



The Pterosaur Database

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Ornithodesmus latidens was later re-named *Istiodactylus latidens*.

Howse S. C. B., Milner A. R. and Martill D. M., 2001.

On the Skeleton of *Ornithodesmus latidens*; an Ornithosaur from the Wealden Shales of Atherfield (Isle of Wight).

By Reginald Walter Hooley, F.G.S.

(read February 5th, 1913.)

[Plates XXXVI-XL.]

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I. Introduction.

The late Rev. W. D. Fox, of Brighstone (Isle of Wight), discovered in the Wealden Beds of brook in that island many associated Ornithosaurian bones. These were acquired by the trustees of the British Museum in 1882, when they purchased his important collection. They are numbered R/176, and classified by Mr. R. Lydekker¹ under *Ornithocheirus nobilis* (Owen) as 'not improbably belonging to this species.'² In 1888 the hinder portion of the skull was shown by Mr. Lydekker to Mr. E. T. Newton, at the time when the latter was preparing his paper on *Scaphognathus purdoni*; and Dr. Henry Woodward permitted it to be bisected longitudinally, so that Mr Newton was enabled to describe the form of the brain.³ No other reference appears to have been made to the fossil until 1901, when the late Prof. H. G. Seeley referred to it in his 'Dragons of the Air' (pp. 173-74), under the name of *Ornithodesmus latidens*, and thus it became the type of that genus. Judging from particulars there given, one would surmise that a much greater portion of the skeleton once existed. At the present time the hinder part of the cranium is the only moiety of the skull to be found; but Dr. A. Smith Woodward informs me that he has heard a tradition that Fox had originally the jaws of this specimen, and that they were lost before the collection came into the possession of the British Museum.

I purpose giving details of the bones comprised in B.M. R/176 for, with those belonging to two other individuals, obtained from the Wealden Shales of Atherfield (Isle of Wight), we have sufficient material to restore the almost complete skeleton of this reptile. The blocks of rock containing the latter have all been recovered from the sea, washed out of an enormous fall of Wealden Shales which occurred near Atherfield Point (Isle of Wight), in the autumn of 1904, the same as that which yielded the skeleton of *Goniopholis crassidens*.⁴

Particulars of the Bones included in the British Museum Specimen, No. R/176

Skull: The back of the skull from the centre of the orbits. Right side badly worn, the left and occiput well preserved.

Vertebrae: A cervical, much crushed, the posterior end nearly perfect. Fragments of other vertebrae are to be seen embedded in the matrix adhering to the odd bones. The notarium with the ultimate process of the right side preserved, and the left side enveloped in matrix. Five consecutive dorsal vertebrae follow the notarium on the same mass of shale. Only their ventral surfaces are exposed. Three and the proximal end of a fourth sacral vertebrae

Sternum: Nearly perfect.

Humerus: The right, minus a fragment of the ulnar process near the condyle. A large portion of the left, with the radial process (deltoid crest) well preserved.

Radius and Ulna: Proximal ends, sections of the shaft, and the distal extremities of both bones.

Carpals: several.

Metacarpals: Proximal and distal ends of wing-metacarpal.

Phalanges: Fragments of the wing-phalanges, proximal ends of both right and left first wing-phalanges. There are also shattered and flattened pieces of limb bones. Where free from a distorted condition, the above are similar in form and measurement to the corresponding bones in the Atherfield fossils.

Particulars of the Atherfield Specimen, No. 1.

This specimen was contained in three blocks and a rounded pebble, which had become thus by attrition on the beach since its fall from the cliff. The three blocks combined had a length of 540 mm. Two of the blocks fitted together precisely, but the third required a section (Which has not been found) to connect it with the other two. As will be proved hereafter, the missing block was originally 89mm. long. The matrix was a very fine silt, containing both carbonate and phosphate of calcium and iron. Its hardness was extremely variable, and as the bones are of papery thinness and very brittle, their removal without damage was a matter of much difficulty. These blocks held the following bones:-

Skull: The greater portion anterior to the orbits.

Vertebrae: An imperfect cervical, the last two cervicals, an almost perfect notarium, and the first four dorsal vertebrae.

Scapula: The left, minus a moiety of the humeral end.

Humerus: the proximal and distal ends of the right, and the distal of the left. As the proximal extremities of the former was lying with its ventral surface exposed, the ulnar and radial processes have been worn to their bases. The concavity between them is filled in by matrix, and overlain by the thin plate of the ventral posterior half of the right ischium. The latter bone was once overlying this end of the humerus, but pressure has squeezed that portion above the remainder of the ischium, so that the humerus appears to be resting on that bone. The removal of this fragment has been found impossible.

Radius and Ulna: The whole of the right radius and ulna, excepting 89mm. (the missing section) from their shafts, and slightly more than the proximal halves of the left.

Pteroid: The perfect right pteroid.

Carpals: All of both wrists, except the left lateral carpal.

Metacarpals: The proximal end of the right-wing metacarpal, and one of the small right metacarpals.

Phalanges: The distal extremity of the first, the major portion of the second and the proximal end of the third phalange of the right wing.

Ischium: The almost perfect right ischium.

Particulars of the Atherfield Specimen, No. 2.

The bones of this specimen are in one block, also obtained from the sea, which has likewise worn away the ends of many of them. That it does not belong to the blocks in specimen No. 1 is proved by its containing similar bones. They lie on a layer of hard blue limestone, but are embedded in the same matrix of silt.

The following bones are preserved:-

Scapula: The humeral end of the right scapula.

Coracoid: The perfect right coracoid.

Humerus: The distal halves of both humeri. The dorsal surface of the left and the ventral of the right are exposed.

Radius and ulna: The proximal ends of the left radius and ulna.

Metacarpals: The distal extremity of the right and the distal third of the left wing-metacarpals.

Phalanges: The proximal half of the right and left first wing phalanges.

II. Description of the Skeleton

The skull is nearest in outline to *Pterodactylus*; but the occiput is square, and not rounded as in the figure and restorations of that genus. The extremity of the snout and the brain-case are the only portions of the skull that are completely enveloped in bone. These two regions are connected dorsally by a triangular bar, and ventrally by thin band-like maxillae. The tip of the muzzle is truncated. Here both upper and lower jaws are moderately convex from side to side, and gently curved longitudinally. There is neither nerve-pore nor foramen visible on the upper and lower jaws.

The upper jaw, 33 mm. from the tip of the muzzle, or above the seventh tooth, becomes laterally compressed – a compression which gradually intensifies until at the commencement of the nares, the sides are decidedly concave. The dorsal outline of the beak makes a very acute angle with the lower jaw, which is straight. There is no supra-occipital crest. The parietal region is but slightly convex from side to side, and, compared with the length of the skull, extremely constricted.

There is no longitudinal arching of the cranial platform or the occiput (Pl. XXXVII, fig. 3). The crown and lateral borders of the back of the skull are semicircular, and the base concave (Pl. XXXVIII, fig. 1). The lower outer border is produced posterior to the condyle. The intermediate area is deeply concave. The brain-capsule is very small.

I estimate the length of the skull to have been 560 mm., and that of the mandibles 423 mm., which I obtain in the following manner. From the angles at which the proximal and distal ends of the humerus, radius and ulna were lying on the blocks, the missing section must have been about 89 mm. long. In the measurements of the skull and limb-bones I have taken this to be the length of the lost section. This would give the humerus the same length as the British Museum specimen, which is 220 mm. long; and, as the preserved portions of that bone in the Atherfield fossil are of the same size, it is no more than what would be expected.

The Vacuities of the Skull.

The External Nares.

The external nares (Pl. XXXVII, fig. 1, n.v.) being not far from the extremity of the snout. They gradually expand backwards 140mm. Here should occur the missing section, and all further trace of their shape and area would be lost, were it not for a moiety of bone (Pl. XXXVII, fig. 4. mx.n.b.) 50 mm. long and 18 mm. deep, attached to the inner face of the maxilla, 236 mm. from the end of the muzzle. This bone shows a thickening at its upper interior edge. The lowest portion of the anterior border exhibits a curved smooth outline, the extreme lower anterior boundary of the antorbital vacuity, for I take this fragment of bone to be the lower end of the maxillo-nasal process. It has on its upper extremity a jagged fracture, thus proving a continuation of the bone in that direction. Perhaps additional proof is added by the beak breaking across, just posteriorly to this process, the weakest place in its length. Again, if the narial opening was confluent with the antorbital vacuity, the great cavity from the anterior border of the nares to the anterior margin of the orbit, taken in conjunction with the weak premaxillar bar and attenuated maxillae, would appear to have

been unable, without a strut, to prevent crumpling on a strain of the jaw in prehension, for the weight of the skull is distributed at both extremities. I believe that the rest of the maxillo-nasal bar has been destroyed, and that the nasal was not confluent with the antorbital vacuity. Granting this, the nasal opening is enormous, subtriangular in shape, slightly oblique in position, and posterior to the teeth.

The antorbital vacuity (Pl. XXXVII, fig. 2, a.o.v.) is large, elongately rhomboid, entirely separated from the orbit and the nasal opening.

Antorbital Vacuity No. 2.

An additional preorbital vacuity (Pl. XXXVII, fig. 2, a.o.v. 2) is situated in front, beneath and confluent with the orbit. It is shuttle-shaped, obliquely placed, and bounded by the jugal above and the quadratojugal beneath. In a profile view of the skull its width appears much less than it is in reality.

The Orbit.

The orbit (Pl. XXXVII, fig. 2, O.) is small, circular, and placed very far behind the mandibular articulation. Except the narrow into the antorbital vacuity No. 2, it is entirely surrounded by bone. The margin is formed by the extreme proximal end of the jugal and a moiety of the lachrymal, the roof by the prefrontal and the frontal, and the posterior border by the postfrontal and postorbital; that is, if we take this buttress to 'include both these elements, as in *Sphenodon*.'⁵ Its lower boundary is formed entirely by the quadratojugal, which here is hollowed as far as the anterior region of the orbit, where a broadening of the bone determines the extent of, but does not complete, the orbital rim. There was no trace of a sclerotic ring.

The Supra-Temporal Fossa.

The supra-temporal fossa (Pl. XXXVII, fig. 3, s.t.f.) is deep, large, and thrown open laterally, because of the supra-temporal arcade rising obliquely forward from the lowest point of the outer edge of the back of the skull. It is bounded on its posterior and lower borders by the squamosal and a process from that bone, and anteriorly by the post-fronto-orbital buttress.

The Infra-Temporal Fossa.

The infra-temporal fossa (Pl. XXXVII, figs. 2 & 3, i.t.f.) is large, directed obliquely, and extends in front of and behind the orbit for equal distances. It is bordered above by the squamosal bar and the quadratojugal, and below entirely by the quadrate. The inner border of these bones forms a rising floor under the posterior end of the vacuity, which prevents its full extent from being observed in a profile view.

