by a successional germ.

n. Primary ridge.

Fig. 3. Vertical section of the crown of an unused tooth, seen by transmitted light, magnified eight diameters.

e. Enamel.

d. Vascular dentine.

p. Pulp-cavity filled with mineral matter.

Fig. 4. A successional tooth of the right side of the lower jaw, with the serrated coronal margin entire, from Brook Point, Isle of Wight. This specimen is identical with the tooth in place (Plate XVI. fig. 1), but must have belonged to a larger individual.

4. The mesial or inner aspect.

a. The anterior margin.

b. The posterior marginal angle.

n. The primary ridge of the enamelled front of the crown.

4ª. The external smooth convex aspect of the same.

p. Pulp-cavity.

Fig. 5. A tooth belonging to the left side of the lower jaw; the apex of the crown partially worn away. This specimen, together with figs. 1, and 4, with numerous vertebræ, a femur 3½ feet long*, and other bones, were obtained from the Weald Clay, forming the cliff near Brook Point, Isle of Wight; the whole probably belonged to the same individual, which must have been an aged reptile of very colossal proportions†.

5. The smooth, convex, outer aspect.

5ª. Oblique view, showing the posterior side and marginal angle, and the ridged enamelled inner surface.

a. The anterior margin.

b. The posterior marginal angle.

f. The fractured extremity of the fang exposing the pulp-cavity (*p*).

Fig. 6. Molar of the left side of the lower jaw: in this example the whole of the

* I have presented this bone to the Hunterian Museum.

† See my Geology of the Isle of Wight, p. 315.

serrated part of the crown is worn away, and the fang absorbed by the pressure of a successional tooth.

6. The smooth convex outer aspect; the worn surface of the crown has two distinct facets, as in the abraded coronal planes of figs. 3 and 4.

6[a]. The inner or mesial aspect of the same.

PLATE XIX.

A portion of the anterior part of the left upper maxillary bone of an adult Iguanodon, from Tilgate Forest: represented of the size of the original*.

Fig. I. The inferior or alveolar aspect, showing the remains of the sockets of ten molars.

f, *f*. Dental alveoli.

x. The intermaxillary articulating surface.

Fig. II. The upper or nasal surface, with deep channels for the infra-orbital vessels and nerves.

a, *a*. The infra-orbital canal.

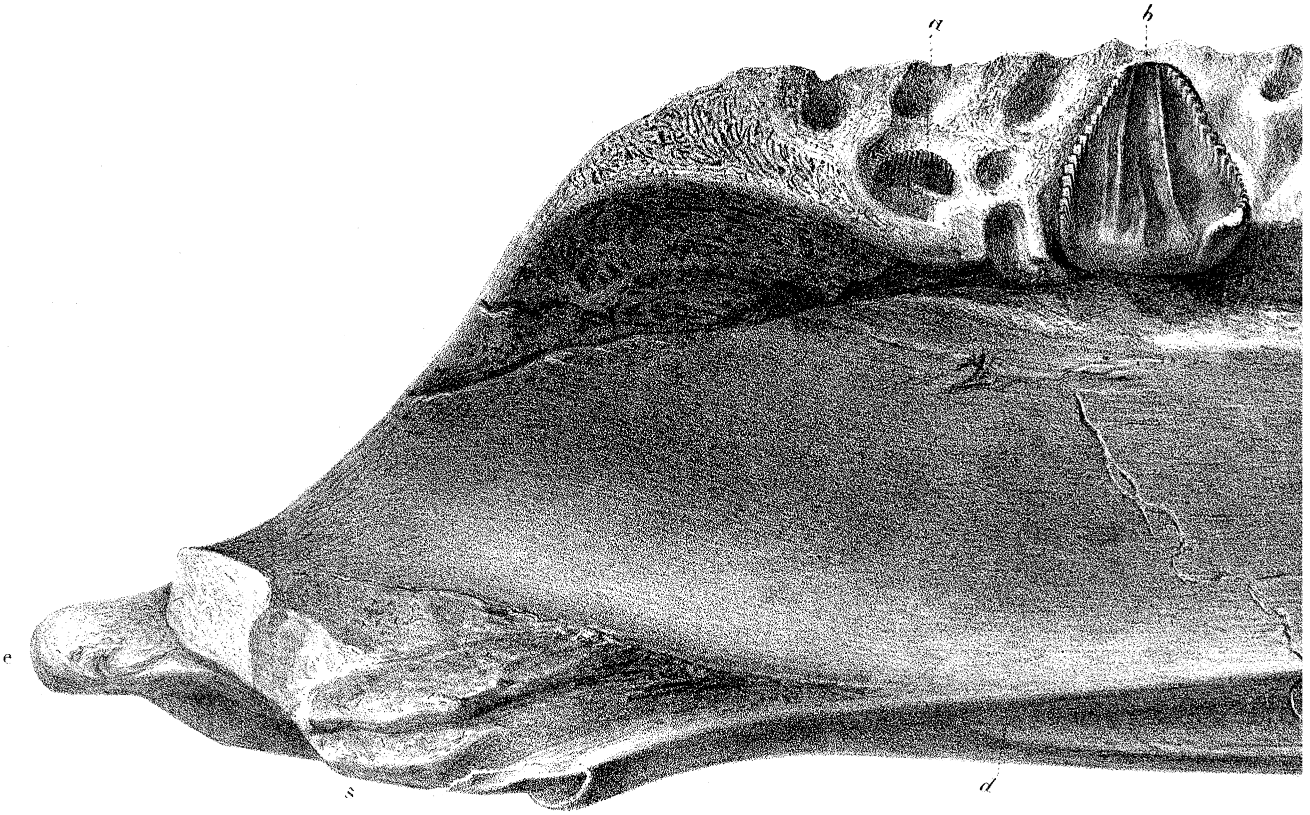
b. Retrograde furrow of the same.

c. A deep concavity in the roof of the infra-orbital canal (see description, *ante*, p. 191).

x. The anterior marginal surface that articulated with the intermaxillary bone.

