IX. *Description of the Skull and Teeth of the* Placodus laticeps, OWEN, *with indications of other new Species of* Placodus, *and evidence of the Saurian Nature of that Genus. By Professor* OWEN, *V.P.R.S., Superintendent of the Natural History Departments in the British Museum.*

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COUNT MÜNSTER, in the year 1830, obtained two specimens of portions of the upper jaw with the palate and teeth, of a vertebrate fossil, from the Muschelkalk member of the Triassic system near Bayreuth, which he described and figured in a brochure, entitled "Fossile Fischzähne von Bayreuth*," referring the specimens to the class of Fishes. They were chiefly remarkable for the large size, and especially the breadth and shortness, of the crowns of the teeth.

Professor AGASSIZ, in the 'Part' of his great work on Fossil Fishes†, which appeared in 1833, and formed the commencement of the second volume, accepted Count MÜNSTER's determination of the foregoing fossils, referred them to the Pycnodont family of the Ganoid order of his System of Ichthyology, and founded on them a genus which he called *Placodus*, a term significant of the broad flat teeth of such supposed fishes. The generic character given by Professor AGASSIZ is as follows:—"Dents polygones, à angles arrondis, dont la surface est aplatée et entièrement lisse;" and he adds, "Rangé par induction dans l'ordre des Ganoïdes; car je n'ai jamais vu les écailles d'aucun poisson de ce genre?" Of this genus he defines two species:—

1. *Placodus impressus*, AG.; characterized by a depression on the middle of the crown of the tooth, from the triassic formation called 'grès bigarré,' at Deux Ponts.

2. *Placodus gigas*, AG.; characterized by the flat crown of the teeth: from the Muschelkalk, Bayreuth. This species is founded on the specimens originally described by Count MÜNSTER.

Professor BRONN, in his 'Lethæa Geognostica,' adopts the systematic position assigned by Professor AGASSIZ to the genus *Placodus*; but he remarks that it is known by little more than the teeth, which are all short and almost flat, from four- to six-sided, with the angles rounded off; and he states that the vertebral column and scales are unknown. Three species of *Placodus* are admitted in this work‡,—*Placodus impressus*, AGASSIZ, from the Bunter-sandstein of Zweibrücke (Deux Ponts); *Placodus gigas*, AGASSIZ, from the Muschelkalk of Bamberg and Bayreuth; and a third species, afterwards called *Pla-*

* Fossile Fischzähne von Bayreuth, 4to. 1830.

† Recherches sur les Poissons Fossiles, tome ii. 1833–43.

‡ Band i. 8vo, 1837, p. 186. tab. 13. fig. 13.

codus Andriani by AGASSIZ, from the Muschelkalk of Laineck, near Bamberg. In another part of the first volume of the 'Lethæa Geognostica*,' teeth of *Placodus* are cited with those of other Ganoid fishes, in an enumeration of the fossils of the 'Salz-gebirge' (Muschelkalk and Keuper divisions of the Trias).

In 1841 I gave a brief summary, in the section of my 'Odontography' on the teeth of Pycnodonts, of the descriptions of the dentition of *Placodus* from the writings of MÜNSTER, AGASSIZ and BRONN, with a copy of the figure of the teeth of the *Placodus Andriani* given by AGASSIZ. Not having then had the opportunity of examining any original specimens of this singular extinct animal, I adopted, the more readily, the current opinion as to its nature, from the statement by AGASSIZ, that the teeth resembled in microscopic structure those of other Pycnodont genera†.

In 1843 Count MÜNSTER published a description and figure of a considerable part of the facial division of the skull of a *Placodus* from the Muschelkalk of Bayreuth, on which he founded a distinct species, under the name of *Placodus rostratus*‡ (Plate XI. fig. 4). This specimen had the upper part of the cranium imbedded and the palatal surface exposed, showing the marginal teeth and the palatal teeth. The latter are six in number, three on each side (ib. *e*, *f*, *g*), in two almost symmetrical series, and demonstrate the absence of any median row of vomerine teeth, such as exists in *Gyrodus* and some other unequivocal pycnodont fishes. The figure of the skull indicates the presence of zygomatic arches, with a curvature and span very difficult to reconcile with the known modifications of the plan of cranial structure proper to the class of Fishes. But it has been only very recently that such specimens of the rare and seemingly peculiarly German triassic fossil have come under my observation, and enabled me to settle the doubts which Count MÜNSTER'S figure of *Placodus rostratus* first suggested.

In the meanwhile the essay by HERMAN VON MEYER, entitled "Fossile Fische aus dem Muschelkalk von Jena, Querfurt und Esperstädt," appeared, in the Part (Fünfte Lieferung) of his 'Palæontographica' which was published in 1849. In this essay new localities of the *Placodus* are made known, *e. g.* the Terebratulite limestone (Terebratuliten kalk) of Zwetzen. The prehensile modification of the crown of the anterior teeth of *Placodus gigas* is well illustrated§: the distinct covering of a clear enamel-like substance on the crown of the tooth is mentioned‖; but no suspicion seems to have crossed the mind of this acute and indefatigable palæontologist of any error in the ascription of *Placodus* to the Pycnodont family of Fishes.

In the month of October last (1857) some fossils from German triassic formations were offered for sale to the British Museum, including specimens of *Placodus* from the

* Band i. p. 138.

† "La structure microscopique des dents est la même que chez les autres genres, en sorte que je ne crois pas me tromper en plaçant ce genre aux confines de la famille des Pycnodontes."—AGASSIZ, tom. cit. p. 217.

‡ Beiträge zur Petrifacten-kunde, 4to. Heft 1843, p. 123. fig. 1. taf. 15.

§ Palæontographica, 4to. 1849, tab. 33. fig. 8.

‖ "Der ziemlich stark Schmelz dieser Zahne ist glatt und schwarz, die davon überdeckte Zahnsubstanz weisslich," p. 198.

Muschelkalk near Bayreuth. One of these included a larger proportion of the cranial structure than in any previously known specimen: it also exhibited the upper surface, which in Count MÜNSTER'S specimen of *Placodus rostratus* was buried in the matrix, and this surface in the fossil in question, now acquired for the Geological Department of the British Museum (Plates IX. and X. fig. 1), showed the character, viz. the external nostrils (*n*), so surrounded as to be decisive of the genus belonging to an air-breathing class of the Vertebrate series. But, besides the external bony nostrils, the specimen presented the orbits, ib. *o*, with a similar continuous border of bone, together with one of the temporal fossæ, *t*, bounded externally by an arch of bone continued from the post-frontal, 12, to the mastoid, 8; below which was the true zygomatic arch (*ib.* fig. 2) formed by the malar, 26, and squamosal, 27, elements, extending from the upper maxillary, 21, to abut against a short thick but vertically descending tympanic bone, 28. The articular surface for the lower jaw, convex from behind forward, was concave transversely at the middle part between two convexities; this strong trochlear form of joint being unknown in any recent or fossil fish. The bony palate (Plate X. fig. 1) showed the same absence of median vomerine teeth as in Count MÜNSTER'S *Placodus rostratus* above referred to; and it also showed a broad pterygoid plate, 24, abutting against the antero-internal side of the fixed tympanic, 28. The sum, therefore, of the characters presented by the skull, as, *e. g.* the nostrils, divided by an ascending process of the premaxillary, 22, and bounded by that bone, the maxillaries, 21, and nasals, 15; the size, shape, and surrounding of the orbits; the magnitude of the temporal fossæ, with their complete double zygomatic outer arches, the condition of the single tympanic bone, and the structure of the bony palate, left no hesitation as to the reference of the genus *Placodus* to the class Reptilia, and herein with nearest affinities to the Lacertian order, and more especially with that modification thereof exemplified by the extinct genus *Simosaurus*, from the Muschelkalk*.