The Bones of the Skull.

The Premaxillae.

The premaxillae (Pl. XXXVII, fig. 5, p.) comprises the whole of the upper jaw anterior to the nares, and include the whole alveolar tract of each side. Dorsally they are produced backwards as a triangular rod, which is nowhere wider than 15mm. This bar is prolonged to the frontal, but to what distance they continue to take a share in it is not clear. The premaxilla-maxillar suture is apparently beneath the anterior edge of the nares.

The Maxilla.

The maxilla (Pl. XXXVII, figs. 2, 4 & 5, m.x.) is an extremely thin, long, narrow bar of bone, of little depth. There is a slight increase in depth at each end, with the posterior extremity the more expanded. Here the inner dorsal margin is raised above the outer, and on its posterior border it is fused to the jugal. Its exterior surface is concave. Near the tip of the snout, and below the anterior end of the external nares, the inner ventral margin is produced inwards, as a sheet of bone, and meets a similar process of the maxilla of

the opposite side, completely roofing the palate. How far backwards this palate was continued, it is impossible to say, on account of the lost section. The maxilla comprises the inferior boundary of the nasal and antorbital vacuities, and extends to the quadrate, without the intervention of the jugal. The maxilla is edentulous.

The Nasal.

The nasal apparently sends down a process to join that of the maxilla, nearly midway between the anterior end of the nasal and the posterior extremity of the antorbital fossa. That this is so seems to be proved by the presence of the maxillar process: for, where the nasal and the preorbital opening is confluent, as in *Pterodactylus*, such a process is not found. The nasals are fused with the backward extension of the premaxillae into a single median ossification. What extent of this dorsal bar they occupy is indeterminable.

The Lachrymal.

The lachrymal (Pl. XXXVII, fig. 5, l.) is situated in the upper anterior corner of the orbit. It looks forward into the antorbital vacuity. It is triangular, with the apex of the triangle pointed downwards, and bifurcated: the two branches unite with the upper end of the jugal, and form together an elongated foramen. Where it shares in the orbital rim, it is strongly convex, and, between here and the prefrontal, concave.

The Frontal.

In the Atherfield specimen No. 1, only the extreme anterior end of the frontal is seen. It commences over the anterior third of the orbits, and here on the right side is a curious mammillated knob of bone (Pl. XXXVII, figs. 2 & 5, b.) over the upper border of the orbital rim, which most probably was paired on the left. Interiorly to this boss, the surface is concave, rising into a feeble convexity on the summit of the cranium. The frontal unites with the lachrymals, prefrontals, and the premaxillar prolongation with a V-shaped suture, the angle being towards the occiput. It lies below the prefrontals and the premaxillar extension, but not beneath the lachrymals along the line of suture. In the hinder portion of the skull in the B.M. R/174 specimen, the extent of the frontal and the other bones of the cranium roof cannot be seen. The cranial platform is quadrilateral space.

The Post-Frontal.

The post-frontal is situated in the corner between the orbit and the supra-temporal fossa. It sends down a process which, in conjunction with the post-orbital (if that bone be present), comprises the posterior boundary of the orbit.

The Parietal.

The parietal arches the skull between the supra-temporal fossae. It is extremely constricted, so that it becomes very concave on its lateral borders. At its junction with the occipital area the bone is raised.

The Squamosal.

The squamosal is situated at the posterior lower angle of the supra-temporal fossa. It sends forward and upwards a process to unite with the post-fronto-orbital bar, in forming the supra-temporal arcade. Below, it is fused to, and rests upon, the hinder end of the quadrate: this forms a strong buttress, upon which the brain case is supported.

The Bones of the Occiput.

The right side of the back of the skull in B.M. R/176 is destroyed, and the left below the foramen magnum is covered by matrix. Nor are any sutures or striae visible on the upper half, so that the extent of the bones is indecipherable. Except a vertical ridge from the parietal border of the foramen magnum, the whole region between the outer borders is concave. The parietal, squamosals, and paraoccipitals have extended

and coalesced into one concave plate, with the post-temporal fossae almost obliterated. The occipital condyle is large, and, as unusual, set at right angles to the skull.

The Vacuities of the Occiput.

The post-temporal fossa of the left side is well exhibited. It is quite small, subcircular, and placed far above the foramen magnum near the upper border of the occiput. The foramen magnum is very large.

The Quadrate.

The Quadrate (Pl. XXVII, figs. 2, 3, & 5, Q.) is extremely long. It articulates with the mandibles as much as 99 mm. in front of the orbit. Its proximal end is remarkably robust, and so the overlying cranium is weak and fragile in comparison. It forms a third of the depth of this part of the skull. Its proximal dorsal half bends inwards under the supra-temporal arcade. Proximally, externally, it is fused with the squamosal process, between which and the paroccipital process it is immovably wedged. It lies under the squamosal, and forms the lowest angle of the posterior end of the skull. In the median region it is much weaker, and moderately thick; its dorsal half loses the inward curve, and the whole lateral surface looks outwards. This continues to the distal end, where the bone again becomes more powerful, with a stout, convex, ventral border. Dorsally here it is ankylosed to the quadratojugal for 51 mm.; proximally to this it comprises the lower boundary of the infra-temporal fossa. From the interior surface at its distal end a strong bar of bone extends 29 mm. upwards and backwards. The angle thus made with the shaft of the quadrate is occupied by a wing of thin bone, which has its origin 86 mm. from the articular end. The pterygoid probably united with the inner angle of this wing, as in *Scaphognathus purdoni* [*Parapsicephalus purdoni*]. The type of *Sc. crassirostris* is the only specimen that clearly denotes the form of the inner side of the quadrate. It exhibits a corresponding wing, although the distal border is not a straight line, but sigmoid, and the wing is apparently developed to the full extent of the bone. The articulation is a plain pulley-joint, above which the quadrate unites with the lower angle of the posterior extremity of the maxilla.

The Quadratojugal.

The quadratojugal (Pl. XXXVII, fig. 2, 3, & 5, Qu.) is a thin moderately-broad bone, rising obliquely from the maxilla to the anterior termination of the squamosal bar, near the hinder border of the orbit. It is ankylosed to the inner side of this bar. For about a fourth of its length it forms then lower boundary of the orbit, and for the remaining three-fourths that of the infra-orbital vacuity. At its lower end it is fused for 51 mm. with the quadrate and at its extremity with the maxilla.

The Jugal.

The jugal (Pl. XXXVII, fig. 2 & 5, J.) is a rod-like hollow bone, except at its lower end, where the inner and outer lateral surfaces are flat. It rises obliquely, yet feebly arched, to the lachrymal. Here it is bifurcated into short branches, the outer being club shaped and passing backwards and downwards, forming a moiety of the anterior margin of the orbit. The inner is rod-like, and connects with the interior border of the lachrymal. The distal termination is V-shaped, one branch joining a raised portion of the inner border of the maxilla and the other being fused with the interior surface of the quadratojugal at its dorsal edge. Its total connexion with the maxilla and the quadratojugal is only 5 mm. long.

The Temporal Arcades.

The jugal, quadratojugal, and quadrate all rise obliquely from the maxilla at nearly the same angle and free one from the other. The jugal takes no share whatever in the upper temporal arcade: this is formed by the quadratojugal and the squamosal bar. The squamosal bar overhangs externally the hinder end of both the quadratojugal and the quadrate. The lower temporal arcade is made entirely by the quadrate.

The Palate.

I have not thought it advisable, owing to its hardness, to clear away the matrix which lies in the angle made by the convergence of the mandibles, for fear of fracturing this end of the beak. On the area of the palate exposed, there is no trace of the internal nasal openings, and it is too near the anterior margin of the external nares for them to be situated in front.

The Mandible.

The mandible (Pl. XXXVII, fig. 1, 2, 4, & 5, mn.) is long, and the symphysis short. The alveolar tracts terminate close behind the symphysis. The rami of the mandibles gradually decrease in depth backwards; but their strength is maintained by a corresponding increase of the width, and at the articulations they are bulbous. Near the symphysis they are convex ventrally; posteriorly they lose this, and become for some distance flat, with a convex upper and lower border. Behind the premaxillae, they lie exterior to the upper jaw. On their inner dorsal margin there is a depressed ledge, on which the maxillae rest, when the jaws are shut. Beneath this shelf, the bone is concave. They terminate far in advance of the orbits. The extent of their different elements cannot be determined.

The Teeth.

There are twenty-four teeth in the upper, and twenty-five in the lower jaw. Only twenty-three of the former are exposed, owing to a slight displacement of the upper jaw; through this derangement the teeth of the right dentary are covered by the matrix underlying the teeth of the right premaxilla, in such a manner that it is impossible to remove it, without endangering the overlying teeth. The hindmost tooth on each side of the lower jaw is posterior to all the teeth of the upper. All the teeth interlock. They are compressed laterally and lanceolate, the smallest teeth being at the tip of the muzzle; these are followed gradually by longer and broader teeth. The two posterior teeth on each side of both jaws are broader, larger, and more bluntly pointed than the rest. A very marked characteristic is that the last two teeth of the mandibles fit into semicircular slots in the upper jaw (Pl. XXXVII, figs. 1 & 5); and the ultimate one of the upper jaw lies exterior to the lower jaw, the lateral outer surface of which is slightly concave to receive it but not slotted. These teeth, in life, must have been visible when the muzzle was closed. They are a little longer than the others. The indentations in the upper jaw give an appearance to the last tooth of being set on the summit of a strong process. The teeth are smooth and free from striae; but, on careful examination, there is to be discovered, on the outer surface of some of them, an incipient median carina. The alveolar borders of the upper jaw, anterior to the slots, are gently convex to the tip of the snout. Those of the lower jaw, immediately in front of the last two teeth, fall abruptly some distance below the plane of the tract occupied by those teeth, and from there they are feebly concave. The posterior tooth of the left dentary is displaced, but attached by matrix to the surface of the bone near the dorsal border of the beak. This tooth is diamond-shaped, both crown and base forming equilateral triangles. All the teeth are vertical, and planted in separate sockets.

The Vertebral Column.

The hinder half of the cervical vertebra in the Atherfield fossil is quite similar to an example in the B.M. specimen R/176. That example is much crushed, and has been fractured and cemented together, so twisted that the dorsal surface of the one portion is followed by the ventral of the other. This is apparently the example figured in Seeley⁶: it is procoelous. The neural arch and spine are missing. In the Atherfield example the neural spine is fairly high and robust, and the neural arches are flat and set at an oblique angle to the spines: They overhang the centrum. The neural canal is large. The centrum is long and narrow, becoming moderately constricted in the central region. Laterally, a deep and open valley traverses its length. Pneumatic foramina occur on each side. The ventral surface of the centrum is flat without any carination, slightly concave at both ends, and at the posterior extremity bifurcated into the usual tuberous processes with the articular convexity between, but dorsal to them. The pre-post-zygapophyses arise laterally near the posterior third of the centrum, and are directed backwards, terminating some distance from the posterior articulation of the centrum. A restored ventral view of this cervical is given in Pl. XXXVIII, fig. 2.

