

of the Society, jealous of its scientific reputation, I thought it better than saying that "the British Museum has just purchased from the Zoological Society the dead body of an animal which was for some weeks living in their Gardens," which would have been the truthful statement; and it appears that Dr. Sclater was himself ashamed of this statement; for he says that it was "sent" to the British Museum, without saying that it was sent for its specific name to be determined, and for purchase. But all the animals which the Museum receives from the Zoological Society (established for the cultivation and extension of zoological science) are purchased; and when the Society was badly off for funds, this was a fair source of income, of which I do not complain.

III.—*Additional Evidence of the Structure of the Head in Ornithosaurs from the Cambridge Upper Greensand; being a Supplement to 'The Ornithosauria.'* By HARRY G. SEELEY, F.G.S., Assistant to Prof. Sedgwick in the Woodwardian Museum of the University of Cambridge*.

[Plates II. & III.]

To the anterior end of the snout and the back of the brain-case belong nearly all the fragments of Pterodactylian skulls hitherto collected from the Cambridge Upper Greensand; and although the snouts are numerous, they never extend backward beyond the denticulate part of the palate or to the narial apertures; while the back part of the head never reaches so far forward as to include the frontal bones; so that the great middle region of the skull, the seat of the orbits and nares, which transforms its characters with successive groups in reptiles, mammals, and birds, remains unknown. And before the general structure of the head can be illustrated by detailed comparisons in this Cretaceous Ornithocheiroid family, we must learn the condition and form of the bones called frontal, nasal, lachrymal, maxillary, malar, vomer, palatine, pterygoid, postfrontal, and the proximal end of the os quadratum. And if one were a believer in the old morphological doctrine that a like conformation of bone in extinct and living animals warrants the presumption of their having had a like grade of organization, it were hard, with these Ornithosaurian snouts before us, and all the vertebrate province assembled, for us to seek their similars from, to pronounce a sure judg-

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ment on their kindred; for there is no snout among living animals like the Pterodactyles'. Even the extinct animals which are already known manifest no signs of kindred. If among the Teleosauria a like progressive enlargement of the first three teeth and then a narrowing of the jaw is seen to show again a character of many Ornithocheiroid jaws, it is but a solitary resemblance; and the Teleosaur's snout, with its terminal single nostril, is in no other way a counterpart. If Ichthyosauria as invariably have the nostril far back from the end of the snout, it in no other way resembles Pterodactyles'; for the premaxillary bones are separate and dense in tissue, and have no sockets, but only a simple groove for teeth. If, in triangular dagger-shape and bone-texture, some of the species recall birds, still birds have no teeth, even the immature parrots showing but evanescent enamelled specks; while other species end their jaws in a bulbous truncate way, which among birds is never seen. And if we seek for a denticulate jaw among lizards, we shall not find the bird-like elongation of snout, or its Teleosaur-like widening or flattening of palate, and not typically socketed teeth. Yet to birds (and lizards) it approximates best, but in such obscure ways as to stand apart with an individual isolation which would admit of its kindred being reptiles, or mammals, or birds, without amazement to the osteologist. It is not a nose that leads.

Similarly, if only the back of the skull had been found, it would have been more a matter of scientific taste than of scientific fact to have said whether it showed stronger similitude to toothless birds like the heron, or a toothless mammal like *Myrmecophaga* or the foetal *Orycteropus**. Therefore to one who would consider these Cambridge exuviae in the old morphological way, estimating the affinities bone by bone and adding them together to get the total affinity, there is room for considerable doubt and justifiable difference of opinion about the restoration of the head and its resemblance to that of other animals.

I have now an opportunity of lessening that doubt by the discovery of the frontal bone. (Pl. II. fig. 1.)

The specimen is referred to an Ornithosaurian because it possesses the peculiar thin, dense, and smooth bone characteristic of the class, which has been found in no other fossils of the Cambridge Greensand; and it is identified as the frontal bone because it resembles the bone so named in certain reptiles, birds, and mammals, and is not like any other element of the skeleton. The fossil is broken both in front and be-

* The occipital condyles are not preserved with the adjacent bones in Cambridge fossils, and the auditory region is filled with phosphate of lime.

hind, but is free from investing phosphate, and so shows both the external and cerebral surfaces. Externally (fig. 1) the part preserved is straight from front to back, with a mesial groove which deepens as it extends anteriorly, so that the two lateral halves of the bone are convex, the anterior groove apparently existing to receive the nasals or premaxillary bone. The outermost lateral parts of the frontal are flattened and directed downward behind, where they widen so as to be inclined to each other at nearly a right angle; they look upward, outward, and slightly forward, rounding into the upper part of the bone. The extreme length of the specimen is $1\frac{1}{8}$ inch. Owing to breakage, its greatest width from side to side is at a quarter of an inch from the hinder termination of the bone, where it measures $\frac{3}{4}$ inch; and then it contracts from side to side in a parabolic curve, which in passing forward approximates nearer to the upper surface of the bone, till the width at the anterior breakage is $\frac{3}{8}$ inch; the bone is V-shaped at the broken end in transverse section.

The external surface shows two or three impressed lines parallel to the mesial groove.

Seen from the side (fig. 2), the slightly concave inferior longitudinal outline of the bone is nearly parallel with the straight superior longitudinal outline, the depth of the bone from above downward in front being more than $\frac{1}{4}$ inch, and the depth behind being $\frac{5}{16}$ inch. The concave lateral outline seen from above (already described) in this view runs diagonally from the front upper corner to the back lower corner of the bone. The long triangular posterior part above this line is the lateral region of the frontal already referred to as bent downward. The anterior subtriangular part below the line is concave from back to front, and concave from above downward in front, where the two sides of the bone meet at the base so as to form in transverse outline a V-like shape. In the anterior part of this concave area are two small oblong perforations for vessels.