* This specimen is in the British Museum.

⁂ The nearly perfect tooth figured in Philosophical Transactions, 1841, Plate VI. figs. 1, 2, 3, is an upper molar of a very young Iguanodon. Fig. 4 of the same plate is the coronal germ of an upper tooth.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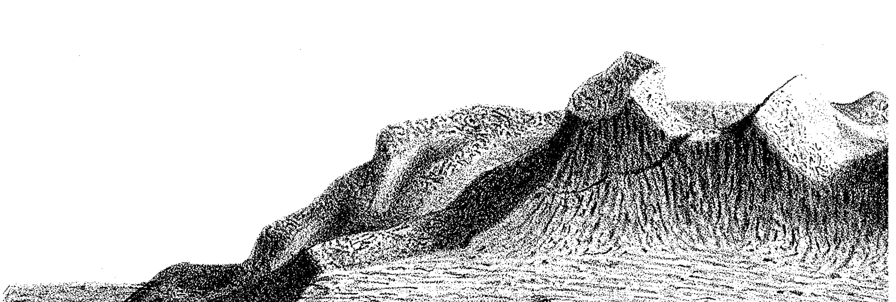

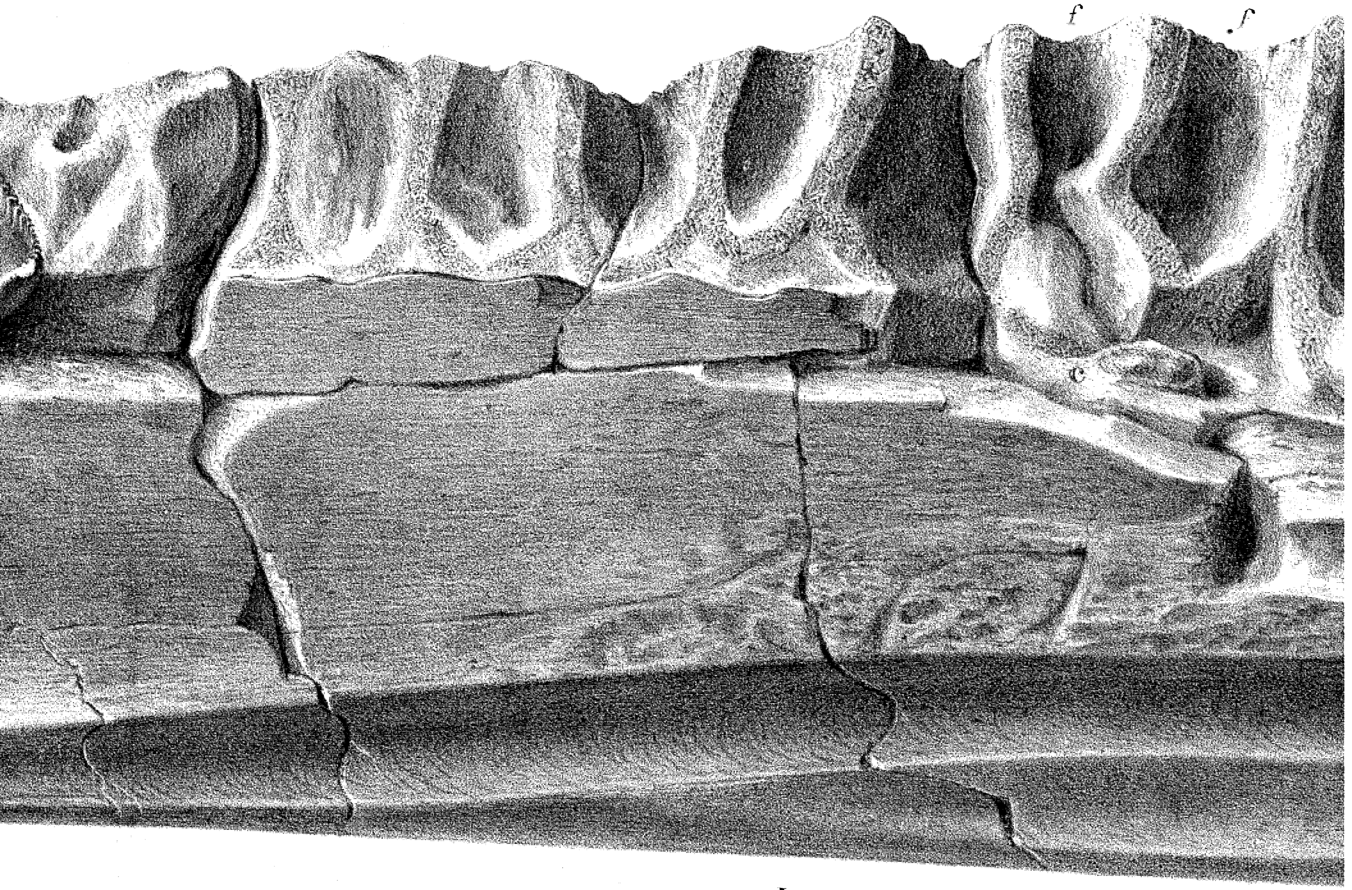

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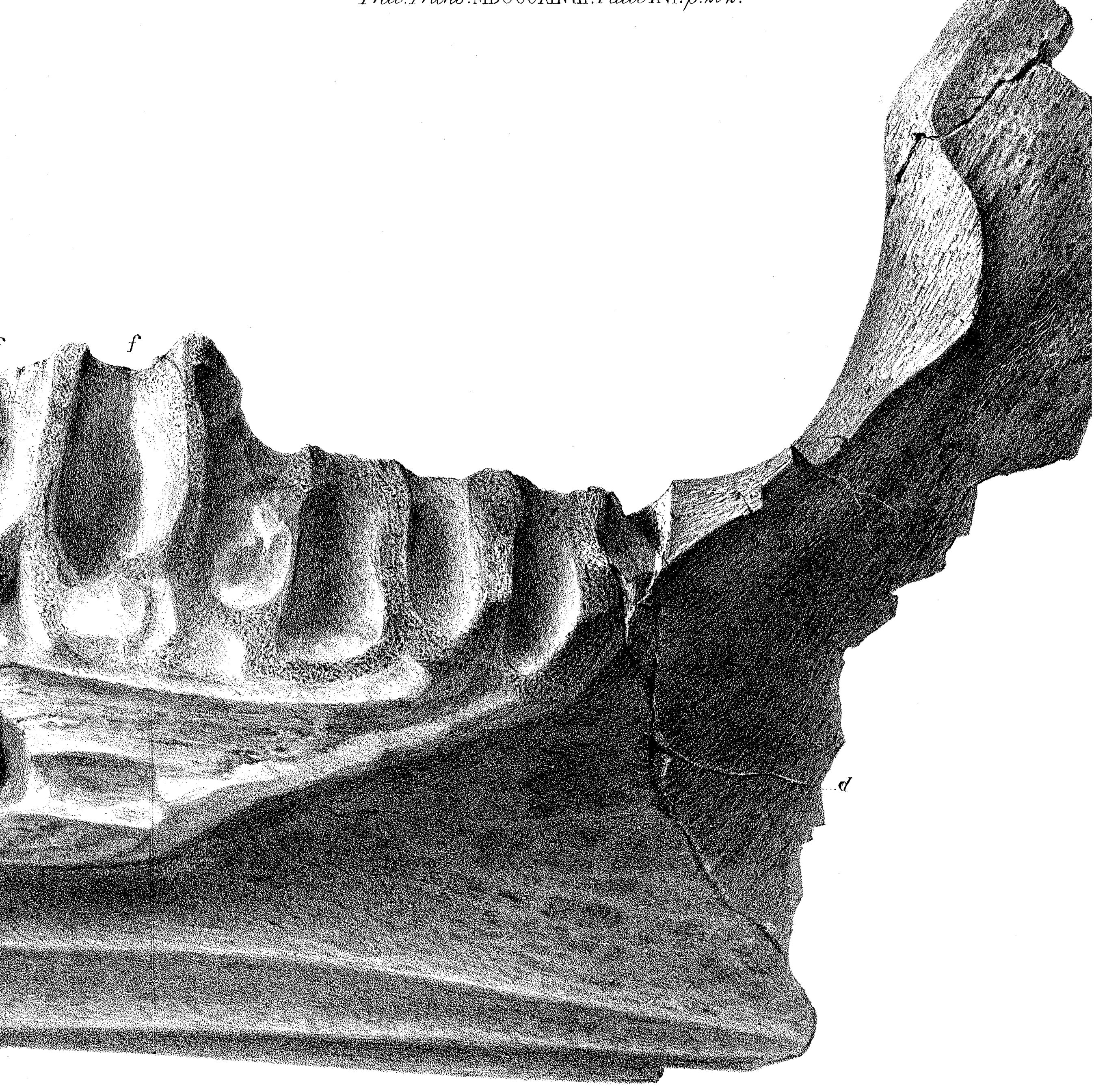
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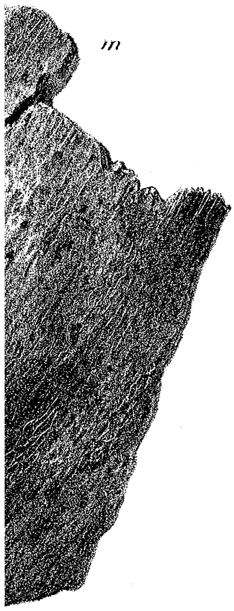