The generic characters of the fossil were unequivocally shown by the shape and relative size of the crowns of the teeth, covered, as in the previously figured specimens, by a black enamel, contrasting strongly with the light grey colour of the fossil bone supporting them. Two slight rectifications of the generic character originally proposed by M. AGASSIZ are necessitated by the subsequent accession of different species. The teeth may present a rounded contour, which is the case in all those of the specimens here described; and the surface of the crown becomes quite smooth only by attrition, the enamel of the newly-risen tooth presenting fine striæ diverging from a central point or fissure. The character on which *Placodus impressus*, AGASSIZ, is differentiated, "une impression ou une sorte de sillon longitudinal qui se voit au milieu de la couronne," is one common to the newly-formed crushing teeth of all *Placodi*.

The species which the specimen under description most nearly resembles in the shape, proportions and arrangement of the teeth, is *Placodus rostratus* of MÜNSTER†: the

* H. v. MEYER, Die Saurier des Muschelkalkes, tab. 20, *Simosaurus Guglielmi*.

† Beyträge, *loc. cit.* Taf. xv. fig. 1 *a* (Plate XI. fig. 4).

specific differences will be pointed out after the description of the teeth as they appear in *Placodus laticeps.*

The teeth of the upper jaw, in this, as in the other known species of *Placodus*, consist of an external or maxillary series (Plate X. fig. 1, *a*—*e*), and an internal or palatal series, ib. *f*, *g*. The maxillary series are supported in a marginal row of alveoli by the premaxillary and maxillary bones: the palatal series appear to be implanted in the palatine and pterygoid bones.

The maxillo-premaxillary teeth are five in number on each side, two, *a* and *b*, implanted in the premaxillary, and three, *c*, *d* and *e*, in the maxillary. The premaxillary teeth are subequal, smaller than the maxillary teeth; their crowns are subhemispheric, that of the first being 4 lines, that of the second 3 lines in diameter: the enamel is worn off from the back or inner side of the crown, showing that the lower jaw was shorter than the upper one. On the inner side of the right premaxillary teeth the crown of a small successional tooth has begun to protrude from the bone: it presents rather strong irregular rugæ diverging from a small central pit: this character has been worn away from the crowns of the teeth in place. The premaxillary teeth, in proportion to their breadth, are longer or project further from their sockets than the other teeth; but none of them present the bent, pointed, prehensile character of the incisive tooth figured in tab. 70, fig. 21 of the 'Recherches sur les Poissons Fossiles,' and referred by AGASSIZ to *Placodus gigas.*

The maxillary part of the marginal series is not continued directly from the premaxillary row, but begins on a plane internal to it, by the breadth of the second premaxillary tooth, *b*. From this point the three maxillary teeth extend outward and backward in a line parallel with that formed by the premaxillary teeth.

The first maxillary tooth, *c*, has a full oval crown, $4\frac{1}{2}$ lines by 4 in diameter. The second maxillary tooth, *d*, measures $5\frac{1}{2}$ lines by $4\frac{1}{2}$ lines in diameter: the longer axis in both teeth is in the line of the series. The third maxillary tooth, *e*, is subcircular, 8 lines in diameter, on the right side; but on the left side the transverse diameter is 9 lines, the other diameter the same as the left tooth.

The palatal series begins on the inner side of this tooth, and consists of two teeth on each side.

The first tooth, *f*, apparently developed in the true palatine bone, 20, has a full elliptical crown, 10 lines by 8 lines: the second tooth, *g*, developed in the broad pterygoid bone, presents a full oval shape, 1 inch 9 lines by 1 inch 3 lines in diameter. The longer axis of both teeth is in the line of the series, and this line is on nearly the same parallel—from within outward and backward—as the premaxillary and maxillary rows. The last large tooth is slightly hollowed, by attrition, at the middle of the grinding surface; the primitive radiating striæ of the enamel are visible only round the margin and sides of the tooth.

All these teeth are implanted by short simple bases in distinct shallow sockets, according to the 'thecodont' type of dentition in the Lacertian order. Evidence has already

been given of their being subject to the same law of displacement and succession as in other reptiles; but this is common to both reptiles and fishes.

The total number of teeth in place in the upper jaw of *Placodus laticeps* is fourteen.

In *Placodus rostratus* (Plate XI. fig. 4), as in *Pl. Münsteri*, *Pl. Andriani*, and *Pl. gigas*, the internal or palatal teeth are six in number, three on each side. In *Pl. rostratus* and *Pl. Münsteri*, the first two palatal teeth are subequal and much smaller than the last great tooth: they are situated on the inner side of the last two maxillary teeth in *Pl. Münsteri*; but are both posterior to the maxillary series in *Pl. rostratus*.

In *Placodus gigas* and *Pl. Andriani*, the palatal teeth (called 'vomerine' by MÜNSTER and 'internal' by AGASSIZ), three in number on each side, are all of large size, slightly increasing from before backward; they are situated close together, forming on each side a series a little curved with the convexity outward, and the interspace between the two series is very narrow. The first tooth is triangular, the second and third are quadrangular; each with the angles rounded, and the transverse diameter exceeding the fore and aft or longitudinal one. The maxillary teeth are much smaller than the palatal ones; have a rounded or subquadrate crown; are four in number; and of subequal dimensions: the series is somewhat curved, with the convexity next the outer alveolar margin; commencing a little in advance of the first palatal tooth, and terminating opposite the interspace between the penultimate and last palatal teeth. The premaxillary teeth, three in number on each side, are more remote and distinct from the maxillary teeth than in *Placodus rostratus* and *Pl. laticeps*. They form an almost transverse series at the fore-part of the upper jaw; and their crowns are more elongated and conical than in *Pl. laticeps*; the prehensile power of the prolonged premaxillary part of the jaw being obviously greater in *Placodus gigas* than in *Pl. laticeps* or *Pl. rostratus*. The size of the last tooth in *Pl. laticeps* surpasses that of any of the teeth in the previously discovered species. In proportion to the entire skull, it is the largest grinding tooth in the animal kingdom, that of the Elephant itself not excepted.

The specific distinction of the fossil exhibiting the true reptilian characters of the genus, and for which I propose the name *Placodus laticeps*, is satisfactorily established by the dental distinctions pointed out in the foregoing comparisons. By some systematists it may even be deemed requisite to separate generically the *Placodi* with two teeth, from those with three teeth, in each palatal series: but *Placodus rostratus* offers a transitional condition in the small relative size of the first two palatal teeth, and in the rounded form of all the teeth, from *Pl. Andriani* to *Pl. laticeps*; and I do not perceive any advantage that would compensate for an additional generic term in the present state of knowledge of the Placodont reptiles.