Seen from below (fig. 3), the surface divides into three distinct portions:—(1) the two external concave strips last referred to, which widen and converge in front. Within these there is (2) a long triangular smooth area with slightly concave lateral margins. The area is slightly concave in length, and deeply concave from side to side. Anteriorly there are in it two large ovate perforations for the passage of vessels; posteriorly the lateral margins are flattened, so that the sharp lateral boundary is there obliterated. And (3) this median triangular area is excavated behind by two semicircular cavities, making it spear-shaped: the cavities are divided by a median smooth

space more than $\frac{1}{8}$ inch wide; they extend some distance forward into the bone; one is excavated for $\frac{3}{8}$ inch; each measures $\frac{1}{4}$ inch from side to side. Seen from behind, their outlines are triangular; they are lined with smooth dense bone-tissue.

Such is this remarkable fossil. A fragment of a second specimen has been placed in my hands by the courtesy of M. R. Prior, Esq., of Trinity College; but as it displays no new structure, I merely mention that it indicates a bone twice as large as that just described, and is perforated on the underside by foramina which are enormously large in proportion, and which are accompanied by many small accessory foramina. On the underside of neither specimen is there any indication of division into separate frontal elements, though externally both show indications of median lateral division.

Now as to the significance of the bone. Its outline recalls the frontal bone of Crocodiles (Pl. II. fig. 4). I figure for comparison the frontal bone of a Crocodile from the upper part of the Tertiary series in the Isle of Wight, *Crocodilus Hastingsiæ*. Externally the Greensand fossil differs in the deep median groove, in the smooth unpitted surface, and chiefly in the lateral parts being directed downward, while in Crocodiles the lateral parts are directed upward. In the Ornithosaur the bone is proportionally longer; and the cerebral part being broken, the resemblance is not so close as it seems to be.

On the interior aspect the concave lateral parts of the *Ornithocheirus* are seen to be represented by similar but deeper concave regions in the crocodile (Pl. II. fig. 4); for they are the upper and inner boundaries of the orbits. Between them is a similar triangular concave area, less well-defined anteriorly in the crocodile because the orbital margins do not converge and meet in front. But here the resemblance ends; for when the bones are compared posteriorly, the crocodile shows no sign of the remarkable excavations seen in the Ornithosaur*.

Among birds the form of the bone is approximated to more closely (Pl. II. fig. 5). There is externally the same smooth surface, the same sort of downward direction of the hinder lateral parts, sometimes the same antero-posterior straightness and mesial depression. These latter characters are not well seen in the common *Gallus domesticus*, and might be better matched in other birds; yet, as the most accessible type, I here contrast (Pl. II. fig. 5) the inner side of the frontal bones in that animal with what is seen in our fossil, premising that,

* In serpents the frontal covers in the cerebral hemispheres in front.

as the fossil is broken behind, this comparison does not determine *exactly* the resemblance and difference between the bones. The lateral orbital spaces are larger and better-marked in the bird, and similarly approximate mesially; but while in the bird the eyes abut against the front of the brain, in the Ornithosaur they are removed further forward, and consequently the triangular space which comes between and behind the orbits in Ornithosaurians is in front of them in birds; and in these animals the bone which I have previously named the ethmoid bone (the orbito-sphenoid of Prof. Owen) is of such shape as would fit on to that space. Finally, the frontal of the bird is largely excavated behind to cover the cerebrum. From the divergence of the excavations in the Ornithosaur frontal, it is clear that they are not for the cerebrum, but for the olfactory lobes in front of the cerebrum, which lobes, when developed, are commonly divided. And if any one will compare the figure of this bone here given with fig. 3, pl. 11 of my book on the Ornithosauria, where is shown the suture of the parietal bones from which the frontals have come away, it will be evident that a considerable piece is wanting from the back of this frontal bone, which, like the bird's frontal bone, is thereby proved, when perfect, to have partly, if not largely, covered the cerebrum. Here, then, with much and close resemblance to the bird, are substantial differences, in an enormous and unbirdlike development of olfactory lobes (with seemingly a covered channel for the olfactory nerve, rare among birds), in evidence of a largely developed and backwardly placed ethmoid and more anterior orbits. Still the resemblance to birds is a true coincidence of functional plan up to a certain point, and altogether different from the resemblance to the bone in the crocodile, which in this point is the most like of reptiles.

If the bone be compared with the frontal of mammals, probably the bird-like rodents, such as the guinea-pig or rabbit, offer the closest similarity of form: the rabbit is to be preferred for comparison. But here, though the general form of the bone would be sufficiently like to admit of comparison, it will be seen that the eye is situated altogether at the *side* of the fore part of the cerebrum and large olfactory lobes, which extend between the orbits; and then the condition of the softer parts of the ethmoid is very different from and not comparable with the condition of the ethmoid in birds, and unlike any known condition in Ornithosaurs. In the interior of the cranial cavity of the rabbit, the development of the olfactory lobes comes much nearer to the ornithosaurian than any thing seen in birds. Yet olfactory lobes are as much a feature of

reptilia and lower animals as of mammals; only in the reptile* they are not closed-in in front by bone, while in mammals they are. But in no sense, except in form, can the olfactory lobes of this specimen be called mammalian; for they obviously never sent filaments direct to supply the olfactory sense, but apparently forwarded the olfactory nerve in a closed tube. Thus in not passing through the ethmoid, but through the frontals, the olfactory lobes approximate towards birds', but differ from all birds', so far as I am aware, in their great size.