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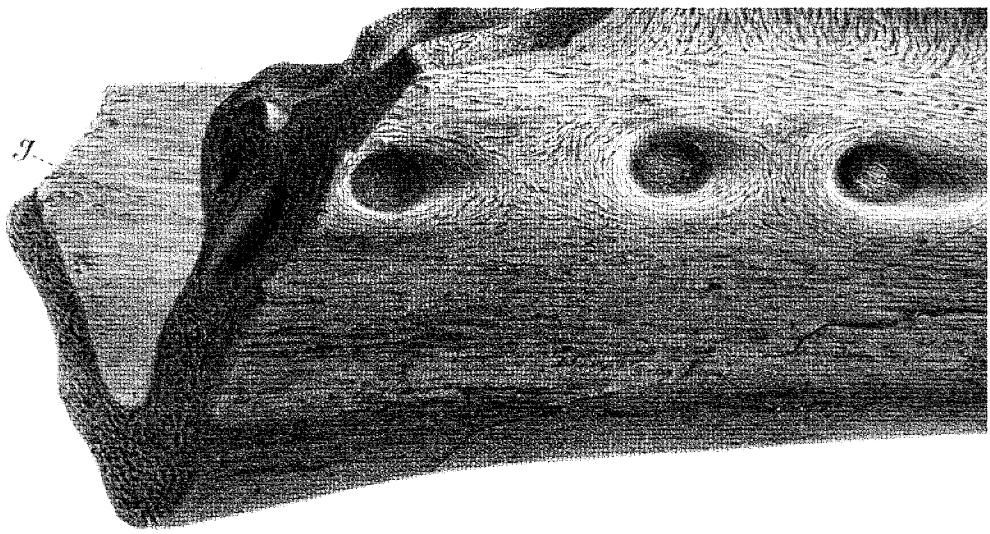

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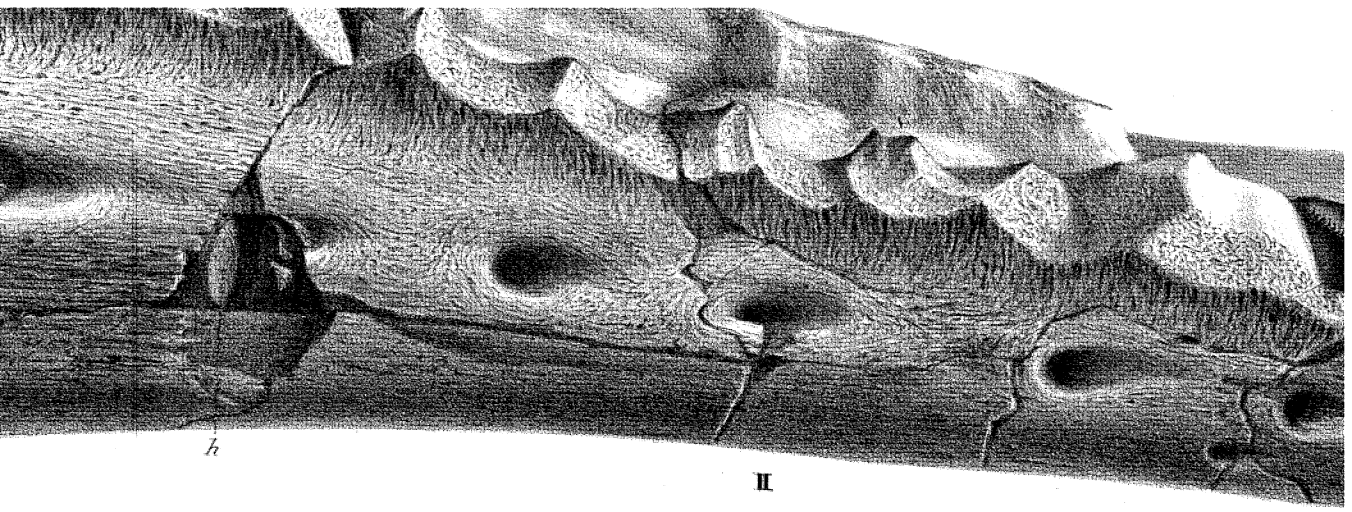
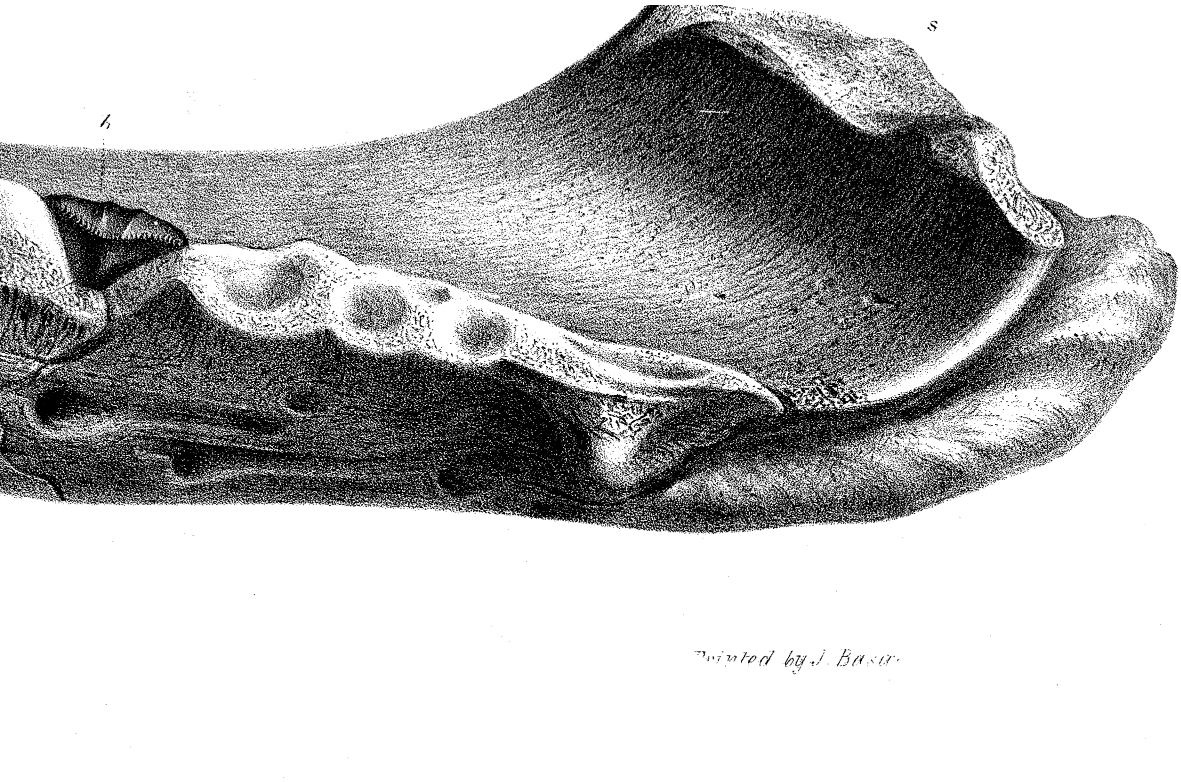