The chief distinctive feature of the cranium of *Placodus laticeps*, is the great proportional size of the temporal fossæ and wide span of the zygomatic arches. The great muscular force applied to work the jaws and their crushing machinery adequately is indicated by this modification. The breadth of the skull at this part equals, at least,

the length, and imparts a triangular form to the whole, viewed from above or below. The name *laticeps* was suggested by this character; but it would apply almost as well to *Placodus rostratus* and *Pl. Münsteri*. In *Pl. Andriani* and *Pl. gigas*, the length of the skull plainly exceeds the breadth.

The apex of the triangle is formed by the premaxillary (Plate IX. fig. 1, 22); it is rounded off: the outer surface of the premaxillary is smooth, and the convex border projects a little way beyond the alveoli of the teeth. It is a single bone sending upward and backward a median process which meets and articulates with the nasals (*ib.* 15), and so forms the partition between the external nostrils.

These orifices (Plate IX. *n*, figs. 1 and 2) are of an oval form with the small end forward, rather sharply defined above, but with the lower border rounding off into the floor of the passage below; about 9 lines by 6 lines in the two diameters. The suture between the premaxillary and maxillary begins about the middle of the lower border of the nostril; that between the premaxillary and nasal is behind the middle of the upper border: the hinder border is formed by the nasal above, by the maxillary below, and by a bar of bone half an inch in breadth, which divides the nasal from the orbital cavity; whether any or what proportion of a lacrymal bone enters into the formation of this bar, the sutural traces are too obscure to enable me to determine. The alveolar border of the maxillary (*ib.* fig. 2, 21), containing the three teeth, *c*, *d*, *e*, forms a slight convex curve downward; then slightly rises and bends rapidly outward to pass into the malar portion of the zygomatic arch, 26. The orbit (Plate IX. *o*, figs. 1 and 2) is subcircular, 14 lines in longitudinal, by 12 lines in vertical, diameter: like the nostril, the upper boundary is sharply defined; the lower border rounds in to the floor of the cavity; the front border shows a middle prominence, low and broad, which contracts as it extends back upon the floor of the orbit.

The interorbital space on the summit of the cranium is slightly convex both across and lengthwise; its breadth is 7 lines, a little increasing backward.

The bony wall of the face below the orbit expands rapidly and spreads outward as it extends backward, dividing about $1\frac{1}{2}$ inch behind the orbit into the upper and lower zygomata. It is by analogy that I conclude these zygomata, which are peculiar to certain Sauria and a few birds, to be composed—the upper one of the conjoined postfrontal and mastoid, the lower one of the malar and squamosal elements. Both zygomata, in *Placodus*, arch outward with a span peculiar for its extent and convexity, the lower arch curving outward by more than its own breadth beyond the upper one. This arch is about half an inch in breadth, its flat surface looking almost directly upward; the margins turned inward and outward: the former is sharply defined. The lower or proper zygoma was evidently of greater breadth than appears in the specimen, for its outer border has been broken away: had it been entire, the breadth of this remarkable skull would have been even greater than it now is. The temporal fossa (*ib.* fig. 1, *t*), circumscribed by the upper zygoma externally, and by the proper cranial parietes internally, is an ellipse, 3 inches in the long diameter, which is in the axis of the skull, and 2 inches

across. The blow which severed the portion of rock, containing the fossil, extended obliquely from behind the right orbit to the back part of the left temporal fossa, and destroyed the upper wall of the cranium proper. The facial part of the skull thus preserved, including the nostrils and orbits, gives the direction of the mid-line of the skull, and demonstrates the reptilian contraction of the cranial cavity; which appears to have measured only an inch across at the middle of the temporal fossæ. The total breadth of the skull here exceeded 8 inches; the total length being somewhat under 8 inches. The small degree of height of the skull, fig. 2, contrasts strongly with these dimensions, especially with the breadth. The vertical diameter of the skull between the orbits is $1\frac{1}{2}$ inch: from the very gradual slope from this part to the end of the mouth, it would seem that the height of the cranium was not greatly increased as it extended backward. The occipital portion of the skull is wanting; and the structure of the base of the skull cannot be satisfactorily made out; the bone and matrix are so blended on the palate and so nearly alike in tint. I believe the inner nostrils to have opened between the two series of maxillary teeth: the matrix can be traced uninterruptedly from the outer nostrils downward and a little backward to this part of the palate: the pterygoid part of the palate behind the last great tooth is $3\frac{1}{2}$ inches across, slightly arched, with the outer angles abutting against the short and thick tympanic, the structure of which has been already described.

For the purposes of future comparison the following dimensions (English, and French metrical) are added to those mentioned in the text:—

		Placodus laticeps.	
From the first premaxillary to the last pterygoid tooth, in a straight line,	in.	lines.	French.
including both teeth	4	4	0·11
Extent of the two premaxillary teeth	0	9	0·018
Extent of the three maxillary teeth	1	8	0·042
Extent of the two palato-pterygoid teeth	2	9	0·07
Breadth between the hindmost premaxillary teeth, including those teeth	1	5	0·035
Breadth between the hindmost maxillary teeth, including those teeth	3	1	0·08
Breadth between the hindmost pterygoid teeth, including those teeth	3	6	0·09
Breadth of trochlear articular surface of the tympanic	1	3	0·03
From the fore-end of the skull to the back part of the tympanic	6	10	0·175
From the fore-end of the skull to the fore-part of the external nostril	0	9	0·018
From the fore-end of the skull to the fore-part of the orbit	2	2	0·05
From the fore-end of the skull to the fore-part of the temporal fossa	3	6	0·09
From the outer margin of one nostril to that of the other	1	3	0·03
From the outer margin of one orbit to that of the other	2	10	0·073
Breadth of the skull across the back part of the nostrils	2	4	0·055
Breadth of the skull across the back part of the orbits	6	3	0·158

(The latter admeasurement gives the peculiarly rapid expansion of the facial part of the skull.)

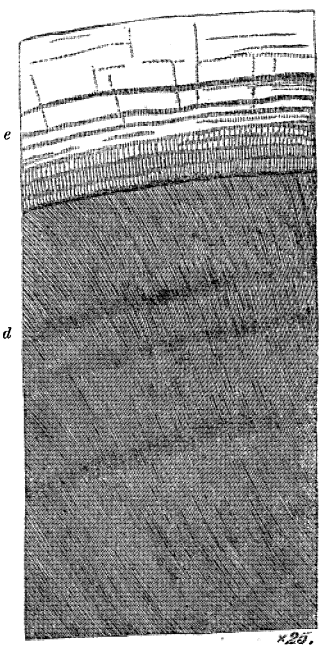
In the German members of the Trias, from which remains of *Placodus* have been obtained, other well-marked forms of the Reptilian class have been discovered, including

the labyrinthodont *Reptilia*, with genera of lacertian affinities, for the knowledge of which we are chiefly indebted to M. HERMAN v. MEYER*.