I conclude, then, that the frontal bone under consideration is only closely comparable with birds', and that it diverges from birds' in ways which are not paralleled in other animals.

Elsewhere I have described and figured all the cranial structures of Ornithosaurians which the Woodwardian Museum contains†; and I propose now, with the notice of an additional imperfect bone which may be the maxillary, to point out exactly how much is known of the Ornithocheiroid brain and skull, and how they resemble and differ from those of other animals—only remarking that the results arrived at can be but of a general nature, since the specimens are few, imperfectly preserved, of different sizes, and obviously belong to two or more genera, each bone perhaps pertaining to a different species.

First, then, to reconstruct the brain. The materials are a transverse section of the brain-case in front of the optic lobes, a natural mould of the upper part of the brain showing the form of the cerebrum and part of the cerebellum, and an indication of the optic lobes on the under surface, an ethmosphenoid bone apparently closing in the brain in front, and part of a frontal bone closing the brain in above; so that, with very unimportant and small parts, the structure of the brain-case is now known.

I suppose the form of the brain-cavity to indicate with approximate accuracy the form of the brain, in which case the Pterodactyle's brain must have been very like what is here drawn (Pl. II. figs. 6, 7); for in only one or two points is there likelihood of error: the cerebellum may be here made too long, and the depth of the cerebrum may be made too little; for there is evidence that it is nearly as deep as it is long.

When the brain is seen from above (fig. 6), there is no difficulty in recognizing it as an evident modification of the avian outline, chiefly remarkable for the enormous size of the cerebral and olfactory lobes, and the small size of the cerebellum, by which

* Serpents not excepted.

† 'The Ornithosauria.'

that organ shrinks away from the optic lobes. Still the differences are only of proportion of parts, and not peculiarities of arrangement. But when the brain is seen from the side, it shows characters which are altogether peculiar to it, in the development of the under part of the cerebrum, by which that part of the brain attains a larger size than any thing seen in birds, and more in accord with the highest mammals than with other animals. Here, of course, the question arises, Is it certain that the parts have been correctly determined (in dealing with such material the question is inevitable), and that what have been called optic lobes are not lateral lobes of the cerebrum, so that, after all, the animal may be a mammal? I can only reply that when the Pterodactyle's skull is compared with the bird's skull, the correspondence of the parts called optic lobes is very close. They are sunk deep into the alisphenoid and squamosal bones, so as to be covered by the thinnest possible film of bone externally, as in birds; a sharp bony ridge divides them from the cerebrum, as in birds; they are as prominent and subhemispherical as in birds, and they are situated almost as in birds; while I fail to find this bony definition of outline in the encasement of the similarly placed part of the mammalian cerebrum; so that I have no doubt at all that these parts of the brain are accurately described by the lettering in the description of Plate II. Every facility is offered at the Woodwardian Museum for the examination of the specimens.

And the conclusion which follows from the facts detailed is that these Ornithosauria, while having a brain moulded upon the bird-type, attained to a condition of cerebral development which would raise them, so far as evidence from the brain went, above birds. In fact, this brain, if brain-form is worth any thing in classification, proves that these animals must take rank immediately above birds, in the same natural group with them.

Now it will be attempted to reconstruct the Ornithocheiroid skull in which this brain was lodged*; and to this end follows a description of what may be regarded as the maxillary bone. (Pl. III. figs. 1, 2.)

Like all Pterodactyle bones, it is fractured. It is a sub-triangular squamous bone, flat externally in antero-posterior direction, perfectly smooth, and very slightly convex from above downward, $1\frac{5}{8}$ inch long at the palatal border. Above this fractured border is an impressed area less than $\frac{1}{2}$ an inch

* The best general restoration of the Ornithosaurian skull is Prof. Owen's, given in pl. 27 of his memoir in the Palæontographical Society's volume for 1851.

wide, margined above by a convex line most impressed behind, and showing at intervals foramina like those seen on the maxillary bone of many of the lizards. In front is seemingly the lower and back part of a perforation which, on the hypothesis of the bone being maxillary, would be the left narial vacuity, showing on its inner side an impressed ovate space. On the upper part of the posterior lateral margin is an angular notch, which may be merely due to fracture or may be the anteorbital or middle hole of the skull. The least distance between these notches is about $\frac{7}{8}$ inch. Internally (fig. 2), between the sides, the bone is convex and rapidly thickens from little more than card-thickness at the palate to nearly $\frac{5}{8}$ inch at a height of $1\frac{1}{4}$ inch from the palate. Externally at about this height the bone rounds upward and inward for a quarter of an inch, and then is truncated, with a small piece of rough surface which looks obliquely outward and forward when the external surface is vertical. On this surface and on a truncated continuation upward of the narial boundary may have rested the nasal bone.

Putting the several known bones together, they appear to indicate a cranium of such a form as is here drawn (Pl. III. fig. 3), the light parts only being known, and the shaded parts put in to complete the outline. Certain black lines running through the shaded parts indicate possible boundaries of bones.

In completing the outlines I have rather followed the authority of German specimens than my own ideas. For instance, behind the orbit and between the frontal and squamosal is a four-cornered space, representing the region in which the postfrontal bone should be applied to the brain-case. The diminutive representative of this bone is apparently seen in many natatorial birds, such as the goose, between the frontal, squamosal, and alisphenoid bones; and in the immature struthious skull Mr. Parker's researches have made its existence evident. In birds the rudimentary bone has no other connexion; but in German Ornithosaurians it is usually of a triangular form, and sends one limb to the quadrato-jugal bone. And this is a point in which all birds differ from Ornithosaurians; for, from the downward direction of the quadrate bone in birds, the quadrato-jugal and malar bones are removed from all relation with the bones of the upper part of the head. Yet seeing that in the Cambridge Ornithosaur the quadrate bone had an articular connexion with the skull, it is inconceivable that the quadrato-jugal should have had a wide union with the postfrontal bone. But if the postfrontal bone is obliterated, and the quadrato-jugal and malar

bones reduced to a rod which united the distal end of the quadrate bone with the palatal margin of the maxillary bone, then there would be nothing to distinguish that part of the Ornithocheiroid skull from the bird's skull. And hitherto no evidence has been found of the existence of either this bone or the malar in Cretaceous genera.