The anterior part of the right side of the Lower Jaw of the Iguanodon Mantelli; from Tilgate Forest.

Fig. 1. Inner or mesial aspect. Fig. 2. Oblique external view.



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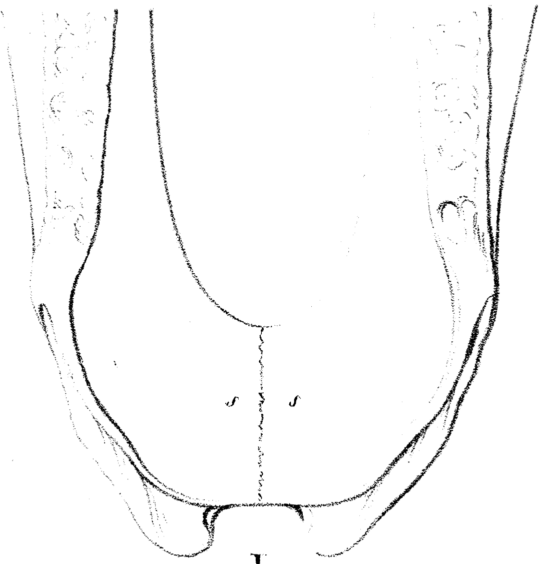

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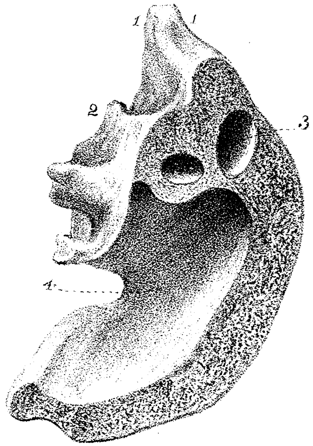

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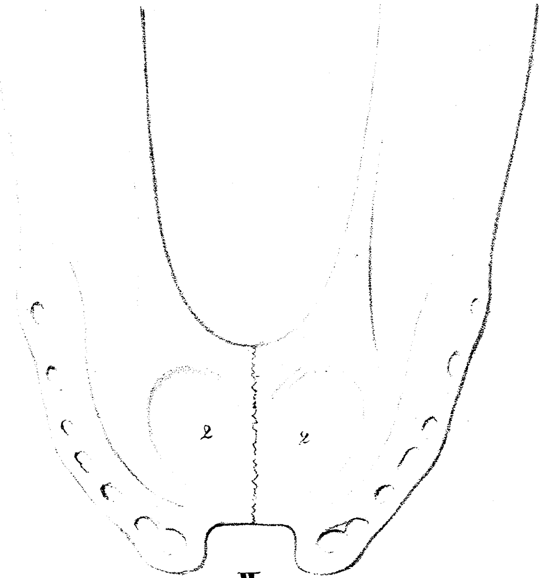