The last two cervical vertebrae have their zygapophyses laterally, and centra ventrally, much waterworn. The centrum of the penultimate is twice as long as that of the ultimate, and the neural spine has a greater longitudinal width; this may be due in some degree to pressure, for this vertebra is much distorted by having been squeezed against the proximal end of the wing-metacarpal which was lying upon it. These vertebrae are shorter and more robust than the cervical above described: they appear to be procoelous. The neural spines are much thickened, especially at their dorsal extremities. The neural arches slightly overhang the centra. The transverse process of the left side of the last cervical is preserved. It shows that the transverse processes were produced outwards, as far as those of the notarium which follow it. They are sent off from the anterior half of the centra. These processes underlie the prezygapophyses, which are produced anteriorly; they are situated at the base of the neural arches, in front of the neural spines. The postzygapophyses are directed backwards, and overhang the posterior end of the centrum, thus forming a space into which the prezygapophyses of the following vertebra enters. The hinder ventral border of the last cervical on the left side has a short, fairly strong, posteriorly directed process, free from the articular surface of the centrum, the hinder extremity of which probably possessed an extra articular facet (exopophysis) as in *Ornithostoma* (*Pteranodon*). An ovate pneumatic foramen lies under the lateral base of the neural arches.

The Notarium.

The notarium (Pl. XXXVIII, figs. 3, 4, & 5) consists of six ankylosed vertebrae. The neural spines are fused into one strung ridge, which, above the first vertebra, is broader than the neural spine of the last cervical; it diminished rapidly, until half as thick over the second, third and fourth, expands again at the fifth and sixth, where it is a third greater than that at the anterior end, and becomes remarkably bulbous. There is no supraneural plate, and the surface of the bone shows no trace of such having come away. The dorsal outline of the fused spines is highest between the third and fourth vertebrae, as in *Ornithostoma*. The facet for the scapula articulation was probably beneath this, where on the right side there is a depression (Pl. XXXVIII, fig. 3, fa.), which, however, is not seen on the left side; but this may be due to pressure. The neural arches overhang the centra, forming a ledge along the median region of their sides. The surfaces of these arches are alternately concave and convex in anterior-posterior extent. The convexities occur where the zygapophyses have fused, and underneath these a series of fossae are found (Pl. XXXVIII, fig. 5, F., F.). Of these fossae that of the first vertebra is the largest, the others decreasing in size to the last vertebra. Probably pneumatic foramina occur within the inter-vertebral fossae, as they are not present elsewhere. On the dorsal surface of the transverse process, the matrix is too hard, and they themselves are too fragile, to permit of its removal, and this is so likewise between the hinder three; but their ventral surfaces have been fully exposed. These processes arise partly from the neural arches, and partly from the centra. In the first notarial vertebra, as in the last cervical, they originate on the anterior half of the centra, and gradually extend more and more on each following vertebra, until in the fifth and sixth their bases occupy the length of the centrum. They are entirely free, one from the other, and are directed slightly upwards. They are arranged in three pairs, and each pair is different in size and form. The first pair are expanded at their bases and outer extremities, and contracted medially. The middle pair are weaker and shorter than the others, and their distal borders are produced posteriorly into a style-like process. The ultimate pair are considerably broader than the rest, are quadrate in shape, and are as long as the first pair. Their ventral surfaces are concave, with a curious downward turning of the anterior edge. This is also seen in the transverse process of the fourth vertebra. The spaces between the transverse process are greatest between those of the first and second vertebrae; between the others they decrease, until between the last two the division has become narrow. The centra are comparatively small; their ventral surfaces are convex from side to side, and feebly concave longitudinally. The first three show a lateral concavity, the last are free from any grooving. On the hinder, lateral, ventral borders of the centra of the first three vertebrae, at their point of union, occur protuberances; these I take to be parapophyses.

The Dorsal Vertebrae.

The dorsal vertebrae are six in number and amphiplatyan. They decrease very rapidly in dimensions backwards. The neural spines are thinner, not so high, and the neural arch less expanded than in the notarial vertebrae. The transverse processes, instead of occupying a horizontal position, as in the vertebrae of the notarium, at once begin to assume an upright one, until in the fourth they are nearly vertical. The

centra are convex from side to side; but, through the rising of their anterior and posterior edges, they are longitudinally more or less concave.

The Sacrum.

Unfortunately, only the fused centra of three, and a portion of the fourth sacral vertebrae are preserved. They gradually lessen in dimensions posteriorly. The bases of the transverse processes are all that remain, and it is impossible to determine the form of the sacrum.

Vertebral Ribs.

Vertebral ribs were lying among the bones near the notarium. They were waterworn. They are short, small, and hollow, and are two headed as in other Ornithosaurs.

The Sternum.

There is no styliform anterior process of the sternum (Pl. XL, fig. 3) such as in all other types is greatly prolonged anterior to the coracoid facets. The keel is as remarkably developed as in the carinate birds. The anterior border is almost vertical; although, ventrally, it bulges slightly in front of the coracoid articular facets. The longitudinal outline rises posteriorly with a sharp curve, and has a greater length than depth. At the posterior end it is a little blunted, by the breaking away of the rind of the bone. It is very robust, especially at the anterior end. In the lateral median region it becomes gently concave. The base of a strong bony process occurs near the centre of each lateral border and appears to have been produced upwards and dorsally to them. Although the edge of the lateral expansion is broken away, the converging surfaces of the bone are divided by so narrow a space that they could not have been produced more than a fraction further. Through this the costal facets are not seen. If they were present, they could only have occupied 18 mm. of the edge, for the rest of the border is too thin and angular for the sternal ribs to have articulated there. The dorsal surface is concave. There is a broadening of the fore part of the keel for the coracoid facets, which are placed below the sternal plate (Pl. XL, figs. 3 & 4, cor. ar. fa.). The right coracoid facet is situated 20 mm. below the sternal plate and 42 mm. above the ventral outline of the keel. In Seeley's figure of this sternum⁷ the coracoid facets are incorrectly depicted as being on the same plane as the lateral expansions. The facets are oblique, the right ventral to the left. They were continued on to the lateral surfaces of the keel: ventral to each is a well developed wing of bone, preventing dislocation of the coracoids. At the posterior termination of each of these is a cavity, determined by Seeley to be pneumatic foramina. This may be so, but they are also cavities which the hinder point of the distal articular end of the coracoids entered when the movements of the wing caused these bones to be at their utmost posterior limit, the walls of these cavities acting as stops. The articulations are pulley-joints. I estimate the true length of the sternal plate to have been 65 mm., and the breadth 44 mm. A restored outline, of half of the natural size, is given in Pl. XL, fig. 5.

The Appendicular Skeleton.

The Pectoral Girdle.

The scapula and the coracoid are strong bones. The former is shorter than the latter. The scapula is fused to the coracoid; the line of suture is horizontal, and both bones here are truncated. Only the preaxial half of the proximal end of the scapula is in union with the coracoid, and here it is bulbous; whereas the free portion is compressed dorso-ventrally, and set at right angles to the glenoid cavity. Its articular surface looks downwards, and forms an extra glenoidal surface (Pl. XXXVIII, fig. 7, ad. ar. sur.). The articular surface of the fused portion is oblique. The glenoid cavity is saddle-shaped. The dorsal surface is convex and the ventral flat, but both become concave near the glenoid cavity. The bone here shows a quadrangular section. The preaxial border immediately behind the glenoid cavity is deeply emarginated, followed by a strong convexity (the acromion process), and that again by a concavity to the distal end. The postaxial border is very concave over its whole length. The distal extremity is considerably expanded; the vertebral margin has a concave facet, apparently for articulation with the notarium. The postaxial border of the proximal end of the coracoid is bent downwards into a kind of lip with a convex articular surface. The

coracoid is moderately curved. It is expanded at both ends pre-postaxial and compressed in the central region of the shaft, the preaxial edge traversing across the bone, until at the sternal end it is in the centre of its ventral surface, which gives the appearance of a twist to the bone. Its sternal articular face is concave pre-postaxially, with its preaxial border produced distally more than the postaxial. Anterior to the glenoid surface of the coracoid there is a triangular inarticular portion, the apex forming the border of the bone. It is produced into a tubercle, between which and the scapula is a groove, which leads into a pit or pneumatic foramen, situated at the base of this triangular area, near the articulation.

The Humerus.

The proximal condyle of the humerus is of the usual Ornithosaurian character, feebly convex on its articular surface, and crescent-shaped in outline, with the horns well splayed out. Near the dorsal border of the preaxial side of the articular surface of the condyle is a strong ridge. The deltoid crest is remarkably developed. It springs powerfully from the preaxial border, at some distance below the head, and curves spirally round the bone until its apex is over the middle of the ventral surface of the shaft. This spiral curve commences 40 mm. from the proximal condyle, and terminates 125 mm. from it. Along its outer curve it measures 75 mm. At its distal end it is 27 mm. above the surface of the shaft. This extremity is claw-like, the point directly postaxially, quite different from those of the other genera where the distal end is more or less obtuse. The ulnar crest is moderately developed. Between the deltoid and the ulnar crest the ventral surface of the bone is concave, but becomes convex as soon as the radial crest is passed. The shaft gradually decreases in size until, in the median region, it has a diameter of 22 mm.; from here it rapidly expands to the extremity, where its pre-postaxial diameter is 64 mm. The bone here is triangular, the apex being on the median line of the dorsal surface. Immediately underlying the apex on the articulation there is a large circular opening into the shaft (Pl. XXXIX, fig. 3, f.). A similar vacuity is found in many of the humeri included in the genus *Ornithocheirus* of the Cambridge Greensand. On the preaxial side of this opening is a small feebly-convex, triangular surface, on which the preaxial moiety of the proximal end of the ulna is articulated. Ventral to it is a moderately developed trochlear joint, oblique, looking outwards, and forming the articulation for the radius (Pl. XXXIX, fig. 3, tr.). On the postaxial side of the central opening is a deep valley (v.), which traverses the ulnar condyle diagonally, from the ulnar tubercle to the central pit. The ulnar tubercle is produced distally; it is strong and claw-like, with a concave side facing the articulation. Two strong ridges border the valley, the upper of which rises vertically from the bottom of the valley, while the lower has a sloping face. The dorsal border of the distal end over the upper ridge is much compressed, buttressing the ridge, and making it appear as if the edge of the bone had been doubled over. The distal extremity is beautifully preserved in the Atherfield specimen No. 1 (Pl. XXXIX, fig. 3), and the proximal ends of the radius and ulna (Pl. XXXIX, fig. 4) are in a like condition. The median area of the dorsal surface at the distal end is much inflated, and slightly concave at the pre-postaxial borders. A very strong epiphysis (Pl. XXXIX, fig. 2, ep.) overlapping the bone is present on the preaxial border of the ventral surface. It formed a support to what must have been a very large tendon, which was inserted in a deep cavity under the inner condyle of the trochlear joint for the radius. This pit is separated by a broad convex ridge from another, situated near, but postaxial to, the median line of the bone. A large pneumatic foramen is present in this cavity. On the postaxial border of the ventral surface, and nearer the distal end than the one on the preaxial, is a ridge (Pl. XXXIX, fig. 2, ri.), the distal termination of which does not follow the border, but passes inwards on to the ventral surface. The ridges and valleys of the distal ventral surface give a sigmoid outline, proximally to which the bone becomes convex. The postaxial border of the distal end is remarkably robust, and produced outwards from the long axis of the bone; while the preaxial is parallel to it. A restoration of the right humerus is given in Pl. XXXIX, fig. 2.