Nothosaurus, *Simosaurus* and *Pistosaurus*, present the same evidences of lacertian affinities in the division of the nostrils by the median extension of the premaxillary backward to the nasals, the same thecodont dentition, and the same circumscription of the orbits and temporal fossæ as in *Placodus*: there is also a general family likeness in the upward aspect of these apertures, accompanying an extreme depression of the skull. The muzzle, though varying greatly in length in these genera, presents the same obtuseness; and the alveolar border of the jaws the same smooth outward convexity which we observe in the *Placodus*. The peculiar confluence of the elements of the upper and lower zygomatic arches, *i. e.* of postfrontal and malar, forming the broad wall of bone behind the orbit, is continued still further backward in *Simosaurus*†. In *Pistosaurus*, the elongated postfrontal, malar and squamosal are united together in one deep zygomatic arch, which has the mastoid and tympanic for its hinder abutment. The lower articular surface of the tympanic bone presents the same trochlear form in *Pistosaurus* and *Simosaurus* as in *Placodus*‡.

The dentition of the triassic Saurians described by v. MEYER, although, like *Placodus*, thecodont in respect of implantation, is of the ordinary lacertian or crocodilian type in respect of form, the crown of every tooth being long and sharp-pointed, adapted to the prehension of fishes or other active vertebrate animals: moreover, they are developed, as in Crocodiles and Enaliosaurs, exclusively in the premaxillary, maxillary and mandibular bones, the palatal bones being edentulous. Besides, however, the instances in modern lacertian genera of palatal teeth, the triassic Labyrinthodonts also exhibit the same superaddition, and the unequal magnitude of some of these teeth may be noticed as presenting an analogy with the dentition of *Placodus*.

Fig. 1.



Dentine and Enamel, *Placodus laticeps*.

The structure of the teeth of *Placodus*, like that in *Nothosaurus* and *Simosaurus*, conforms to the ordinary crocodilian and lacertian type. The dentine (fig. 1, *d*) is of the hard unvascular kind, and the crown of the tooth is covered by a moderately thick well-defined layer of true enamel (fig. 1, *e*). This enamel, in the newly-formed tooth, presents numerous, close-set, fine irregular striæ or rugæ, radiating from a central groove or pit on the summit: the teeth are subject to the same succession and displacement as in the *Reptilia* generally.

* Die Saurier des Muschelkalkes. Fol. 1847–1855.

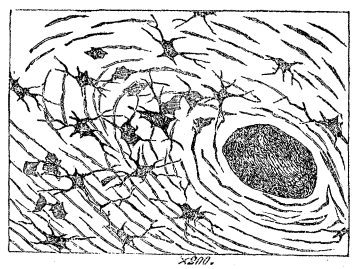
† Ib. tab. 20. fig. 1, and tab. 65. fig. 2.

‡ Tab. 21. fig. 3.

The dentine presents, under an adequate magnifying power, extremely fine, numerous and close-set dentinal tubuli, without admixture of medullary canals: they radiate from the wide and shallow pulp-cavity, with a corresponding feeble divergence, at right angles to the outer surface of the tooth. The tubuli are, at first, straight; but show two slight primary bends near the periphery of the tooth. They present a diameter of $\frac{1}{20,000}$th of an inch, with interspaces varying between two and three times that diameter; they divide once or twice in their course: a few secondary branches were discernible near the periphery of the dentine. The difference between this dentinal structure and that of true pycnodont fishes is seen in the larger relative size and much closer arrangement of the dentinal tubuli in those fishes, and their apparent composition of a closely twisted bundle of smaller tubes, owing to the oblique direction and number of the branches sent off into the intertubular substance*. The terminal branches into which the tubuli resolve themselves penetrate, in Pycnodonts, the clear substance which is analogous to enamel, but is a continuation and slight modification of the intertubular or basement tissue of the entire tooth. In *Placodus* the layer of enamel (fig. 1 *e*) is as distinct as in the Monitor or Crocodile. It is a very dense and compact substance, in which a structure of fibres, vertical to the surface, is but faintly discernible near the dentine.

The osseous tissue of *Placodus* (fig. 2) exhibits concentric layers around the Haversian canals, the area of one of which is shown in fig. 2. The lacunæ or bone-cells, of a size and shape closely resembling those of the Plesiosaurus and Crocodile, have diverging tubuli larger than in Mammals, with a more wavy course and fewer ramifications. The tubuli are much more numerous in the best-preserved and prepared slices of bone than in the specimen figured; which shows, however, the characteristic reptilian size and irregular or subangular contour of the bone-cell.

Fig. 2.



Osseous tissue of jaw, *Placodus laticeps*.

We cannot contemplate the extreme and peculiar modification of form of the teeth in the genus *Placodus* without a recognition of their adaptation to the pounding and crushing of hard substances, and a suspicion that the association of the fossils with shell-clad mollusks in such multitudes as to have suggested special denominations to the strata containing *Placodus* (*e. g.* Muschelkalk, Terebratulitenkalk, &c.), is indicative of the class whence the *Placodi* derived their chief subsistence.

No doubt, the most numerous examples of similarly-shaped teeth for a like purpose are afforded by the class of Fishes, as, *e. g.*, by the extinct Pycnodonts, and by the Wolf-fish (*Anarrhichas lupus*) and the Cestracion of the existing seas. But the Reptilian class is not without its instances at the present day of teeth shaped like paving-stones, of which certain Australian lizards exhibit this peculiarity in so marked a degree that the generic name *Cyclodus* has been invented to express that peculiarity†. Amongst extinct Reptiles, also, a species of lizard from the tertiary deposits of the Limagne, in

* See 'Odontography,' pl. 33.

† Ibid. pl. 66. fig. 7.

France, presents round obtuse teeth, of which the last, in the lower jaw, is suddenly and considerably larger than the rest *.

Mandible, or lower jaw.—Count MÜNSTER obtained from the Muschelkalk of Bayreuth a portion of one ramus of a lower jaw with three teeth in place, which M. AGASSIZ has figured in tab. 70, figs. 15 and 16, of his great work on Fossil Fishes †; referring it to *Placodus gigas*. From this specimen M. AGASSIZ concludes that there was but one row of teeth in each ramus of the jaw ‡. The three teeth in place are of large size and subquadrate form: a fourth smaller tooth appears on the surface of the bone, at a lower level. This M. AGASSIZ considers an incisor; but certain appearances in the specimens, presently to be described, lead me to regard it as a successional anterior molar, exposed in its formative cavity by fracture or abrasion of the bone at that part. M. AGASSIZ, indeed, remarks on the peculiarity of its implantation in the outer border of the jaw §. Its crown is obtuse, and of half the size of the foremost of the three teeth in place.

There is no character adduced in the text or plate in proof of the piscine affinities of the above fossil jaw.

Four specimens of portions of lower jaw form part of the collection of Muschelkalk fossils from Bayreuth, in addition to the cranium of the *Placodus laticeps*, now acquired by the British Museum.