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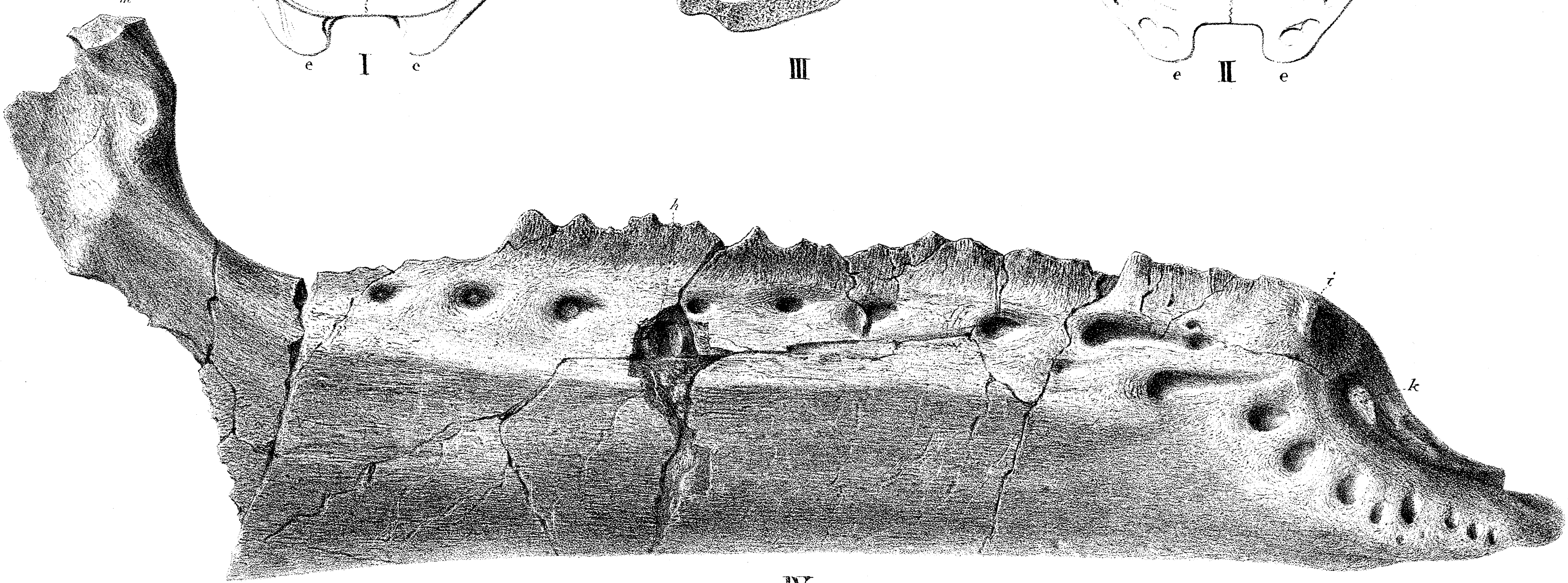

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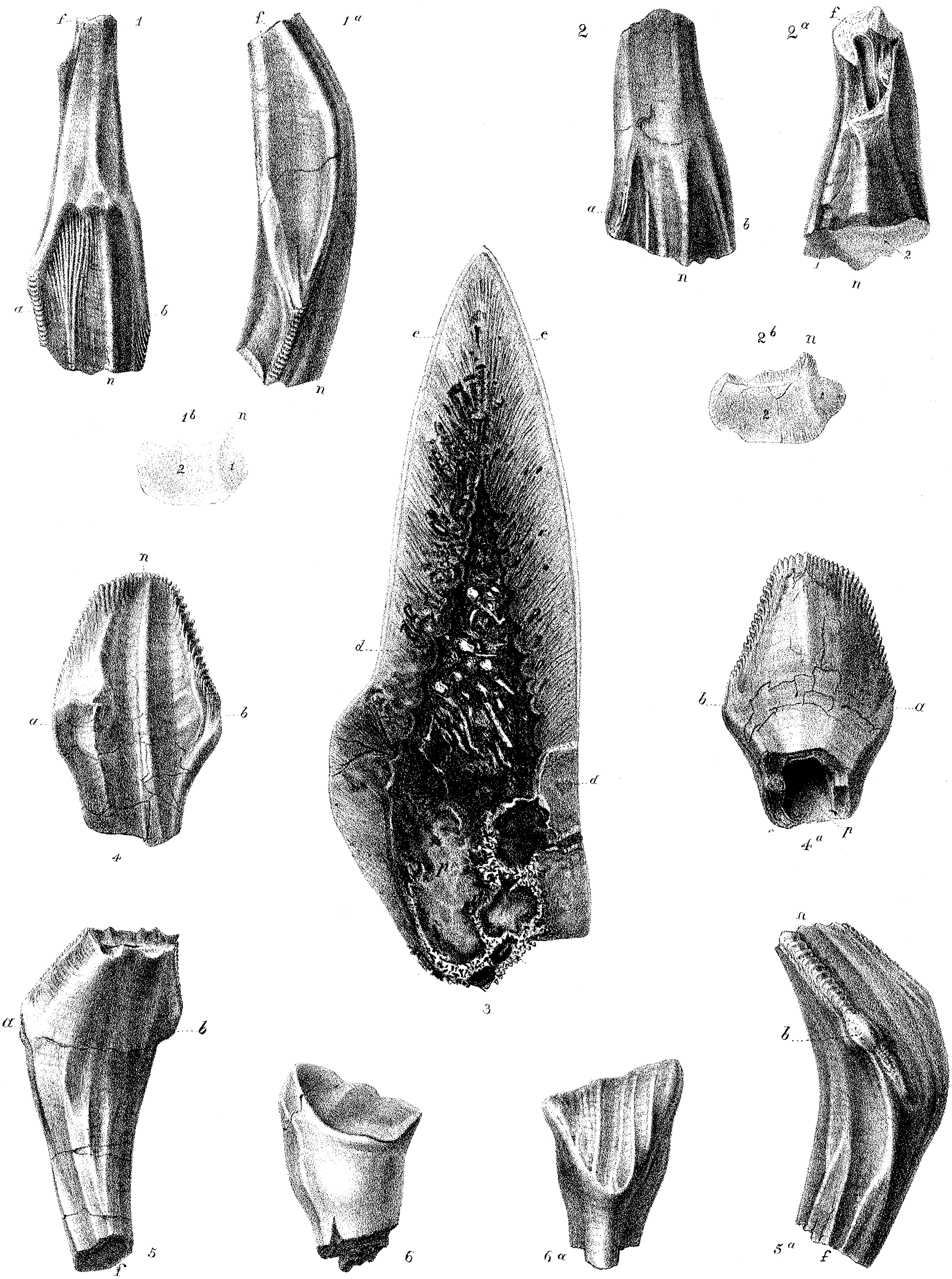