The Radius

The radius (pl. XXXIX, figs. 5 & 6, R.) is slightly shorter than the ulna, and very much less in diameter throughout its length. Proximally, it is ventral to the ulna, and placed on the preaxial side. From here it gradually rises and crosses over the shaft of the ulna, until the distal end is entirely dorsal to it, and occupies the central half of the ulna, the remaining quarters of that bone being visible on each side. The proximal articular surfaces fit the trochlear on the preaxial ventral border of the distal end of the humerus. Proximally, the radius is compressed dorso-ventrally and expanded pre-postaxially. Its dorsal surface is convex, while the ventral is concave, and convex on its pre-postaxial border. The last-named quickly becomes an angular ridge, which is continued distally for a short distance; then the whole bone

becomes circular and rod-like, until it approaches the distal end, where it gradually expands pre-postaxially. The distal articular end is a simple convex pulley. On the postaxial side of the dorsal surface of the distal end there is a well-developed longitudinal ridge, and the striae made by the fibres of a muscle traversing the bone from the preaxial border are visible. On the ventral surface of the postaxial border there is a longitudinal groove.

The Ulna.

The ulna (Pl. XXXIX, figs. 5 & 6, U.) is a very powerful bone. In the median area of the shaft it has a diameter three times greater than that of the radius. The shaft is straight, but an expansion of both articular ends gives a somewhat curved outline to the pre-postaxial borders. The proximal end (Pl. XXXIX, fig. 4) is roughly triangular, the apical side being on the dorsal surface. There is no olecranon. On the preaxial side of the articular surface is a triangular area, in extent equal to a third of the articulation: this is weakly convex, obliquely placed, and looks ventrally. The remaining two-thirds of the articulation constitute a platform which is raised above the other third and looks distally. In the centre of this space is a high and strong V-shaped ridge (Pl. XXXIX, fig. 4, R.) with the angle directed postaxially. The ventral branch articulates in the valley (Pl. XXXIX, fig. 3, v.) on the distal end of the humerus. Thus the overlapping dorsal edge of the humerus enters the two branches, where they converge at the angle. On the dorsal side of the angle of the V is a shallow concavity, in which the tubercle of the ulnar condyle of the humerus rests, and acts as a stop to any dislocation in a preaxial direction, as the angle of the V does in the opposite. Along the postaxial half of the V, and ventral to it, is a curved groove, in which the convex ventral border of the postaxial side of the humerus articulates. A pneumatic foramen is present in the centre of the ventral surface of the shaft, near the articulation. Distal to this is a high robust ridge (Pl. XXXIX, fig. 6, ri.), extending some distance down the bone. The crown of the ridge is highest near its distal termination, and its top bends over, forming on its preaxial side a slightly-concave surface, against which the radius rested. The section of the bone here, *minus* the ridge, is circular, gradually becoming oval in the median region of the shaft, and this in its turn gives place to a quadrangular section as the distal end is approached. At the distal end the bone is expanded pre-postaxially: the dorsal surface is flat, the ventral concave, and the pre- and postaxial borders convex, although these surfaces have raised and concave areas. On the dorsal surface, towards the postaxial border, is a longitudinal ridge (Pl. XXXIX, fig. 5, ri.): against it the radius lies, and is thus supported and stiffened by a ridge on the postaxial ventral surface of the proximal end, and also by a similarly-placed ridge on the dorsal surface of the distal end. On the ventral side, near the postaxial border at the distal extremity, is a circular facet (Pl. XXXIX, fig. 6, fa.) with a flat articular surface raised above the bone, placed obliquely, looking preaxially, and continuing distally to a convex condyle on the articulation. This forms a very prominent feature. The preaxial border is very deep; 40 mm. from the distal end its dorsal margin is produced into a wing, which, rapidly expanding outwards, extends to the distal end: here the whole border is swollen, and terminates in a tubercle directed distally and moderately produced. By this arrangement, on the distal preaxial border an elongated concavity is formed; this has a roughened surface, and forms the insertion for a powerful tendon⁸. The postaxial distal border is convex, and is not expanded outwards to as great an extent as the preaxial. As at the proximal end, the distal extremity comprises the whole of the pre-postaxial extent of the articulation. Here the radius articulates dorsally to the ulna. On the articular surface of the distal extremity, postaxially to the tubercle, a deep, circular, basin-shaped pit occurs; this is followed by a trochlear joint extending to the postaxial border. The inner condyle of this trochlear is an oval-shaped convexity, situated medially, with its long axis directed pre-postaxially. The convex outer condyle is continued obliquely on to the ventral surface of the shaft, where it looks preaxially.

The Carpus.

The carpus consists of three distinct bones – a proximal, a distal, and a lateral carpal. The proximal and distal carpals are much wider than long, and the lateral longer than wide. The proximal articular surface of the proximal carpal is greater in area than the distal, causing the outer face of the bone on all sides, more or less, to slope inwards, towards the distal articulation; in the distal carpal this feature is reversed, and thus there is a constriction towards the proximal articulation. All the surfaces of the carpals are very complex. The preaxial border of the proximal carpal is produced outwards into an elongated process of bone, truncated at its extremity. This has on its proximal surface a spherical knob of bone (Pl. XXXIX, fig. 8, A), which articulates in the circular pit on the distal articulation of the ulna (Pl. XXXIX, fig. 7, A). The dorsal

surface of this process is concave, and here occurs a subcircular pneumatic foramen. This surface articulates apparently with the lateral carpal. From this preaxial process on the ventral side the bone narrows, first showing a convexity followed by a concavity, afterwards enlarging considerably in a proximal and postaxial direction to the border. This expansion (Pl. XXXIX, fig. 8, C) articulates with the convex condyle of the distal end and the circular facet on the ventral surface of the ulna (Pl. XXXIX, fig. 7, C, & fig. 6, fa.), and in a proximal and distal direction is produced for the length of the distal carpal, articulating with it on its inner face. The dorsal preaxial border is remarkably raised proximally into a strong buttress, which juts out as a wedge-shaped piece of bone, anchylosed to the carpal. The butt-end of this wedge has a concave groove, in which the radius articulates (Pl. XXXIX, fig. 8, D). From this buttress to the postaxial border the bone narrows, and the surface is mainly convex, without any peculiar feature. A process similar to that on the proximal carpal occurs on the preaxial border of the distal, directed also preaxially, and possessing, on its proximal surface, a facet for articulation apparently with the distal end of the lateral carpal. On its preaxial dorsal half, for the same distance as the buttress for the radius on the proximal carpal, the bone is produced outwards and distally in such a manner that the two form a deep quadrangular cavity. Whether a sesamoid bone occupied this hollow it is not possible to say; however, it is suggestive, for such have been found near this point in the German specimens. The postaxial half of the dorsal surface is nearly flat. The bone gradually expands from the preaxial to the postaxial border, which is produced distally outwards. The postaxial border is the apex of an angle, formed by the conjunction of the ventral and distal articular surfaces, which gradually converge together to this point. The articulation for the radius on the proximal carpal is an elongated groove, parallel to, and near, the dorsal surface, and midway between the pre-postaxial borders (Pl. XXXIX, fig. 8, D). That for the ulna is much more complex (Pl. XXXIX, fig. 8, A, B, C). It consists preaxially of a hemispherical knob (A), dorsally to which is a small concavity (E); postaxial and ventral to the knob is a large basin-shaped concavity (B), followed by a ridge, and that again by a concave surface (C), having its postaxial, and a portion of the ventral, margin so raised that its articular surface is oblique to the main articulation. This surface comprises the postaxial moiety of the articulation. The knob (A) fits into the pit or socket on the preaxial side of the distal end of the ulna (Pl. XXXIX, fig. 7, A). The concavity (B) articulates with the convexity on the distal end of the ulna (Pl. XXXIX, fig. 7, B), and the raised surface of the concave postaxial surface of the articulation (Pl. XXXIX, fig. 8, C) articulates with the circular facet on the ventral surface near the postaxial border of the ulna (Pl. XXXIX, fig. 6, fa.); while the rest of the concavity articulates with the convexity on the postaxial extremity of the ulna. The distal articulation of the proximal carpal, and the proximal of the distal carpal cannot be seen, as the bones are cemented together by the matrix; yet, so close are they in all perceptible characters to some of those from the Cambridge Greensand, that no doubt can be entertained as to the similarity of their articulations.

The distal articulation of the proximal carpal, as seen in the Cambridge specimens, comprises two transverse concave surfaces divided by a ridge, the dorsal one being only half the extent of the ventral. The smaller is oblique, looking outwards, and the larger distally; but, as it terminates at the distal end of the wedge-like prolongation on the postaxial edge of this carpal, it becomes raised here, and also looks outwards.

The proximal articular surface of the distal carpal has convexities corresponding to the concave surfaces of the distal end of the proximal carpal. Thus a trochlear joint is formed, with a pre-postaxial movement. The distal articulation of the distal carpal is beautifully seen in the Atherfield specimen No. 1. Nearly in the centre of the articulation is a very large and deep circular pit (Pl. XXXIX, fig. 9, D), the diameter of which is 17 mm. Dorsally to this is an elongated, narrow, shallow and concave, articular surface, placed obliquely, so that it looks both upwards and distally (O). This takes no part in the articulation with the wing-metacarpal; it is dorsal to it, and on a different plane. The small metacarpals articulated here. On the preaxial side of the central cavity and ventral to that just described, is a triangular area, the ventral angle of which is continued round the central pit; ventrally to this the bone expands, and then narrows and extends as a curved bar to the articulation for the small metacarpals, and thus the central cavity is completely bounded. All these surfaces slope inwards, forming a socket (Pl. XXXIX, fig. 9, B) in which the main proximal end of the wing-metacarpal articulated. In addition to these surfaces there is a quadrangular articular facet (Pl. XXXIX, fig. 9, A) below the plane of the others, and more proximal, also for articulation with the wing-metacarpal (Pl. XXXIX, fig. 10, A); but, as will hereafter be shown, not during flight, as that would have been impossible, and to perform an entirely different function. The lateral carpal is a small shovel-shaped bone, but may have approximated closely to the American forms in life, as it is slightly

waterworn on the side on which the emargination occurs in those genera. It is longer than wide, and has a depth about half its length. It fits in between, and presumably articulates with, the two elongated processes thrown out, on their preaxial borders, by the proximal and distal carpals.