The first of these mandibular specimens (Plate X. figs. 6 and 7), includes part of the left ramus and a smaller portion of the right ramus united by the hinder portion of the symphysis, *s*, *s*. In the left ramus the first (*a*) and third (*c*) teeth are preserved, in the right ramus the first (*a*) and second (*b*) of the three large subquadrate teeth which are figured in the mandibular fossil described by M. AGASSIZ.

These teeth are somewhat smaller in the present specimen and are differently shaped. The grinding surface of the last (fig. 7 *c*) is almost a complete square with the angles rounded off, measuring 1 inch in length, and 1 inch $\frac{1}{2}$ a line in breadth; the inner border is one line longer than the outer border. In the *Placodus gigas* the corresponding tooth is 1 inch $2\frac{1}{2}$ lines in length, and 1 inch 3 lines in breadth: the inner border is 4 lines longer than the outer one, and the angles are more rounded off than in the present specimen. The second (penultimate) tooth in the present specimen (fig. 7, *b*) resembles in shape the last: the length and breadth are each 11 lines. In *Placodus gigas* the corresponding tooth is notably broader than it is long, and the inner border is longer than the outer one. The first tooth on each side, in the specimen under description

* GERVAIS, Zoologie et Paléontologie Françaises, pl. 64, figs. 5–7.

† Recherches sur les Poissons Fossiles, 4to. tom. ii.

‡ "Il est évident d'après cela, que chaque branche de la mâchoire n'avait qu'une rangée de larges molaires, et que les rangées externes manquaient complètement."—Recherches sur les Poissons Fossiles, 4to. tom. ii. p. 219.

§ "Ce que est remarquable, c'est que cette dent soit implantée en quelque sorte au borde externe de la mâchoire," ib. p. 219.

(figs. 6, 7, *a*), is a successional one, not having risen into place, and with the crown showing the fine radiating irregular rugæ: its breadth much exceeds its length, being as $10\frac{1}{2}$ lines to $6\frac{1}{2}$ lines, and the latter dimension is along the inner border, which is double the extent of the outer rounded border; the grinding surface is rather triangular than quadrate. In *Placodus gigas* the corresponding tooth does not present such a disproportion between the outer and inner borders, but preserves more of the transversely extended quadrate form. By the comparison of the above three principal crushing teeth of the lower jaw, therefore, the fossil under consideration is specifically distinct from *Pl. gigas*. It may belong to the species called *Placodus Andriani*; but, if distinct, it is most probable that the three close-set, large, broad and flat-crowned teeth were opposed to three similarly shaped and aggregate teeth, such as are seen in *Placodus gigas* and *Placodus Andriani*.

In the specimen (Plate X. figs. 6 and 7), the symphysis (*s*, *s*) has been broken across immediately in front of the first of the three teeth: its breadth at this part is 2 inches 3 lines; its depth is 10 lines. The rami of the jaw, after they become free, expand in depth, retaining a breadth or thickness of $1\frac{1}{2}$ inch; are flattened or broadly rounded below; are thus of peculiar massiveness and strength, adapted to the support of the large crushing teeth; and the rami diverge at an open angle which relates to the characteristic breadth of the skull in the *Placodi*. Only the dentary elements are preserved; the alveolar border extends 4 lines beyond the last of the grinding teeth, forming a flat ledge of that breadth; the corresponding projection in the larger mandible of *Placodus gigas* is of about half the breadth. The inner border of the last tooth almost overhangs the vertical inner wall of the ramus. The symphysis seems to have developed a low median ridge along its under surface.

It is possible that the specimen here described may be part of the under jaw of a *Placodus Andriani*; but, as the two other mandibular rami next to be described have the same claims to such relationship from the size and form of the grinding teeth, and one of them an additional claim through a structure of the jaw-bone, I am induced to indicate the species presenting the peculiarly thick, massive proportions of the mandibular rami above described, as *Placodus pachygnathus*.

The specimen (Plate IX. figs. 3, 4, 5 and 6), is the middle portion of the left ramus of the mandible, with the last three large grinding teeth *in situ*: it consists of the dentary element, showing the same angular notch in the vertically extended back part which may be observed in *Nothosaurus* and other Muschelkalk Saurians*. The upper border of the dentary in *Nothosaurus* rises behind the last tooth into a low analogue of the coronoid process, and a similar modification exists in the present mandible, and obviously to a greater extent, but the summit of the process is broken off; the fore-part of its base is continued, as in *Placodus gigas* and *Pl. pachygnathus*, forward upon a ledge of bone outside the alveoli of the last two teeth: the breadth of this ledge is equal to that in *Pl. gigas*†.

* H. v. Meyer, Die Saurier des Muschelkalkes, tab. 3. fig. 2. † Agassiz, tom. cit. tab. 70. fig. 16

The three grinding teeth are relatively much smaller, as the following dimensions show:—

	Pl. gigas. in. lines.	*Pl. bombidens.* in. lines.
Vertical diameter of the jaw behind the last tooth . . .	1 3	1 9
Antero-posterior extent of the three grinding teeth . . .	2 9	2 2
Antero-posterior extent of the last grinding tooth . . .	1 $2\frac{1}{2}$	0 10
Antero-posterior extent of the middle grinding tooth . .	0 $10\frac{1}{2}$	0 $7\frac{1}{2}$
Transverse extent of middle grinding tooth	0 14	0 10
Antero-posterior extent of first grinding tooth	0 $7\frac{1}{2}$	0 6
Transverse extent of first grinding tooth	0 $11\frac{2}{3}$	0 9

The inner half of the last tooth of *Placodus bombidens* (Plate IX. fig. 5, *c*) is broken away, but its relatively smaller dimensions in the remaining part are decisive against its specific identity with the *Pl. gigas*.

The crown of the penultimate grinder (figs. 3, 4 and 5, *b*) is peculiar for its great degree of convexity, especially in the transverse direction. The median transverse furrow from which the rugæ of the enamel have radiated is still discernible on the worn crown, as are the rugæ themselves on the inner part of the crown.

Beneath the anterior tooth, *a*, the crown of its successor, *a'*, is exposed in figs. 4 and 6, the enamelled summit of which is complete; it is of the same size as the tooth it is about to displace, and this is important in estimating the value of dental characters in regard to difference of size. For, had the present fossil belonged to a young animal, not fully grown, the successional teeth would probably have been larger than their predecessors; or if, as in the case of most fishes, growth of body had continued throughout life, some indication of a maintenance of proportion with augmenting general bulk might have been expected in the successional teeth. I conclude, therefore, that we have in the portion of jaw here described, a part of a full-grown animal of its species, and that the dental characters exhibited are specific.

The mandible begins in advance of the first grinding tooth to bend a little outward, and this indicates an expansion of the fore or symphysial part of the jaw, analogous to that of the premaxillary part of the jaw in *Placodus Andriani**. The fore-part of the angular element of the jaw appears below the back part of the dentary, to which it articulates by suture; and here the under part of the angular shows a sutural surface for the splenial element, indicative that this element appeared in a slight degree upon the outer surface of the ramus.

All these indications of the compound structure of the mandible concur with the characters of that part in *Nothosaurus* and some other triassic Saurians.