In another point of some importance there is a lack of evidence : no trace has been found of the existence in Cambridge fossils of the middle hole of the skull between the orbit and nares ; and as the perforation does not exist in the Ornithosaurs *Pterodactylus longicollum* and *P. Kochi*, I have not outlined it in the diagram.

So that, to state the case of these Ornithosaurs separately, on the evidence at present known, it is found that the only points in which the skull differs from that of birds, are in the vertically expanded quadrato-jugal bone and the apparent expansion of the ethmoid to close in the front of the brain. Yet these characters, though minor in kind, are a wide divergence from birds, the latter one being seemingly unparalleled among Vertebrata, and the former implying an expanded squamous malar bone, and probably a developed postfrontal. Therefore there is reason to anticipate that in these bones Cambridge Pterodactyles will be found to approximate towards other Ornithosaurs, and, like them, to diverge from birds. It may then be appropriate to examine into their bearing on the animal's affinities.

In the first place, so far as can be judged from published figures, there is no absolutely conclusive evidence in any Pterodactyle whether the malar bone has a distinct existence ; it might even be united to the maxillary, or, with less improbability, to the quadrato-jugal. Perhaps the strongest evidence for its separate existence is offered by the Cambridge specimens, where the quadrato-jugal appears to form part of the basal margin of the orbit, and clearly receives a bone in front which must also have entered into the orbit, while apparently nearly the whole of the maxillary is occupied in forming the back of the nostril, and there is no reason for suspecting that it extended back to the orbit ; so that the existence of a separate malar bone is highly probable. And although no one can be more convinced of the fallacy of reasonings founded on imperfect knowledge of facts (the arsenal of erroneous ideas), I think that the existence of this malar bone may, on the evidence, be assumed.

It is evident, then, that by the existence of a quadrate and quadrato-jugal, these animals differ from mammals, where sometimes, as among ruminants, the malar unites with the

(downward and forward process of the) frontal behind the eyes, and completes the orbit. The malar bone by itself, if distinct, might be compared to the mammalian malar.

In lizards malar, quadrato-jugal, and postfrontal bones exist, but their relations are different from what is seen in *Ornithosaurs*. The lizard quadrate is commonly vertical, and the quadrato-jugal is attached to its proximal end, while the orbit is completed after the mammalian plan by the (post-) frontal and malar, and the quadrato-jugal does not penetrate the suture between these bones, as it does in *Ornithocheirus*.

In Crocodiles there is still the same series of bones, with the malar and quadrato-jugal squamous: but they do not come near to Pterodactyles; for the quadrate is directed backward, while in all *Ornithosaurs* it is directed forward; and the quadrato-jugal, although attached throughout its length to the quadrate, does not enter into the orbit, but into the temporal fossa, and it cannot be said similarly to divide the postfrontal and malar bones.

In the Rhynchocephalia, typified by *Sphenodon*, there is but one bone between the maxillary and the vertical quadrate; and that bone Dr. Günther names the malar. But at the back of the orbit the postfrontal and malar bones are separated by a bone named by Dr. Günther the quadrato-jugal, which meets the squamosal behind, but is entirely separated from the quadrate bone; so that among none of the types which are correctly called reptiles is the resemblance to our *Ornithosaurians* very close.

In birds it is certainly more distant, owing to the rod-like form which these bones take; but if the bones had assumed a squamous character, and united with the upper boundary of the orbit, the skull in these matters would be essentially avian. Accordingly, with such wide divergences from all other animals, coupled with its own peculiar characters dependent upon the forward direction of the quadrate bone, and the uncertainty about the precise condition of the bones in *Ornithocheiridæ*, I find a difficulty in arriving at any more definite conclusion than that the general relation of these bones is more like what is seen in reptilian types than among birds and mammals. But in no reptile is there a similar condition, and perhaps the nearest reptile type is *Sphenodon*.

No *Ornithosaurian* hitherto figured displays the true structure of the palate. The most instructive specimens are those figured in the well-known memoirs of Goldfuss and Quenstedt. And as Prof. Quenstedt's description of the skull in his *Pterodactylus suevicus* makes known some points which do not appear in Von Meyer's general account, I translate what is said

upon the subject in the special monograph '*Ueber Pterodactylus suevicus*'* :—

“The head, 5 inches 10 lines (Paris) long, has suffered somewhat through pressure, and might therefore be considered inferior in some respects to that of [*P.*] *crassirostris*. Also all the teeth have fallen out; I have vainly endeavoured to trace their alveoli. It is noteworthy that the points of several of the teeth appear to be cut off. The fang and crown can be recognized; and the enamel is not in ridges, but only in wave-like folds.