The Metacarpal.

The proximal end of the ulnar metacarpal is well seen in the Atherfield specimen No. 1 (Pl. XXXIX, fig. 10); and the distal is fairly well seen in the Atherfield specimen No. 2. Its exact length cannot positively be determined, for a portion of the shaft is missing. If we judge from the great size of the proximal end and the much reduced distal extremity, and produce their borders at the required angles to connect them, its length would seem to be about 215 mm.,⁹ or roughly half that of the ulna: this is far from what it should be, if it followed the structure of the short tailed forms, where the metacarpal is not shorter than the antebrachium. However, in *Ornithostoma*,¹⁰ which is a short-tailed, 'the bones of the forearm [are] . . . shorter than [the] wing metacarpal.' The proximal end is remarkably robust, and occupies the full width of the distal carpal articulation. From the preaxial side, the articular surface is convex for two-thirds of its extent; this is followed by a deep valley. Postaxially to this, is a flattened oval facet (Pl. XXXIX, fig. 10, A), which does not look proximally as the others do, but has its ventral edge raised and the dorsal depressed, so that its articular surface is oblique to them, and looks outwards and upwards. Half of its area lies outside the line of the postaxial border of the bone, although that border branches out and supports it. When the two-thirds are in articulation with the distal carpal, this facet is free, and thus takes no share in the joint. It articulates with the flattened oblique facet, proximal to the main articulation of the distal carpal on the dorsal surface of that bone (Pl. XXXIX, fig. 9, A), and then only when the metacarpal is directed backwards, and is rotated in a postaxial direction. Such a position would be assumed in folding the wing. The distal articulation is an obliquely-placed trochlear; it is very similar to the examples of this end of the metacarpal from the Cambridge Greensand, figured by Owen and Seeley. The dorsal and preaxial borders of the bone are moderately convex. The dorsal surface at the proximal end possesses a deep concavity on each side, and a convexity in the centre, which gradually dies away distally. The proximal lateral borders of the bone are much raised, especially on the preaxial margin. With this area (Pl. XXXIX, fig. 10, C), the splint-like small metacarpals were situated; their position is above the plane of the ulna, and in the same line as the radius. The small metacarpals are only preserved in fragments; the proximal end of one is lying in the concavity on the dorsal surface of the wing-metacarpal. It is a very small rod-like bone, with a little thickening at the articular end pre-postaxially, and a convex articular surface. Their number is not known.

The Pteroid.

The right pteroid (Pl. XXXVI, fig. 1, pt & Pl. XL, fig. 1) was lying parallel to the radius, with its proximal end overlapping (15 mm.) the radius and over the position of the lateral carpal. The last-named bone had become displaced. The pteroid is of the usual whip-like form. It has a flattened expansion at its proximal end, tapers to a point at the distal, is hollow, of small size, and a fourth of the length of the antebrachium. The dorsal border of the expansion is convex, the ventral is compressed and flat. The outer surface has produced longitudinal muscle striae; the inner is a very shallow concavity, in the centre of which is an oval foramen 9 mm. long and 4 mm. wide.

The Wing-Phalanges.

All the wing-phalanges are hollow. The portion preserved of the right first phalange (Pl. XL, fig. 2, W.ph.) is 330 mm. long. The general form of the bone is of the usual type. The proximal articulation is three times the diameter of that of the centre of the shaft. The articular surface for the ulnar metacarpal is concave, and extends along the ventral half of the bone. Immediately dorsal to this occurs the usual epiphysis, which is more pointed, and directed to the dorsal side, than in other forms. Lying externally to this, and occupying the space between it and the dorsal borders, there is a small and deep semicircular emargination (Pl. XL, fig. 2, sc.e.), bordering on the dorsal edge by an outgrowth of the bone, directed dorsally. In this a small rod-like bone (Pl. XL, fig. 2, s.b.) is placed and perhaps articulated. Both right and left wing-phalanges possess this bone. The proximal end of the right first wing-phalange preserved in the B.M. R/176 specimen has two small, rounded, splint-like portions of bones, abutting against the dorsal half of the articulation.

The Second Wing-Phalange.

The second wing-phalange (Pl. XXXVI, fig. 1, 2 w.ph.) seen in the Atherfield specimen No. 1 is not entire, on account of the missing section. Both articular ends are expanded. There is a great variation from the other wing-phalanges in the form of the shaft; the bone is triangular, the apex being on the dorsal border; the preaxial and ventral surfaces are concave (The latter more so than the former), and the postaxial convex. It soon passes into this form at the proximal end, and as quickly resumes the normal shape at the distal. This peculiarity is not occasioned by crushing. The bone is much thicker than in other parts of the skeleton.

The Third Wing-Phalange.

The portion recovered of this phalange (Pl. XXXVI, fig. 1, 3 w.ph) is 127 mm. long. It is convex dorsally and ventrally, and concave pre-postaxially.

The Fourth Wing-Phalange.

No trace of this wing-phalange has been found.

The Pelvic Girdle.

The Ischium.

The ischium (Pl. XL, fig. 6) is a deep, thin sheet of bone. The dorsal border is produced in front of the acetabulum. The posterior end sends up a spur, which comprises the lower portion of the posterior margin of the acetabulum. On the anterior ventral border of the plate of the ischium is a fissure determining the extent of the fused pubic bone. No foramen is discernible.

Prepubic Bone.

No prepubic bone has been discovered.

The Femur.

The femur (Pl. XL, fig. 7) is long, straight and slender. Both extremities are robust, and the median region of the shaft is attenuated. The head and neck are terminal to the shaft, and the former is hemispherical. There is a large trochanter and a deep trochanteric fossa.

The Tibia.

A portion of the proximal end of the right tibia (Pl. XXXVI, fig. 2, ti), 115 mm. in length, is lying with its postaxial border exposed, between the quadrates. The articular surface is moderately concave, with little elevation of its margins. The proximal end is moderately robust. The postaxial surface is concave, and the other surfaces are convex. The perfect bone probably almost equalled the femur in length. It is hollow, but the bone is thicker than the bones of the wing. Another portion of a limb-bone (Pl. XXXVI, fig. 2, ti), which I take to be also a part of a tibia, lies across the right quadrate and the proximal end of the right tibia. If it be the distal end of the same tibia, it must have been broken before petrification. There is no trace of a fibula.

Summary of the Characters.

Skull large, somewhat bird-like, cranium not arched longitudinally, no backward projecting occipital crest, occiput concave and reptilian, muzzle elongated. Length of skull = 560 mm.; mandibles = 420 mm. The alveolar border ends in front of the nares and 28 mm. behind the symphysis. Number of teeth, 24 in the upper, and 25 in the lower jaw, all lancet-shaped, compressed laterally, and interlocking. Posterior teeth

larger than the anterior. The last tooth of the upper jaw overlaps the lower, and last two of the lower fit into slots in the upper jaw. All the teeth are placed vertically. No rising of the alveolar rims. Anterior nares large, oblique, looking outwards, near the tip of the muzzle, and separated from the antorbital vacuity. The antorbital vacuity is the largest fossa in the skull, and not confluent with the orbits. Orbits very small and circular, and placed far back in the head. Orbital rim incomplete. No sclerotic ring. Infratemporal fossa oblique, extended both in front and behind the orbits. A sixth vacuity (infra-orbital) occurs under, and confluent with, the orbits. The beak, anterior to the nares, and the brain-capsule are the only portions of the skull that are completely encased in bone. Dorsal bar ridging nares and antorbital fossae, triangular, with no lateral expansion. The jugal is entirely separated from the supra-temporal arcade, and the jugal and quadratojugal from the infra-temporal arcade. The jugal forms merely a small moiety of the anterior border of the orbit, and is connate, at its lower extremity only, with the quadratojugal and quadrate. The jugal, quadratojugal, and quadrate are directed obliquely backwards; all connect with the maxilla. The quadrates articulate with the lower jaw, far in advance of the orbits, by plain pulley-joints. The lower temporal arcades are formed entirely by the quadrates. Length of symphysis = 70 mm. Six vertebrae in the notarium; no supra-neural plate. The transverse processes are free from each other; the anterior and posterior pairs are of the same length, the median shorter and smaller. Six free dorsal vertebrae. Sternum with a greatly developed bird-like keel, but no anterior spine-like projection. Little lateral expansion of the sternal plate. The coracoid articular facets overlap, and are prolonged on the lateral surface of the keel. Radial crest of the humerus spiral, and directed distally. Humeral articulation with the ulna a compact hinge-joint; with the radius a well-developed trochlear. Radius much smaller than the ulna, and extremely attenuated in the median region of the shaft. Radius decussating the ulna, passing from a ventral preaxial to a complete dorsal preaxial position. Head and neck of femur terminal.