It is very probable that the fossil just described may belong to the species called *Placodus Andriani*. Provisionally it has been entered under that name in the 'Catalogue of the British Museum Series of Fossils.' Should ulterior acquisitions prove it to belong

* Agassiz, tom. cit. tab. 70. fig. 8.

to a different species, the term *bombidens* would best express what seems to be the specific peculiarity in the shape of the surface of the grinding teeth.

The third portion of the lower jaw (Plate XI. figs. 1, 2 and 3) differs from both of the last described, and from that of *Placodus gigas*, in the absence of any ledge outside the last molar tooth; the outer alveolar wall of which, as well as that of the next tooth, descends sheer upon the outer surface of the ramus.

The present specimen is chiefly instructive for the extent and height of the coronoid process, 29′, and for the additional evidence it yields of the compound structure of the mandibular ramus.

The angular element, 30, is preserved for an extent of nearly 4 inches behind the last molar tooth: the osseous substance is plainly traceable in the matrix midway between the tooth and the broken angle of the jaw, so as to give a vertical extent of $3\frac{1}{2}$ inches to this part of the ramus, which much resembles in general shape what is called the ascending ramus of the jaw of a carnivorous quadruped. At its upper half the outer surface is flat, the lower half is convex, and this undulates by a slight concavity as it extends forward into the again convex outer surface of the horizontal ramus supporting the teeth. The fore-part of the angular piece, 30, is wedged between the dentary, 32, and splenial, 31; the surangular, 29, is interposed between the angular and the upper and back part of the dentary, 29′: the summit of the coronoid process appears to be contributed by the surangular. The joint-part of the articular element seems to be accidentally lost; it was not brought out in the extent to which the matrix could be safely removed from the present specimen. The concave inner surface of the angular element, 30, and the suture between it and what I take to be the fore-part of the surangular element, 29, are well shown. The inner plate of the splenial has been removed: the articular surface for the splenial element, and a vascular longitudinal groove which that element would have covered, are exposed on the inside of the dentary part of the horizontal ramus.

In this part of the jaw two teeth—the last (*c*) and penultimate (*b*) grinders—are in place: both are of subquadrate form, and in this respect, as well as size, resemble the same teeth in *Placodus pachygnathus*, from which species, however, the present much differs in the shape of the jaw.

The last tooth (*c*, fig. 2) has been but recently acquired; the rugæ being obliterated from only a small proportion of the middle of the crown, where there is a depression of a somewhat crucial figure. This tooth measures 1 inch along the inner border, and the same across the crown; the outer border is $9\frac{1}{2}$ lines in extent.

The next tooth (*b*, fig. 2) has been worn smooth and flat; its outer part is broken away; the extent of its inner border is 10 lines; its breadth 11 lines. Beneath it on the surface of the dentary, left uncovered by the missing splenial piece, the inner side of the enamelled crown of a successional tooth (*b′*, fig. 3) is exposed. The inner border of the crown of both teeth a little overhangs the inner wall of the jaw.

The development of the parts of this compound jaw for the attachment of muscle

harmonizes with the expanse of the temporal fossa and the size of the zygomatic arch, and with the force required for the due working of the extraordinary teeth which are developed in it.

The depth of the ramus behind the last molar is 1 inch 10 lines.

It may be concluded, from the size and shape of the two molars in place in the present jaw, that it belonged to a species which, like *Placodus gigas* and *Pl. Andriani*, had similarly-proportioned teeth in the upper jaw, and not to species in which, as in *Pl. rostratus* and *Pl. laticeps*, the last tooth is considerably larger than the one in front of it. From *Placodus pachygnathus* it differs, not only in the absence of the ledge outside the last tooth, but by the commencement of the symphysis in advance of the second tooth. The species which it indicates may be named *Placodus bathygnathus*.

The last fragment of a *Placodus* from the Muschelkalk of Bayreuth, which will be here noticed, is a small portion of jaw containing three teeth (Plate X. figs. 2, 3, 4 and 5). These are subequal, and, as compared with those last described, of small size: in this respect, as in their shape, they correspond with the marginal teeth of the upper jaw of *Placodus gigas*.

The bone is preserved on one side only, and for the extent of about an inch, gradually thinning off into the mass of matrix which chiefly constitutes the specimen.

If this free bony surface belongs, as I surmise, to the upper and outer part of the upper jaw, the crowns of the teeth project further beyond the free outer alveolar margin, as in fig. 4, than they appear to do in the figure of the upper jaw of *Placodus gigas*, in the 'Poissons Fossiles' of M. Agassiz. At the same time, the crown and working surface of the crowns of the teeth look downward, as they ought to do on the above supposition of the natural aspect of the exposed surface of the bone.

On making a vertical section of one of the three teeth *in situ* (fig. 5), a cavity of reserve, *f*, was exposed above and on the inner side of the tooth in place, containing half of the crown of a successional tooth, *d*, with the well-defined enamel contrasting with the dentine.

Herman v. Meyer, the historian of the extinct Saurians of the continental Muschelkalk, has made us familiar, by means of his exact descriptions and beautiful figures*, with the genera *Nothosaurus*, *Pistosaurus* and *Simosaurus*, the precursors and near allies of the long-necked *Plesiosauri* of a subsequent mesozoic age.

The evidence which has been adduced in the foregoing pages establishes, I trust, an addition to this series, of a Saurian genus, unique in its order for the singularity of its dentition. It is remarkable that, hitherto, no vertebræ or other bones of the trunk or limbs have been found so associated with the teeth of *Placodus*, as to have suggested their belonging to the same species. Usually, after the indication of a reptile by detached teeth, the next step in its reconstruction is based upon detached vertebræ. The twelve or more evidences of *Placodus*, afforded by bone as well as tooth, are all portions of the skull.

* Die Saurier des Muschelkalkes. Fol. 1847–55.

It is possible that some of the singularly modified vertebræ from the Muschelkalk, indicated by v. MEYER under the generic name of *Tanistropheus**, and the family one of *Macrotracheliens*†, may belong to the *Placodus*; and the same surmise suggests itself in reference to some of the limb-bones from the Muschelkalk that cannot be assigned to other known Saurian genera. I shall be amply repaid if the present labour which has been devoted to the rectification of the class affinities of the *Placodus*, should tend to accelerate the acquisition of fossils further advancing our knowledge of its Reptilian structure.

The obvious adaptation of the dentition of *Placodus* to the crushing of very hard kinds of food, its close analogy to the dentition of certain fishes known to subsist by breaking the shells of whelks and other shell-clad Mollusks, and the characteristic abundance of fossil shells in the strata to which the remains of *Placodus* are peculiar, concur in producing the belief that the species of this genus were reptiles frequenting the sea-shore, and probably good swimmers‡. But as, at present, we have got no further than the head and teeth in the reconstruction of this mesozoic form of conchivorous Reptile, I will conclude with a remark suggested by the disposition and form of the teeth. In all the species, under the rather wide range of specific varieties of the dentition, there are two rows of the crushing teeth in the upper jaw, and only one row in the lower jaw, on each side of the mouth; and the lower row plays upon both upper rows, with its strongest (middle) line of force directed against their interspace. Thus the crushing force below presses upon a part between the two planes or points of resistance above, on the same principle as that by which we break a stick across the knee; only here the fulcrum is at the intermediate point, the moving powers at the two parts grasped by the hands. It is obvious, that a portion of shell pressed between two opposite flat surfaces might resist the strongest bite, but subjected to alternate points of pressure its fracture would be facilitated.