“The lower jaw, 4 inches 5 lines long, displays the lower surface in a way hitherto unequalled. The symphysis alone measures 1 inch 8 lines, and is 6 lines wide behind. The symphysis proves how accurately Münster has expounded the lower jaw. Its surprising resemblance to the upper beak of a water-fowl was calculated, however, to lead any one to Wagner's different interpretation†. There is no trace whatever of a suture in the symphysis; and no nerve-pores, found so numerous in birds, can be seen at the foremost extremity. The indents further back appear to be chiefly due to pressure. A transverse section shows clearly that the whole symphysial region is parallel to the upper surface. The part which is arched over is made up of several elements, although it is difficult to obtain a true conception of their outlines. In continuation of the dentary bone (1) lies the superangular bone (4), with the angular bone (2) continuous with them on the inside. The thickened articular bone, at the proximal end, cannot be mistaken; its small hindmost continuation was somewhat larger in the living animal. Although one fancies one sees the hollow of the articulation, it is to be presumed that it did not lie on that side, but underneath, on the side which is averted from the eye.

“The upper jaw, again, has in front very much the form of a beak; but, unfortunately, the anterior end has suffered from a forcible twisting. The bone is therefore seen from above in front; and the further back it goes the more it is seen from the side. The nasal bones are well defined, and as the front end of the bone near them is perforated like the lower jaw, it seems as if the entrance to the nostril had been here, as is the rule with birds. In that case the aperture, which occurs fully 2 inches behind the extremity of the jaw, would have nothing to do with the anterior nares. In the forward part of this hole lie two bones, similar to each other (16), which become thinner further back: they are the vomers. On the hind part of the

* 4to (Tübingen), 1855, pp. 38–40.

† Akademie zu München, vi. p. 156.

nasal bone hangs down a triangular bone (2), which recalls to mind in a lively way the lachrymal bone in birds. But as there is a very strong process (19) of the jugal bone rising up towards it, the eye-hole may perhaps have been thus closed in front. The skull then would have had three holes, as was first so excellently demonstrated by Goldfuss:—the nostrils, supposed to be isolated in the anterior end; the middle, elongated, triangular hole; and the cavern of the eye. This latter is well defended on the hinder side by an elevated ridge of the frontal bone. I could not find the sclerotic circle of the eye in it; but several bones, which I have exposed as much as possible, are lying scattered in the eye-hole, as follows: the slender bone at the top (6), which is prolonged under the lachrymal bone, may be the sphenoid; the two triangular bones (25) are the pterygoids; in front of them lies a similar bone with three concavities (22), which from its position is to be regarded as the palatine bone. A sure foundation is found in the uncommonly strong quadrate bones (26); the left one is still in its natural position, but the right one lies in the hollow of the eye, with its articular surface facing the process of the jugal bone. The head measures only 4 inches from the articular surface of the left quadrate to the extremity of the beak; and one is therefore led to suppose that the lower jaw must have projected somewhat more than the upper jaw. The occiput, however, extends backward in a remarkable median crest, which has not previously been figured in any species: it might easily be overlooked, from its thinness; but its existence cannot be doubted. Including it, the whole length of the head amounts to 5 inches 10 lines. Above it lies a fractured bone, which can only be interpreted as the parietal bone. As the head has also suffered somewhat from the twist already mentioned, one is also able to see at the upper margin fractured pieces from the right side. At first I thought of exposing these also, but now think it more prudent to leave them alone for the present.”

I have reproduced this passage because the specimen to which it relates shows the bones of the palate better than any other species, and not because Prof. Quenstedt's interpretation seems to me accurate. The numbers upon the bones in the figure are those used by Cuvier; but I would suggest the following modified interpretation, as in accord with the fuller knowledge gained since the monograph was written. If the small anterior depressions are correctly identified as nares, about which I entertain no doubt, then the bone marked 3 is evidently the nasal. This identification is probable, because the teeth are limited to the extremity of the snout, and entirely

in front of the nares; from which circumstance the inference may be made that the premaxillary bone did not extend far backward, and formed the front of the nostril; so that, with the toothless maxillary forming the side border, the nasal bones might well close it behind. The bone marked 7, though named frontal in the text, would, from the number, seem to be intended for the parietal; it appears to me to correspond in function, by making the upper border of the orbit, with the frontal bone. The bone 8, evidently intended for the supraoccipital, seems to me, both from the figure and a cast of the original specimen, to be the entire side of the cerebral region pressed flat. I should interpret it as consisting of the parietal bone in the upper part, and of the squamosal in the lower part, which gives attachment to the quadrate and malar bones. The little bone (23) just above the proximal ends of the malar and quadrate, is probably intended for the squamosal; from the analogy of all other Ornithosaurs and lizards, I should rather name it the post-frontal. And with regard to the palatal bones, if they in any way resemble those seen among birds and lizards, they must certainly have a different naming from that detailed. I think the bone 22, regarded as the palatine, would be better identified as the lachrymal. The triangular bones (25) may well be the pterygoids, as Quenstedt names them. The angle of the triangle at one end of the long side would meet the quadrate; one of the short sides of the bone would unite mesially with the similar side of the other pterygoid bone; and both would have their other short sides looking backward, while the angle at the other end of the long side would meet the palatine bones in front. Considering the position of the latter bones in birds and reptiles, I have no hesitation in identifying the long slender bones marked 16 as the palatine bones. The small bone (6) named sphenoid I should rather identify as the right quadrato-jugal.

This interpretation enables me to offer a restoration of the Ornithosaurian palate (Pl. II. fig. 8), which can only be reconstructed on the basis of the bird's palate; for the form and relations of the pterygoid and palatine bones are very similar to what is seen in many natatorial birds.

It will be impossible, on comparing the figures, to discover any character, in which the Ornithosaur cannot be paralleled by birds, which would separate it as more than a different and not distantly allied genus, both the forms and arrangement of the bones being paralleled in many natatorial birds. Yet too much stress must not be laid upon these important characters in the way of affinity, because lizards also approximate to-

wards birds in the plan of their pterygoid and palatine bones, though there is nothing so typically bird-like in their form, arrangement, and proportions as in the *Cycnorhamphus*.