III. Mechanism of the Skull and Joints and Movements of the Limbs.

The skull is beautifully adapted to combine strength with lightness. It is a mere framework of triangles, either in section, laterally, or at the base. It is constructed entirely on the cantilever principle. One end of the cantilever carries the beak and the other the brain-case, with the fulcrum at the mandibular articulation. The position of the teeth at the tip of the long jaws is mechanically bad, as with the tension on the back of the skull, exerted by the necessarily powerful neck-muscles, combined with the weight and strain of any large prey struggling in the jaws, the beak would tend to break midway between the tip and the fulcrum. To counter this, the premaxillar bar is triangular and the maxillae are band-like, with the wider diameter vertical. These bones are hollow, and are supported and braced by the maxillo-nasal bars. A long muzzle would seem to have been more favourable for procuring food. The use of the teeth at the extremity of such a beak would be great if the diet consisted mainly of fish and the smaller reptilia, and was seized in flight. The teeth are admirably fitted for that purpose, their interlocking gin-like arrangement being perfect for prehension, so much so that no prolongation of the occipital crest, as in *Ornithostoma (Pteranodon)*,¹¹ to permit of a greater development of the temporal muscles, was necessary. This was an adaptation for the same purpose by different means. Length of beak is seen in such birds as herons, storks, etc., which favour a like food, or as in the skimmer, *Rhynchops*, as mentioned by Dr. Eaton (*loc. Cit.*). That the reptile dipped occasionally in the water in pursuit of its prey is likely, but the 'power of swimming' which Buckland¹² thought that the Ornithosauria had, could not have been possible, for not only were the limbs included in the pteridium, but the elbow-joint only allowed a hinge-like movement dorso-ventrally, and the nature of the articulation of the carpus and the wing-metacarpal with the first wing-phalange precluded the backward motion required. The highly developed keel of the sternum proves the reptile to have been of very powerful flight, and it is interesting to recall the opinion of Hermann von Meyer¹³ with regard to the known Ornithosauria in 1859, that they could not have been migrating animals, because there was no keel. The evolution of the keel had been accomplished by the Wealden Period. The position of the coracoids in flight seems to have been at right angles to the keel, that is, with their articular ends on the coracoid facets of the keel opposite one to the other, and the scapulae articulating with the dorsal vertebrae. The arc-shaped coracoid articular facets on the keel appear not to have been solely for purposes of flight, for the semi-revolution would weaken rather than strengthen the act, but to allow of the coraco-scapular arch being drawn forwards. The free articular portion of the scapula at right angles to the coracoid moiety of the glenoid cavity probably gave rotating freedom to the humerus in an anterior-posterior direction, opposite to the supero-inferior movement in the act of flapping the wings. The ordinary saddle-shaped glenoid cavity permitted a much greater freedom of movement up and down, than from side to side; wherefore I suggest

that the additional surface was primarily evolved to allow of the humerus being directed forward parallel with the long axis of the body, by a slight twist of the wings. Such a position was necessitated and assumed when the reptile was hanging from a rock or bough. During suspension the coracoids would also be drawn forwards, until their sternal ends overlapped one above the other as the peculiar coracoid articulations permitted. Those forms possessed the coracoid articular facets looking 'dorsad and laterad' on an anteriorly-directed styliiform process were certainly not adapted for this purpose, unless crushing has altered their position and extent.

The elbow comprises a compact hinge-joint, with perfect rigidity while the limb was used in flight, and, when necessary, complete flexibility. The strong buttress of bone formed by the doubling-over of the dorsal border of the distal articular extremity of the humerus seems to have originated through the great stress here during flight. The oblique ridge-like epiphysis on the proximal articular surface of the ulna articulated in the valley below the buttress, its dorsal face rested and was held under the ventral wall of the buttress, protecting the joint from upward dislocation. The claw-like postaxial condyle of the humerus, placed against the facet of the postaxial side of the ulna, prevented outward displacement, and the V-shaped ridge on the preaxial moiety of the articular surface of the humerus precluded inward shifting. Any upward, outward, or inward thrust at the elbow would not under ordinary usage disturb the joint. No rotating movement of the elbow was possible. Although the radius decussates the ulna no pronation or supination such as occurs in man was possible, for the human radius crosses in an anterior, while that of *Ornithodesmus* does so in a posterior direction; neither does the radius cross so far that its distal end reaches the opposite side as in man, nor is any rotatory motion possible, for it articulated with the proximal carpal in a deep transverse groove. Moreover, its flat ventral surface rested upon a similar surface on the dorsal side of the ulna. Such a flexibility would weaken, not strengthen the wing for flight. This decussation afforded a strut or support in the downward flap of the immense wings.

The folding of the wing was performed by the help of the three joints of the wrist and that of the wing-metacarpal with the proximal phalange. By the particular form of the ulna articulation with the proximal carpal, the first joint had the power not only of a hinge-like motion dorso-ventrally, but also of a peculiar turn in a downward and backward direction. This was achieved by aid of the pit-and-ball articulation, and by the articulation of the postaxial articular surface of the ulna, on the ventral surface of that bone, with the raised ventral border of the proximal carpal. At the median joint (a trochlear) of the wrist the only movement possible was pre-postaxial, and thus the reverse of that of the elbow which was dorso-ventral. At the distal carpal and wing-metacarpal joint a rotatory motion was possible. On a turning and bending-back of the wing the two additional articular surfaces on these bones came into union, and continued the bend originated by the proximal joint of the wrist, in such a way that the carpus formed a sort of elbow enabling the wing-metacarpal and phalanges to take an upward position. By the aid of the distal wing-metacarpal and proximal phalange pulley-articulation, the distal portion of the wing could be carried at any inclination in a pre-postaxial arc. The arrangement of the first and second joints of the wrist prevented either inward or outward dislocation. In all the forms the wing has been made to bend posteriorly from the wing-metacarpal and the proximal phalange-joint, but this was not the case here. Dr. Plieninger¹⁴ considers that in *Rhamphorhynchus kokein* the chief articulation of the wing was less at the elbow and wrist, much more between the fifth metacarpal and the wing-finger phalange; and Prof. Williston¹⁵ thinks that in *Ornithostoma* there was very 'little movement in the wrist, considerable in the elbow, and very much in the shoulder.'

It would be interesting to know whether the robust longitudinal ridge (Pl. XXXIX, fig. 6, ri) on the ventral surface of the ulna, near the proximal end, occurs in many genera. Here, it appears, the biceps-tendon was attached, and not to the radius: for there is no tuberosity or cavity for its insertion apparent on the latter bone, if, indeed, it were not otherwise too weak to withstand the strain of flexing the lengthy limb with its patagium.

Both extremities of the ulna and the proximal end of the wing-metacarpal occupy the whole of the pre-postaxial diameters of the articulations, so that the wing was carried by the humerus, ulna, wing-metacarpal and phalanges, the radius only acting as a strut, and the small metacarpals and phalanges giving no assistance. Weak as are the small metacarpals, yet for all such purposes as suspension they would be sufficiently powerful to brace the manus in supporting the reptile, and their position, dorsal to the ulnar metacarpal, would be an aid to the grasp. Certain it is that the articulations of the wrist would permit the

wing, when not extended, to be not only bent backwards parallel with the body, but also twist in a posterior direction, freeing it from all interference with the action of the other metacarpals. Prof. Williston thinks that, if *Ornithostoma* 'hung in the upright position when at rest, it is difficult to see where the head was stowed away' (*loc. cit.*). In *Ornithodesmus* it would have been easy for the head to be placed over or under the brachium, or drawn by the retraction of the neck on to the shoulders with the skull held upwards.

The femur, with its terminal head and neck, could only be carried at right angles to the long axis of the body, and its inclusion in the patagium made impossible anything but a sluggish forward and backward motion in ambulation. The bending of the leg to reach the ground took place at the knee-joint in a lizard-like manner. In recent reptiles and mammals, where the thigh is carried at right angles to the body, the neck and head of the femur are terminal or nearly so; and in birds and mammals, where it takes a vertical position, they are more or less at right angles.

IV. Morphology and Comparisons with other Species.

The region between the snout and the occiput is highly modified, beyond all analogy with any known skull of the recent or fossil Reptilia. A straight dorsal outline of the beak is also found in *Pterodactylus*, *Campylognathus* (*sic*), *Rhamphorhynchus*, *Ornithostoma*, and *Nyctosaurus*. In this respect *Ornithodesmus* varies from *Dimorphodon* and *Scaphognathus crassirostris*, where the beak is boldly convex, and approaches *Sc. purdoni*, where the beak has only a moderate convexity and is much more elongated. The concave reptilian occiput also closely resembles that seen in this species, and reminds one vividly of the Lacertilia, as, for example *Lacerta ocellata* and *Varanus varius*, and the Rhynchocephalian *Hatteria punctata*.

The Nares.

The nares differ from those of other species in their greater area and close proximity to the extremity of the muzzle, although their position is posterior to the teeth. They are large, and situated near the end of the snout in *Dimorphodon*; but they are nearly vertical, and occur above the central lateral alveolar border. In *Scaphognathus crassirostris* they are smaller, and have the same inclination and position as in *Dimorphodon*. Like features obtain in *Sc. purdoni*, but they are further from the tip of the jaws, and by their continuation behind the teeth approximate to *Ornithodesmus latidens*. In *Rhamphorhynchus gemmingi* they are much reduced in dimensions, and terminate before reaching the last teeth. All these agree with *O. latidens* in having the nares separated from the antorbital fossae by a long bar. In *Pterodactylus antiquus*, *Pt. Kochi*, and *Pt. suevicus*, the nares occur some distance behind the teeth, and are confluent with the antorbital vacuities. In *Ornithostoma* and *Nyctosaurus* they are very small.

The Antorbital Vacuity.

The antorbital vacuity is greater in extent then, and dissimilar in form to, that of any other species.

The Antorbital Vacuity No. 2.

No Ornithosaur has anything approximating the remarkable infra-orbital fossa of *Ornithodesmus latidens*. The extraordinary transposition of the bones that form its boundaries gives it a unique character. Apparently the origin of this vacuity is the closing-in of the bones surrounding pear-shaped orbits, as in *Dimorphodon*, leaving an opening below the eyes; but the form of the bones and their positions are quite different. In the latter the jugal is V-shaped, forming the anterior and lower boundaries; and the quadratojugal is triangular, comprising a moiety of the posterior border, and uniting with the supra-temporal arcade, both bones being vertical.

The Orbit

In *Dimorphodon* and *Scaphognathus* the orbit is in front of the articulation of the quadrate with the mandible, and in *Pterodactylus*, *Ptenodracon* (Lydekker), *Rhamphorhynchus*, and *Nesodactylus* the orbit is above the articulation. It is posterior in *Ornithostoma*, but in *Ornithodesmus* it is, relatively, more so. In

the latter the orbit is widely removed from the anterior nares, which in *Ptenodracon* and *Ornithostoma* are in close proximity, much more separated, and still more than in *Rhamphorhynchus*, *Scaphognathus*, and *Dimorphodon*. A great peculiarity is the extraordinarily-small moiety of the orbit formed by the jugal, and also that this should be in the anterior margin only – not below and behind, as would have been supposed by analogy with other species. So far as I am aware, there is no skull recent or fossil which has anything conforming to this. In 1870 Owen¹⁶ remarked on the complete orbital rim, and that the lower border was mainly formed by the jugal. In *Ornithodesmus* the rays or runners thrown out by the jugal and quadratojugal over the infra-orbital vacuity apparently represent a vestige of the once complete orbit. The reduction in size and the alteration of the position of these bones have been caused by the elongation of the muzzle drawing these bones forward. In *Scaphognathus purdoni* the orbital fossa is the largest aperture in the skull, and the bones are arranged according to the plan of *Dimorphodon*. There is no closing-in of the bones that form their boundaries, but the modification which eventually produced this effect in *Ornithodesmus* was in progress.

The Supra-Temporal Vacuity.

The supra-temporal vacuity is greater in depth and more externally open even than in *Scaphognathus*, where it is deeper than in any other genus.

The Infra-Temporal Vacuity.

The extension of the infra-temporal vacuity, both anterior and posterior to the orbit, is another exceptional character. The nearest approach is found in *Pterodactylus antiquus*, where it lies obliquely below the hinder half of the orbits. It is interesting to note that it occurs before and beneath, but not behind, in the Dinosaur *Diplodocus*.