DESCRIPTION OF THE PLATES.

PLATE IX.

Fig. 1. Upper surface of the skull of *Placodus laticeps*, OWEN.
Fig. 2. Side view of the same skull.
Fig. 3. Outside view of part of the lower jaw of *Placodus bombidens*, OWEN.
Fig. 4. Inside view of the same jaw of *Placodus bombidens*, showing a successional tooth.
Fig. 5. Upper view of the same jaw of *Placodus bombidens*.
Fig. 6. End view of the same jaw of *Placodus bombidens*, showing the formative cavity of the successional tooth, *a'*.

* Die Saurier des Muschelkalkes. Fol. 1847–55, pp. 42, 128. † Ibid. p. 165.

‡ The *Nothosaurus* and some other reptiles of the Muschelkalk seem to have had limbs resembling the paddles of the *Plesiosauri*.—H. v. MEYER, *op. cit.* p. 33.

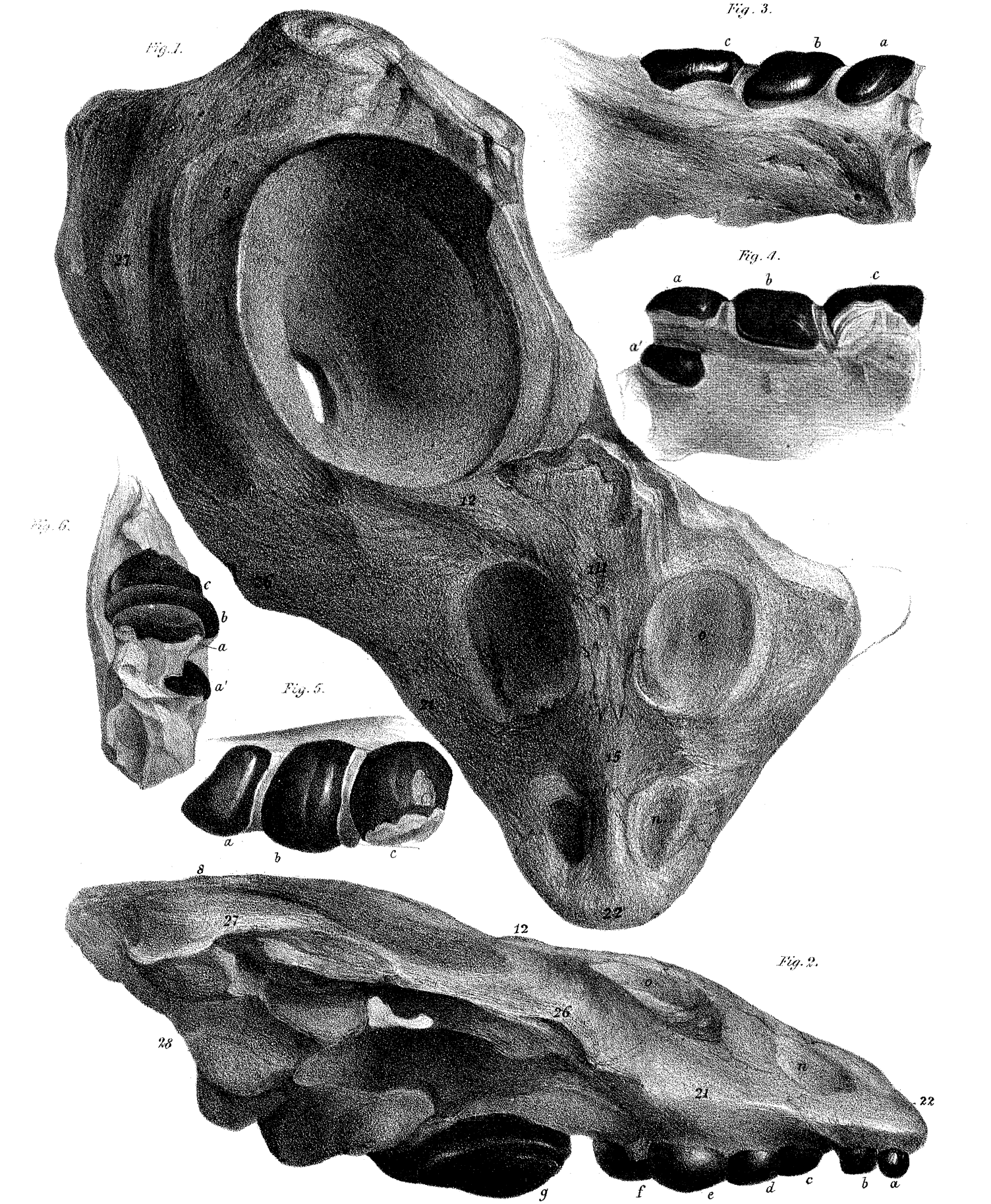
PLATE X.

Fig. 1. Under view of the skull, with the dentition, of *Placodus laticeps*.
Fig. 2. Inner view of a portion of the upper jaw, with three marginal teeth, of *Placodus gigas*, AGASSIZ.
Fig. 3. Grinding surface of the same teeth.
Fig. 4. Outer view of the same portion of jaw and teeth.
Fig. 5. Section of a tooth and part of the jaw of the same specimen, exposing a formative cavity, *f*, with a successional tooth, *d*.
Fig. 6. Portion of mandible, with teeth, of *Placodus pachygnathus*, OWEN.
Fig. 7. Upper view of the teeth in the same fossil.

PLATE XI.

Fig. 1. Outside view of a part of the mandible and teeth of *Placodus bathygnathus*, OWEN.
Fig. 2. Grinding surface of last and penultimate tooth of *Placodus bathygnathus*.
Fig. 3. Inside view of the dentigerous part of the mandible of *Placodus bathygnathus*, exposing part of a formative cavity and tooth-germ, *b'*.
Fig. 4. Under view of the skull, with the dentition, of *Placodus rostratus* (MÜNSTER, 'Petrifacten-kunde,' taf. 15).

All the figures are of the natural size: they were not reversed in the drawing, so that the 'right' in the text and specimens is the 'left' in the plates.