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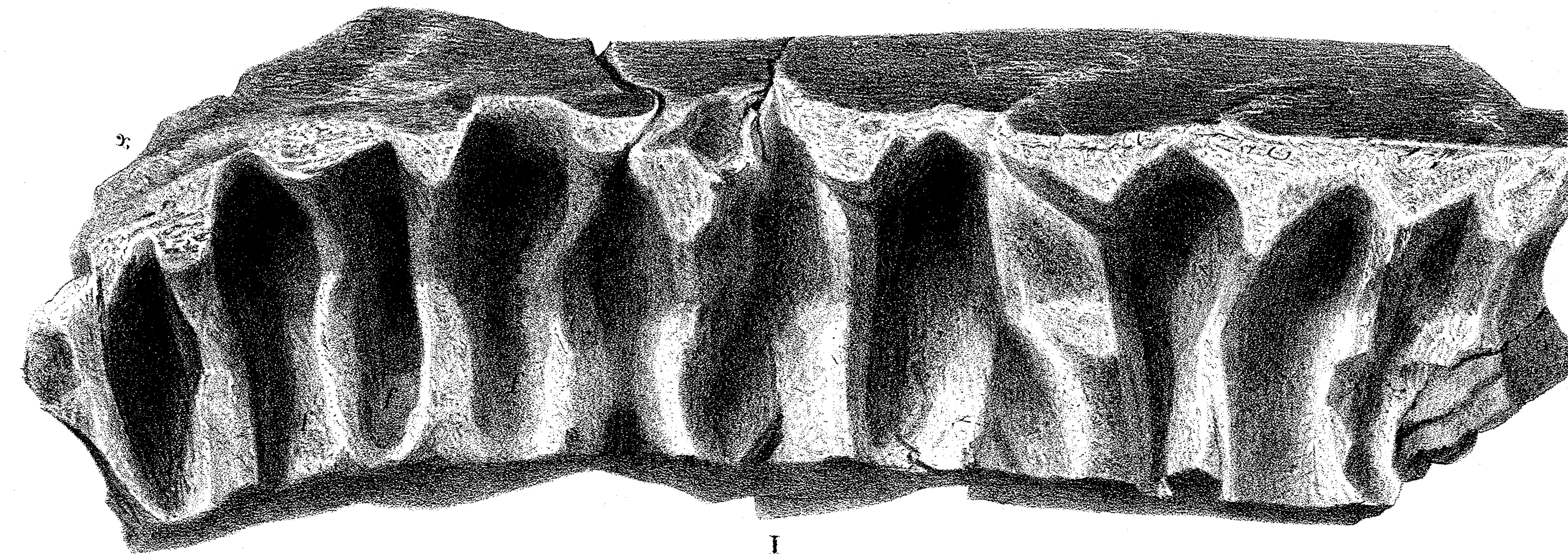
Teeth of the Iguanodon