Another point necessary to a knowledge of the skull is the composition of the lower jaw. And although only the dentary and articular ends are known in the specimens from the Cambridge Greensand, I propose to examine how much they really make known. First, there is the dentary bone, which never shows any indication of being composite: although numerous specimens have been examined, there is never the slightest trace of a median suture. The bone, in the only example which is at all perfect*, has the palatal surface much longer from back to front than the inferior surface, the dentary bone being comparatively small, not extending further back than do the teeth, and being underlapped throughout the greater part of its short length by other elements of the lower jaw. There is no direct evidence whether any of the Greensand species had the bone prolonged backward beyond the symphysis.

The largest fragment of the articular end at present known (Woodwardian Museum, J. c. 12. no. 1) has been figured by Prof. Owen in his Monograph on *Pt. simus*, published by the Palæontographical Society, 1860. It is broken in front, and shows on the upper part of the inner surface an area from which a bone has come away. This bone, which did not reach up to the superior border of the jaw, I think may have been a backward process of the dentary element. From front to back the exterior surface of this portion of the jaw is convex, and the interior surface concave (as much so as is usual among water-birds), suggestive of a median approximation. Another and small fragment (Woodwardian Museum, J. c. 12. no. 4) exhibits another sutural surface, which demonstrates that a straight suture, parallel to the inferior margin, and looking obliquely outward and upward, divided the lower *angular* bone from the upper *surangular* bone: the angular bone is the broadest from side to side; it is flattened underneath; and a concave channel runs along its inner surface from behind forward; the surangular bone is much the deeper from above downward, especially on the exterior surface, and some distance in front of the articulation it is compressed from side to side; so that while the limit of the bones is only marked by a slight groove externally, internally the strong projecting ridge of the angular bone gives the surangular an appearance of being deeply excavated. This bone

* Ornithosauria, pl. 12. fig. 1.

contributes the anterior boundary to the articular surface for the quadrate. The articular bone in its anterior part rests upon the angular bone, but behind the articulation the specimen is fractured. In passing backward the depth of the jaw becomes much less as it nears the articulation; here the bone widens and extends inward precisely as in birds: the heel behind the articulation is of varying length and form.

In every respect this structure is like that of a bird*, if we except the want of evidence of the existence of the opercular bone; but as it is possible that the interior surface which I have attributed to the dentary bone may be for the opercular bone, the correspondence may be more perfect than I have supposed it to be. If there were only four elements in the lower jaw, the whole arrangement would be very like that seen in turtles.

If, now, we endeavour to form a conception of the Ornithocheiroid head in its structural resemblances to other animals, we see that the entire skull, so far as known, is formed after the manner of birds in every region, except in the malar, quadrato-jugal, and postfrontal bones, which, though of the reptile type, are not similarly placed in any reptile, and must therefore be regarded as an Ornithosaurian modification of the bird's skull. The lower jaw may be Avian or Chelonian. The teeth must be regarded as Ornithosaurian, curiously combining Reptilian and Mammalian characters.

The points in which the Cambridge head certainly differs from other types are not important. They consist, if my identification is right, in the brain being closed by a bony mass in front, which extends forward partly between the orbits. This structure has not been figured in any of the true Pterodactylidæ, and does not appear to be constant in the Ramphorhynchidæ, and seemingly is equally inconstant in Cambridge genera. But in the one specimen in which such a mass occurs it is very wide from side to side, is ankylosed with what I interpret as the fore part of the sphenoid, and furnishes the authority for the convex mammal-like under part of the brain; and the bone also resembles the preorbital part of the ethmoid in the duck and in many birds. This resemblance is, indeed, so close that, but for the detailed correspondence of the base of this fossil specimen (Ornithosauria, pl. 11. fig. 7) to the base of the sphenoid in the back of an Ornitho-

* In 'The Ornithosauria' it is stated (p. 92) that the six elements of the lower jaw may be counted on each side. It would have been more accurate to have said five; for the separation of the coronoid from the articular is not well made out.

saurian skull, I should have adopted it. And still it is a point that requires additional evidence to pronounce upon decisively. Should the bird-like interpretation (to which, from the forward position of the orbits &c., I least incline) eventually prove tenable, it would take away the evidence for the anomalous cerebral characters which have already been dwelt upon, and bring both brain and brain-case into a more absolute conformity with birds than I have felt justified in assuming. Still no such bone has ever been found in Pterodactyles, and at present there is no proof that it existed.

The only other point in which Cambridge specimens appear to differ from those of Germany is the squamous character of the quadrato-jugal bone*.

I come to the last word about the skull, not because our knowledge is completed, but because there are no more bones. New specimens in time will fill in the lacunæ which have been indicated, and modify our doubtful determinations; but so much of the skull is now known that no specimens can unsettle or invalidate its avian affinities. And if a controversy nearly as old as modern zoology thus ends, it is because the more philosophical and severe science of our time has taught us to find an animal's place in nature by study of the common plan on which it is built, rather than in the old morphological way, which would predicate an entire organism from the form of a quadrate bone or a caudal vertebra. And the result gives strength to an old law of Cuvier's, which hitherto has never failed—that the pneumatic skeleton is always associated with avian organization. So that henceforth, just as we infer from the double-fanged tooth the lungs and heart, and brain and reproduction, of a mammal for the animal to which it belonged, so now we may infer for the animal which had limb-bones with pneumatic foramina the organization and systematic grade of a bird. Side by side with birds, the Ornithosauria are a monument of the faithfulness of Nature to her laws, and a new pledge to the student that she never will betray the heart that trusts her.