The Supra- and Infra-Temporal Arcades.

The exclusion of the jugal from the upper temporal arcade, the extension of the quadrate to the maxilla, and the squeezing-out of the jugal and quadratojugal thereby are surprising characteristics and isolate *O. latidens* from every known family. Hermann von Mayer¹⁷ described the jugal of *Pterodactylus longirostris* (syn. *Pt. antiquus*) as forming the under and greater part of the anterior boundary of the orbit by a strong, pointed, outgrowing process. In *Pt. scolopaceps* (syn. *Pt. kochi*)¹⁸ he gives an almost similar plan; and the jugal in *Pt. crassirostris*¹⁹ (syn *Scaphognathus crassirostris*) he describes as a four-branched bone forming the under half of the orbits. Thus there is no arrangement approaching to that which obtains in *Ornithodesmus latidens*; but *Scaphognathus purdoni* reveals at least an incipient stage. Mr. Newton²⁰ says that the jugal in this species is 'a V-shaped bone,' and that the hinder branch 'has its posterior edge occupied by the quadratojugal.' Dr. G. Baur,²¹ in some pertinent notes on Mr. Newton's paper, remarks that

'the tendency of the quadratojugal in *Scaphognathus* to separate the post-orbital from the jugal is very remarkable.'

This process of the exclusion of the jugal from the supra-temporal arcade is apparently an adaptive result. In *Ornithodesmus* the prolongation of the facial portion of the skull is about 5½ times that of the cranial, and in *Pterodactylus antiquus*, the nearest to it in shape, 3½ times; while in *Scaphognathus crassirostris* it is 1¾ times. This proportion in the two last-named permits of the vertical position of the jugal process, to meet the lachrymal; but in *Ornithodesmus latidens* the proportion of the length of the beak to that of the cranium is so much greater, that not only the jugal, but also the quadratojugal and quadrate have become elongated forwards, until the entire jugal, the greater part of the quadratojugal, and the quadrate are in front of the orbit. The posterior production of the maxilla to the quadrate has not originated this disposition of the jugal, for the position of the hinder extremity of the maxilla in *Pterodactylus* and in *Scaphognathus* is the same as in *Ornithodesmus*, namely, beneath the posterior third of the antorbital vacuity; and this is its location in *Pterodactylus antiquus*, *Pt. kochi*, *Pt. suevicus*, *Dimorphodon*, *Rhamphorhynchus*, and *Ornithostoma*: it cannot be directly for the reduction of the weight of the skull, for in *Dimorphodon* the maximum had almost been attained. It must be that the prolongation of the beak, which was more favourable to the reptile in procuring food, has drawn out and displaced the jugals, the quadratojugals, and

the quadrates, to the extreme. The great length of the lower temporal arcades in anterior-posterior extent is in striking contrast with their shortness in *Pterodactylus*, *Scaphognathus*, *Dimorphodon*, *Ptenodracon*, *Ornithostoma*, and *Nyctosaurus*.

The Maxilla.

In *Pterodactylus*, *Rhamphorhynchus*, *Ornithostoma* and *Nyctosaurus*, the jugal and quadratojugal intervene between the maxilla and the quadrate, or are situated in front of the articulation of these bones. In *Scaphognathus purdoni* both the jugal and the quadratojugal are some distance in advance of the articular end of the quadrate underlying the centre of the orbit, where the maxilla terminates. The quadratojugal is vertical and triangular, its comparatively-broad base completely shutting out the maxilla from the quadrate; but here is to be seen the initial stage of the union of the maxilla with the quadrate, which was finally attained in *Ornithodesmus latidens*.

The Nasal.

The nasals in *O. latidens* have on each exterior border of the sigmoidal ventral surface an eave-like edge, which is evidently the vestige of a once greater lateral expansion. In *Scaphognathus crassirostris* and *Dimorphodon macronyx* the nasals spread out as a roof over the antorbital fossae. In *Scaphognathus purdoni*²³ their extent has been thought uncertain, as the bone has come away from the areas of their positions. On a careful examination of the original specimen in the Museum of Practical Geology, Jermyn Street, London (now held at the BGS, Keyworth), I found that by the grooving and the direction of the striae on the underlying matrix, the plan of the bones could be made out. The areas in question were not only covered by portions of the nasals and prefrontals, but also by the anterior ends of the lachrymals; and the singular fact of the bone having come away from two such symmetrical areas appears to be accounted for by the outline being determined by the thickening and strengthening of the bones forming the upper boundary of the orbit, the antorbital fossae, and the dorsal ridge of the beak. The premaxillary bar is seen to be produced to the frontal, separating the nasals. Where the latter unite with the premaxillae a channel occurs. The nasals are comparatively large bones. The prefrontals by rising processes border the orbits and meet apophyses from the frontal, excluding the nasal from the orbits. The main portions of the prefrontals are wedge-shaped, and are produced forwards, terminating between the nasals and tongues sent out by the maxillo-nasal bars, on their union with the nasals. These maxillar processes are united ventrally to the anterior horns of the crescent-shaped lachrymals, which are situated in the upper corner of the antorbital vacuities, form moieties of the orbital rims, and meet the ascending branches of the jugals with their posterior horns. The fractured edges, and the markings on the matrix, appear to prove that the frontal does not reach as far as Mr. Newton suggests. He thinks that it separates the prefrontals from the orbits, but it does not apparently do this for more than 3 mm. anterior to the fracture. The nasals thus occupy their usual position interior to the prefrontals. Such being the case, they are situated as in *Scaphognathus crassirostris* and *Dimorphodon macronyx*.

The Quadratojugal.

The union of the quadratojugal with the maxilla, as has been pointed out by Dr. Baur²⁴, is a character of the Sauropoda: he instances *Diplodocus*. It is seen in the Ornithopoda, for *Iguanodon* reveals a like arrangement, and also in the Amphibians *Chelydosaurus vranyi* (Fritsch) and *Dendrerpeton pyriticum* (Frisch). The quadratojugals of *Dimorphodon macronyx* and *Scaphognathus purdoni* are triangular plates and placed vertically, and therefore differ from the quadratojugal of *Ornithodesmus latidens*. In *Rhamphorhynchus*, *Ornithostoma*, and *Nyctosaurus* they more or less approximate to this form.

The Quadrate.

Zittel²⁴ notes, as a character of the Pterosauria, that the inferior articular surface of the quadrate finishes in front of the middle of the orbit; thus, if we accept *Ornithostoma*, where it is slightly in front, *Ornithodesmus latidens* is quite peculiar. The manner of the proximal union of the pterygoids with the quadrates of the European forms is as yet obscure, but there is not much doubt that distally it is effected in both *Scaphognathus* and *Ornithodesmus* by means of a rod-like bar from the pterygoids. The plain pulley-articulation of *O. latidens* is very different from the spiral groove of *Ornithostoma* (*Pteranodon*).

The Teeth.

The arrangement of the hinder teeth is unique. Several of the teeth of the upper jaws of *Dimorphodon* and *Scaphognathus* overlap the lower jaws. The teeth of *Pterodactylus antiquus* and *Pt. suevicus* occur much in advance of the nares, whereas in *Ornithodesmus* the nasal opening begins near the last teeth. In the former genus the teeth are short and conical, thus differing from the lancet-shaped teeth of *Ornithodesmus*. These lancet-shaped teeth are vertically placed, set in the alveolar border with great regularity, and these conditions, combined with their complete interlocking constitute exceptional traits. The nearest approach is found in some of the fragments of jaws from the Cambridge Greensand that are included in the genus *Ornithocheirus*. In the type-specimen of *Scaphognathus purdoni* the alveoli appear to show that the teeth were slightly compressed laterally, and thus are nearer the dentition of *Ornithodesmus*.

The Notarium.

It is curious that in the process of development of a notarium *Ornithodesmus* should differ so much from *Ornithostoma* (*Pteranodon*). This is shown in the absence of the supra-neural plate and of the fusing of the extremities of the transverse processes by a band-like ossification. In *Ornithostoma* the scapular union took place on the supra-neural plate, and in *Ornithodesmus* on the fused neural spines. In the former, eight vertebrae comprise this compound bone; in the latter, six. In the former, the transverse processes of the first three vertebrae are fused with stout ribs; in the latter this feature is not seen. In *Ornithostoma* the transverse processes are of the same length; while in *Ornithodesmus* the median pair are shorter than the others. The reason of this is not apparent. The style-like process from the posterior side of the extremities of two of these may be an incipient stage of their fusion.

It appears from the notarium of *Ornithodesmus latidens* that the six anchylosed centra, described by H. G. Seeley as the sacrum of *O. clunivulus*²⁵, belong to the notarium. Whether they belong to the notarium or to the sacrum, they are specifically separated from the former by the following characters: the centra of the first and second vertebrae are comparatively flat and broad, with a pronounced longitudinal valley on the ventral surface of the third to the sixth, and the last four are broader and flatter than the first two. The valley is absent in *O. latidens*, and the ventral surface of all the vertebrae are convex from side to side and concave longitudinally.

The Sternum.

In *O. latidens* alone, among all known forms, is there a carina for the whole length of the sternum developed so highly, so arched, and with the lateral expansion so narrow, as to approximate very closely to the similar structure in birds. It would seem that the expansion of the lateral plates decreases, as in birds, in ratio to the height of the keel. In *O. latidens* the position of the coracoid facets differs from that seen in birds. According to Seeley²⁶, the articular surfaces 'obliquely overlap, practically as in wading birds like the heron.' In *Ardea cinerea* (*The Grey Heron*), as in all those birds that I have examined, whether in the fine series preserved in the Museum of the Royal College of Surgeons or elsewhere, the articular surfaces of the coracoids are situated not on the keel, but on the anterior border of the lateral expansion, and separated in nearly all forms one from the other by bone. They must necessarily be oblique, for the lateral expansions are also. In the heron the extreme inner angle of one coracoid decussates over the other, and both are wedged into the edge of the sternal plate in such a manner that they cannot move farther in an inward direction. Moreover, the articular surface is not produced beyond them, and thus absolutely prevents an inward, rotating movement past the keel. The only motion possible is an outward one, the sternal end of the coracoid sliding along in the articular groove, which has projecting edges to keep it in position. In *O. latidens* the mechanism is very different from that observed in *Ardea cinerea*. In lieu of an articulation in a straight line directed obliquely on the anterior margin of the sternal plate, we observe a semicircular free surface permitting an extraordinary rotation movement of the coracoids around the anterior edge of the keel on to its sides; also it was possible for the sternal ends of the coracoids to decussate completely, and not, as in herons, only the inner third of the articular surface, which does not extend the full width of the bone. Dr. Plininger²⁷ well shows how uncertain has been the knowledge of the exact position of the coracoid articulations; he points out that Goldfuss located them in two little fossae on the dorsal side of the sternum, and H. von Meyer, in *Pterodactylus*, in a similar place, on the ground or the

position of the coracoids. In *Ornithostoma*²⁸ and in *Nyctosaurus*²⁹ Prof. Williston says that they ‘look dorsad and laterad.’ The anterior process in both these genera projects in front of the sternum, and very close to that characteristic of the *Rhamphorhynchus* type, is therefore far removed from that of *O. latidens*. In the examples of the sternum from the Cambridge Greensand described by Seeley, the anterior outline of the anterior process is directed obliquely forward from the lateral expansions, not vertically as in *O. latidens*; and the form and position of the coracoid facets differ. Dr. Plininger³⁰ has well described the form of the sternum of both long- and short-tailed forms. It is quite evident from my description and the figures (Pl. XL, figs. 3, 4, & 5) of *O. latidens* that it is impossible to include it with either of these two types. In the type-specimen of *Scaphognathus crassirostris*³¹ the form of the sternum cannot be accurately determined, as it is lying under the flattened skeleton, and the aspect is therefore probably the dorsal. According to Hermann von Meyer³², the sternum appears as a broad rhomboidal shield with rounded ends. The sternum is not known in *Scaphognathus purdoni* or *Dimorphodon*.