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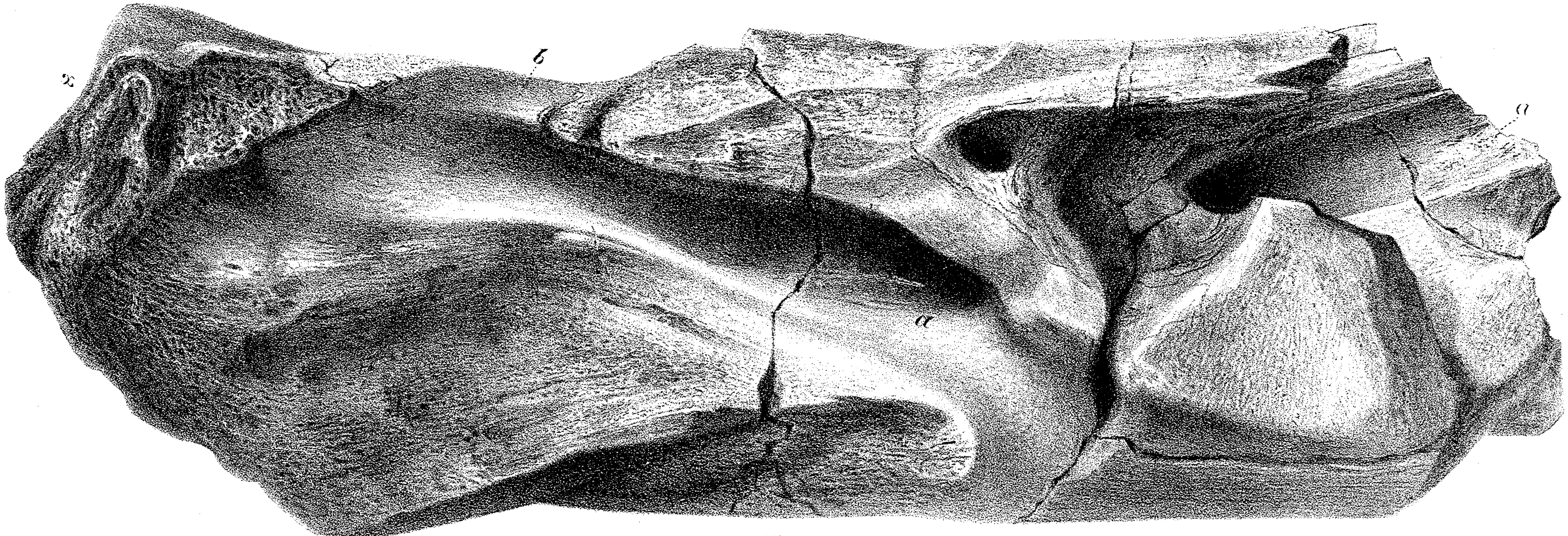
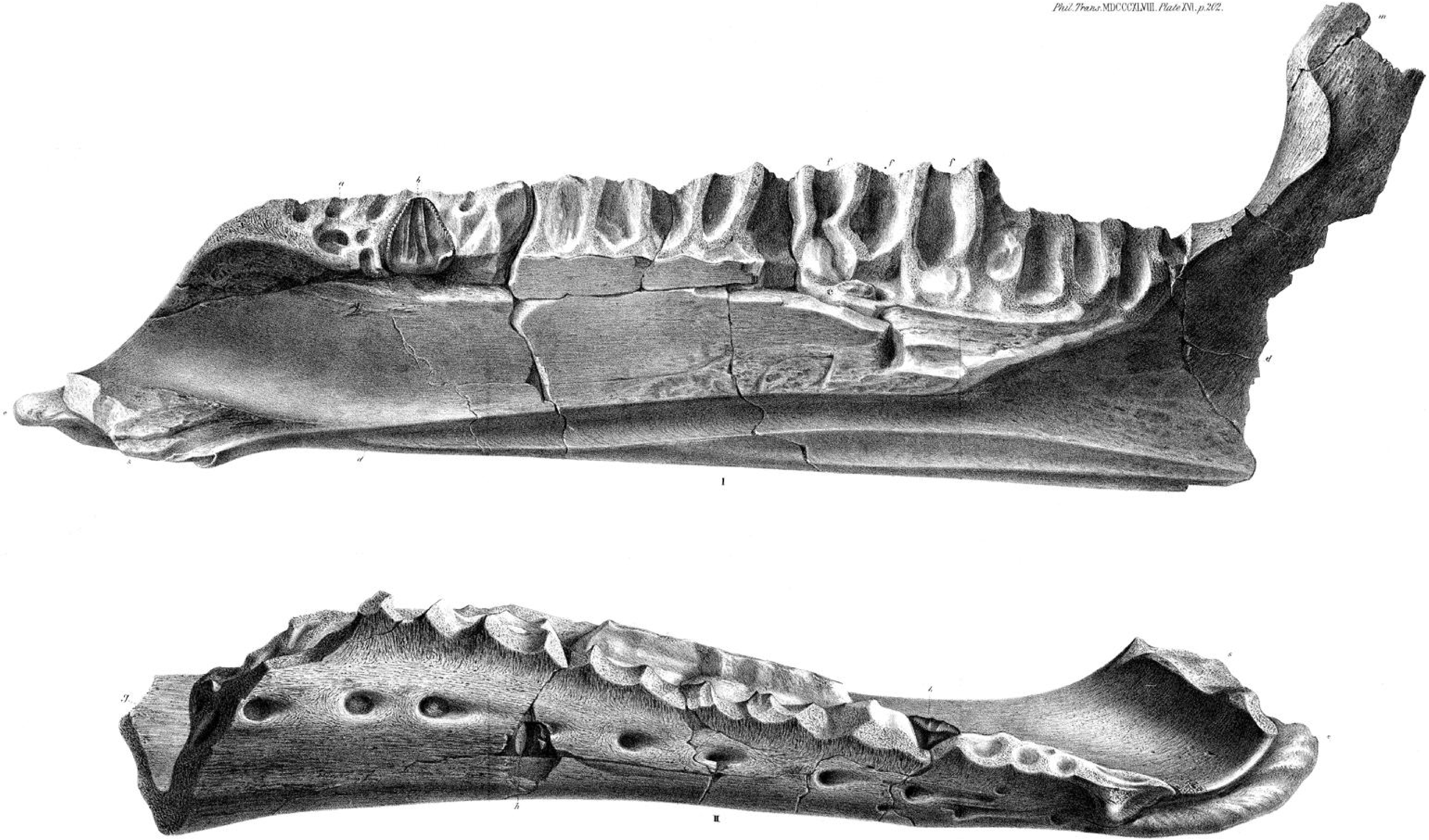


II

Dinkel del: et lith.

Printed by J. Basire.

Portion of the Upper Jaw of the Iguanodon.



Dinkel del et lith.

Printed by J. Basire.

The anterior part of the right side of the Lower Jaw of the *Iguanodon Mantelli*; from Tilgate Forest.

Fig. 1. Inner or mesial aspect. Fig. 2. Oblique external view.