* A new genus appears to be constituted by some (three) portions of jaws from the Cambridge Greensand. Unfortunately, the extremity is not preserved. They have the ordinary dagger-shaped snout, but appear to be entirely destitute of teeth. I provisionally name the genus *Ornithostoma*.

Another unnamed generic type is typified by *Pterodactylus longicollum*, *P. rhamphastinus*, and the two species included under the name of *P. Kochi*. In this genus the middle hole of the skull is entirely wanting. For it I suggest the name *Diopecephalus*.

EXPLANATION OF PLATES II. & III.

PLATE II.

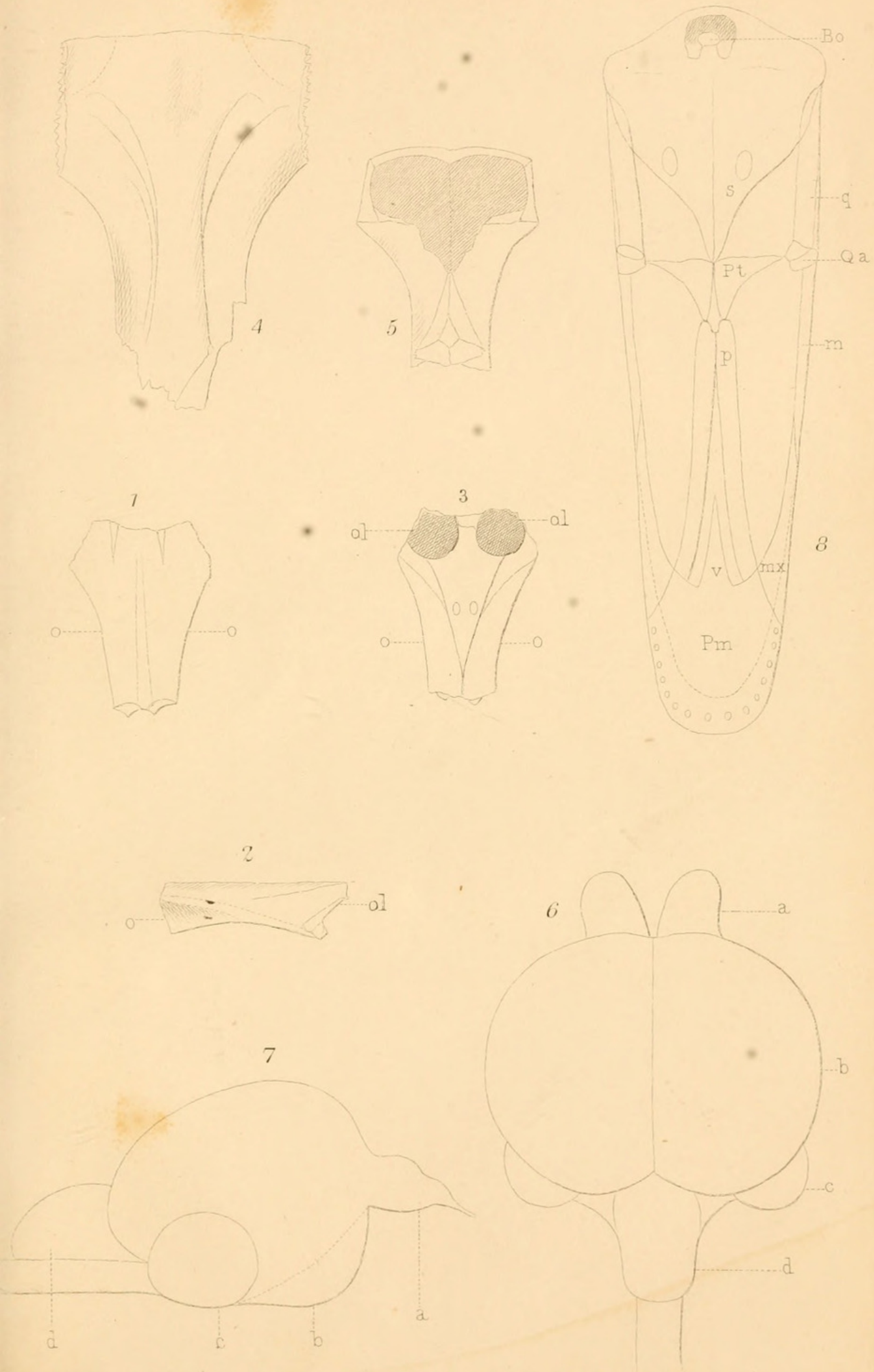
- Fig. 1.* Upper surface of the anterior part of the frontal bone of an Ornithosaur.
- Fig. 2.* The same fragment, seen from the side.
- Fig. 3.* Interior aspect of the same specimen.
In these figures *o* marks the upper boundary of the orbit, and *ol* the region occupied in the fragment by the olfactory lobes.
- Fig. 4.* The corresponding interior aspect of the frontal bone of *Crocodylus Hastingsæ*.
- Fig. 5.* Interior view of the frontal bones of a chicken. The shaded part marks the cavity occupied by the fore part of the cerebrum—a part which is not preserved in the fossil, fig. 3.
- Fig. 6.* Restoration of the form of the cerebral cavity in the Ornithosaurians from the Cambridge Upper Greensand; outline, seen from above.
- Fig. 7.* Restored form of the cerebral cavity of an Ornithosaur, seen from the side.
In these figures *a* marks olfactory lobes; *b*, cerebrum; *c*, optic lobes; *d*, cerebellum. A dotted line is introduced between *c* and *a*, which would give the cerebrum a form more like that of a bird, and which possibly may prove to be its true shape.
- Fig. 8.* Restoration of the palate of the Ornithosaurian *Cynorhamphus suevicus* (Quenst.): *Bo*, basioccipital; *s*, sphenoid; *Q*, quadrate bone; *qa*, quadrate articulation; *Pt*, pterygoid; *P*, palatine; *V*, vomer; *Pm*, premaxillary; *Mx*, maxillary; *m*, malar.