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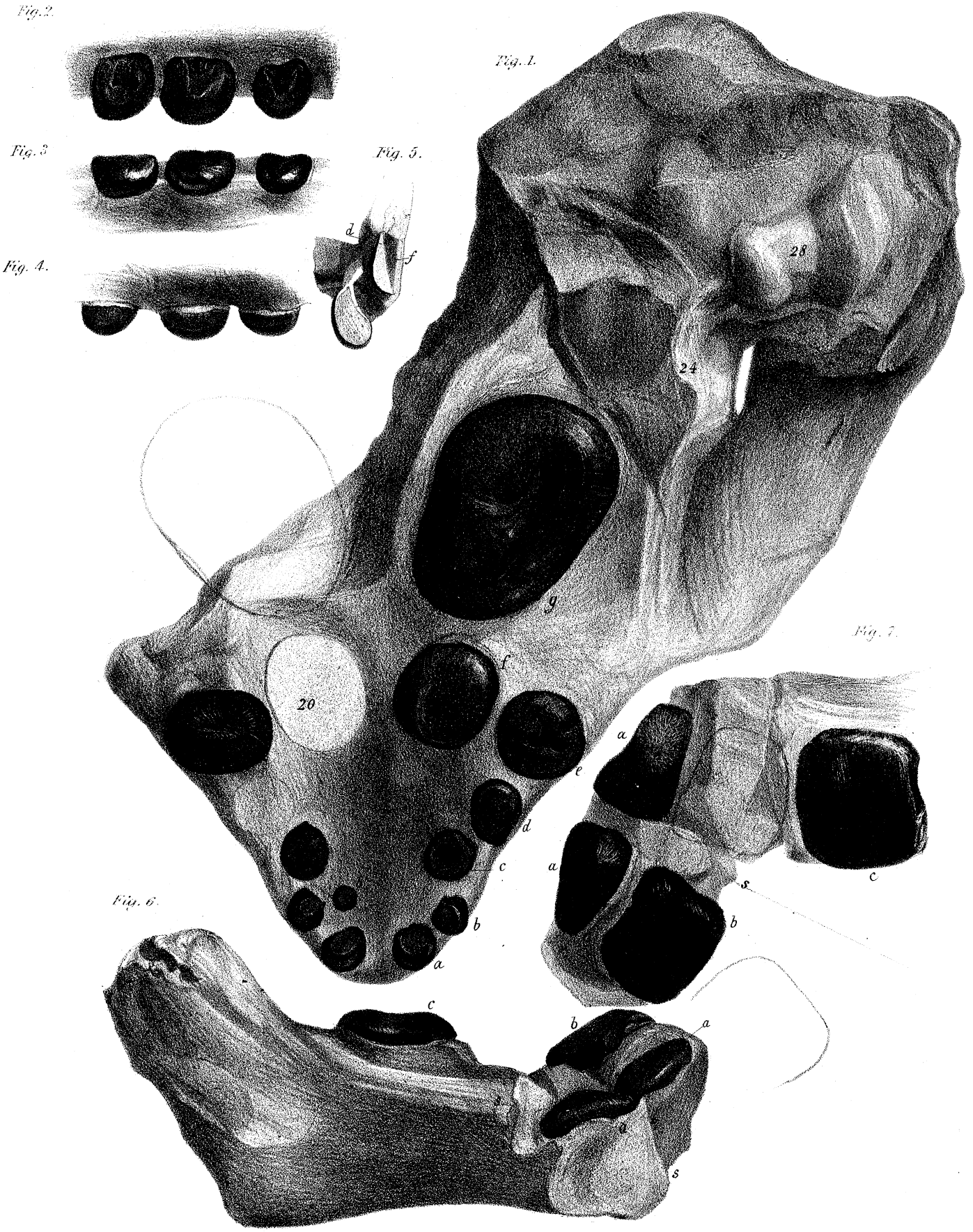

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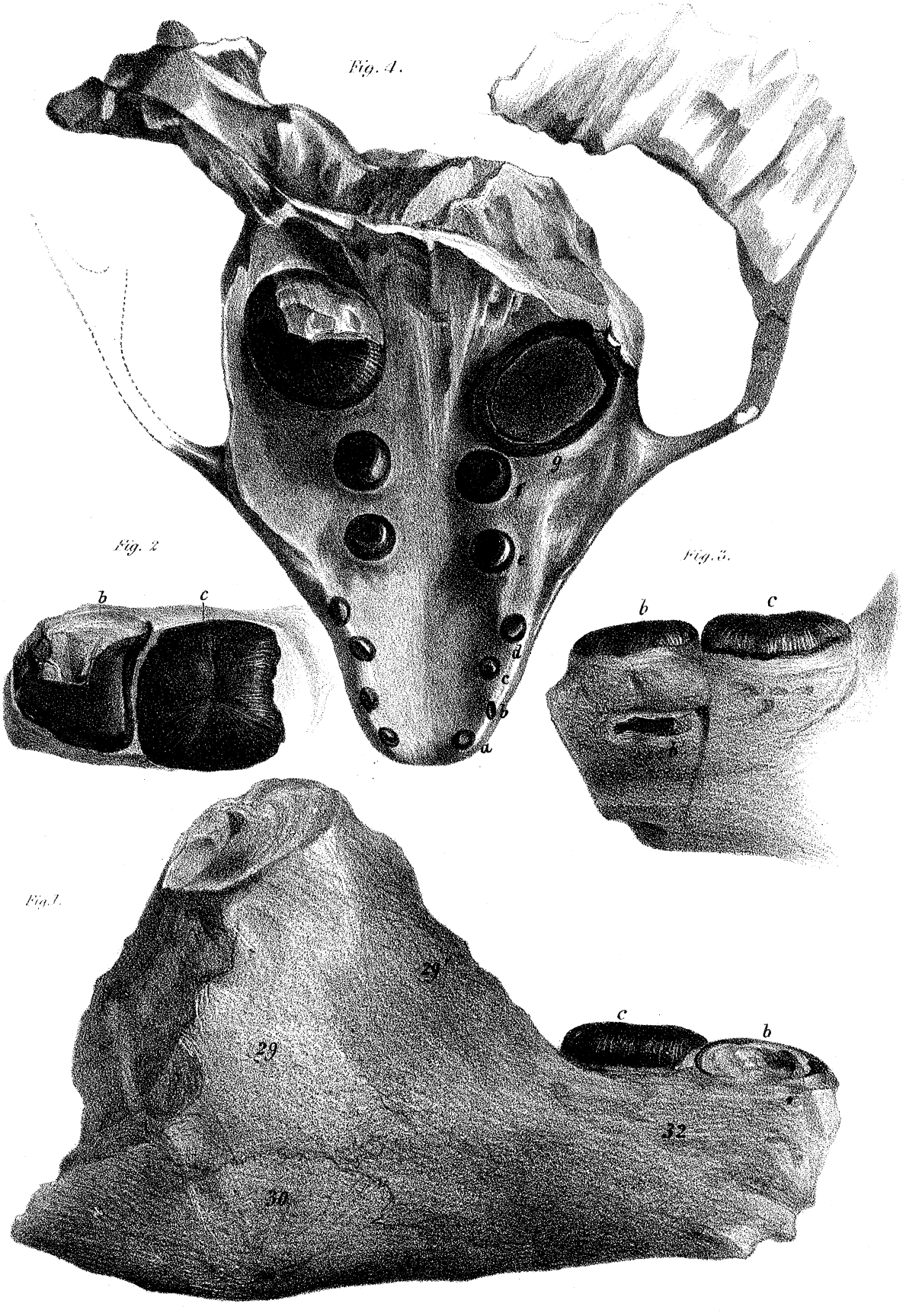

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