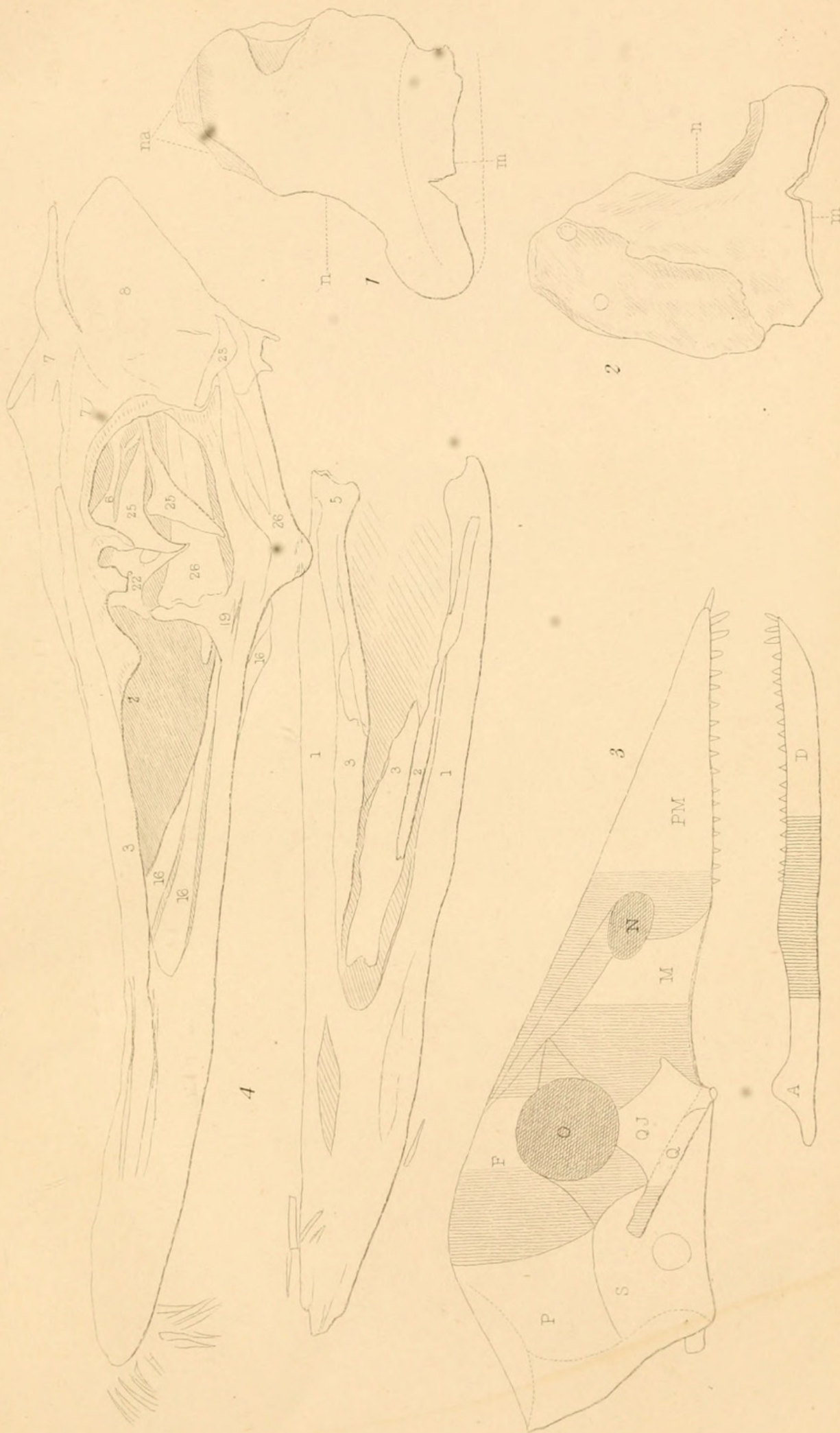
PLATE III.

Portion of a bone supposed to be the maxillary bone of an Ornithosaur.

- Fig. 1.* External appearance.
- Fig. 2.* Interior appearance.
m is towards the maxillary border; *na*, a surface (perhaps articular) towards the nasal bone; *n*, part of the boundary of the nasal aperture. The inner surface of the bone is a good deal invested with phosphate of lime.
- Fig. 3.* Diagram side view of the Ornithocheiroid cranium, the shaded parts being at present unknown: *s*, squamosal; *P*, parietal; *F*, frontal; *Q*, quadrate bone; *QJ*, quadrato-jugal; *M*, maxillary; *PM*, premaxillary; *D*, dentary, *A*, articular end of lower jaw; *N*, nostril; *o*, orbit.
- Fig. 4.* Copy from Prof. Quenstedt's figure of the head of *Cynorhamphus suevicus*: 3, nasal bones; 7, frontal; 8, parietal and squamosal bones; 23, postfrontal; 26, quadrate; 6, quadrato-jugal; 19, malar; 2, lachrymal bone; 22, lachrymal bone; 25, pterygoid; 16, palatine.

From this specimen is made the restoration Pl. II. fig. 8.







Seeley, H. G. 1871. "III.—Additional evidence of the structure of the head in Ornithosaurs from the Cambridge Upper Greensand; being a supplement to 'The Ornithosauria'." *The Annals and magazine of natural history; zoology, botany, and geology* 7, 20–36. <https://doi.org/10.1080/00222937108696309>.

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