All the specimens of other genera, where the sternum is well displayed, can be assigned without doubt either to the long- or to the short-tailed forms.

The keel of the sternum of Ornithosaurs has apparently a totally different morphological origin from that of birds. Most authors have thought that the anterior spine is homologous with the inter-clavicle; some aver its homology with the episternum of crocodiles and the manubrium of birds. The facts certainly appear to prove that it is the interclavicle, primarily of dagger-like shape, and occupying, with its posterior end, the ‘primordial cleft’ of the sternum, and that the coracoids rested directly on the dorsal surface of the spine with the scapulae arched in the primitive position towards the vertebral column. Under the influence of flight, the interclavicle became arched in front and gradually pushed backwards, until we find it in *Ornithodesmus* vertically at right angles to the lateral expansions, instead of on the same plane, and thus occupying the same position as the keel in birds. As the interclavicle bent posteriorly under the pressure, the coracoids worked their articular facets at first to look obliquely outwards and at last laterally, thus rendering possible movement from in front to the side, and bringing the free ends of the scapulae into conjunction with the neural spines of the vertebrae.

There are several examples of the interclavicle retracting in a forward direction, until but a vestige remains – caused mainly, I believe, by the action of swimming, the limbs with their backward thrust stimulating the forward thrust of the ends of the coracoids, until they unite, thereby squeezing out, as it were, the interclavicle. In the Ichthyosauridae the coracoids are in conjunction behind, and separated in front by the interclavicle; and in the Plesiosauridae the coracoids, with the exception of an anterior fissure, unite through the greater part of their length. They only require the keystone of the interclavicle, which undoubtedly in an earlier ancestor, at least, divided both the pre-coracoids and the coracoids. In the Nothosauridae the coracoids unite in the median line, without a cleft, the vestige of the interclavicle being found as a keystone at the united end of the clavicles, the ‘omosternum’ of Hulke. In birds the articulation of the coracoids on the grooved antero-lateral margins of the sternum is reptilian; while in Ornithosaurs it is on the interclavicle, which is neither reptilian nor avian, but Ornithosaurian, and a unique modification.

The Shoulder-Girdle.

Scapula and Coracoid.

In *Scaphognathus*, *Dimorphodon*, *Pterodactylus*, and *Rhamphorhynchus* the shoulder-girdle is more primitive than in *Ornithodesmus*, *Ornithostoma*, or *Nyctosaurus*, lacking the high specialization of these genera, and more or less retaining a splint-like form. Remarkable variation in detailed characters is found in species of the same genus, as for example, *Pt. suevicus* and *Pt. longicollum*. The main difference between *Ornithodesmus* and *Ornithostoma* and *Nyctosaurus* is the rather slender process in the two last-named described by Prof. S. W. Williston³³ as found in the inner angle of the fused bones enclosing the foramen. He mentions, too, that a similar process and foramen are seen in a Cambridge Greensand example described by Owen³⁴, who assigns this girdle to *Pterodactylus sedgwicki* (syn. *Ornithocheirus sedgwicki* Seeley sp.). Dr. Plininger³⁵ also notes its occurrence in *Pt. suevicus*. The foramen seen in these specimens is clearly the remnant of a cleft that once existed between this process and the girdle, and there

is much to be said for Prof. Williston's suggestion that it is 'possibly a vestigial clavicle.' It I understand correctly, the line of union between the scapula and the coracoid in *Ornithostoma* runs horizontally across the glenoid cavity. In that respect it is similar to *Ornithodesmus* and *Nyctosaurus*, and different from both these in the line being transverse and like a Cambridge Greensand example figured by H. G. Seeley³⁶.

The Humerus.

The great development and spiral curve of the deltoid crest distinguishes *Ornithodesmus* from all other genera. The only humeri that I can discover which have a somewhat similar spiral curve, although in not so great a degree, are those from the Lower Chalk of Bluebell Hill, Burham (Kent), in the British Museum (Natural History), and numbered respectively R/ 1935 and R/1357. The very high specialization of the distal end cannot be compared with that of any known genus. The distal end of Humerus R/37 in the same Museum approximates to it. Distal ends of humeri from the Cambridge Greensand, in the Sedgwick Museum, show it in an incipient degree. The German forms, where the distal end can be examined, possess a trochlear joint with the radial condyle greater than the ulnar.

The large circular foramen on the articular surface of the distal end of the humerus of *Ornithodesmus* is certainly very curious. Possibly a synovial gland was located here. It is represented by a pit or depression in *Ornithostoma*³⁷.

The Radius.

The remarkably reduced dimensions of the radius, when compared with the ulna, form a unique character. It is an interesting parallel modification with birds. The proximal articulation is more specialized, and consequently differs from the simple and almost flat face of the proximal end of the radius in other genera. Probably it will be found that the decussation of the ulna by the radius is not peculiar to *Ornithodesmus*. It certainly occurs among the Cambridge Greensand specimens. In the distal ends of the radius and ulna of *Pterodactylus compressirostris* from the Chalk Pit, Burham (Kent), which have been figured by Owen³⁸, the radius is seen decussating the ulna. On the first plate the ventral, and on the second the dorsal, surfaces of both bones are exhibited. Seeley³⁹ has called attention to the fact that the fossil in fig. 1, pl. xxiv of Owen's 'Cretaceous Reptilia' is 'figured for the humerus' and, further, that 'less well-preserved bone in that figure exhibits the ulna in its true position behind the radius': this, I think, should read 'the radius in its true position behind the ulna.' In view of the similarity of the humeri from the chalk-pit, there cannot be much doubt that they belonged to the genus *Ornithodesmus*. In the reconstruction of the hand of *Rhamphorhynchus kokeni* by Dr. Plieninger, the distal end of the radius is partly behind the ulna, but in all other figures of restorations the radius is placed at the distal end parallel with the ulna. These reconstructions have been made from specimens in which the bones are compressed and displaced.

The fact that proximally the radius is in front of (ventral to) the ulna has long been known. As the distal end of the radius gradually worked into a dorsal position, either the proximal carpal expanded dorsally for the new articulation (the ulna by expansion at the distal end taking the place of the former radial articular surface), or at one period the radius articulated with a separate carpal, which, under the same influence, followed the radius, and became fused on the original dorsal surface of what is now the one proximal carpal bone. The latter, I think, was the case.

The radius and ulna are not separated in the central region of their shafts, as in birds.

The Ulna.

The Ulna is more reduced in the median region of the shaft, more expanded at the extremities, and has more highly-specialized articulations than in any other known example. The proximal articulation is far removed from the trochlear joints of the European and American specimens; but some of the Cambridge Greensand specimens included in the genus *Ornithocheirus* exhibit it, although either in an incipient or in a degraded stage.

The Pteroid Bone.

Dr. Plieninger⁴⁰ says that, in the long-tailed forms, the pteroid is a short compressed rod, in the short-tailed forms slender and thin. *Ornithodesmus* possessed the type of the long-tailed forms. In *Nyctosaurus*⁴¹ the pteroid is greatly developed, and the proximal end on the lateral border has a wing-like projection at right angles to the shaft, which is not seen in *Ornithodesmus*.

As the question of whether the pteroid is the first digit or a separate ossification is still open, it will be as well to state what light is cast on the point by the study of *Ornithodesmus*. I have before stated that the proximal end was overlapping by 15 mm. the distal end of the radius. On its interior concave face there are signs of muscle-striae, while there are on the exterior surface lines converging proximally and apparently continued round the border of the bone, the whole appearance suggesting that the bone was affixed by muscular attachment. Moreover, the extreme proximal exterior surface is bevelled off, in such a manner that the edge is quite sharp; whereas, if articulating with the lateral carpal, it would at least be obtuse. The peculiar, large, oblong foramen on the inner surface is perhaps not pneumatic, but rather incomplete ossification for the adhesion of the investing tissue. Dr. Plieninger, in common with the majority of authors, believes the pteroid to be a turned-back thumb, as suggested by Herman von Meyer. I Agree with Prof. Williston (loc. supra. cit.), that it is 'an entirely distinct ossification': because, if we concede that it is the thumb thrown back, we must explain how such a modification was accomplished. The thumb would assuredly be the first digit that would be used in clinging to rocks or boughs for support, and thus would have no incentive to reflex, as it would be, on account of the wing, the nearest and best digit to set in action for the grasp. We must suppose that both the 'thrown-back thumb' and the wing-finger were included in the patagium, leaving the intermediate digits free; and, if the former were reflexed, why not the latter? or, if the wing-finger be the fourth finger, as it would be if the pteroid is not the thumb, why is not the fifth finger found reflexed, as the pull would be as great on the one as on the other? According to this theory, the so-called 'pteroide' described an arc, until its present position was attained. There is nothing to prove that the wing-membrane was anything more than a fringe (if that) down the preaxial border of the arm, and this would not provide the powerful stimulus for so extraordinary a change: the stress would be so insignificant, that it cannot be conceived how it would be necessary as a stay, or as a means of stretching the narrow frill of the wing. Nor, in the position in which it is always found, nearly parallel to the antebrachium, could it enlarge or stiffen the spread of the wing in flight. What, then, are the causes which by their action produced such an effect? We have good reason for looking upon the 'pteroide' as an ossified extensor-tendon: for the enormous disrupting strain on this sinew by the weight of the lengthening wing-digit, when cleaving the air in flight, would set up an irritation within the tendon itself, which would cause ossification to take place. Thus, naturally, the end of the ossification furthest away from the place of attachment of the tendon would have a pointed whip-like extremity, by the gradual lessening of the stimulus towards the shoulder.

The Carpus.

The general form of the carpals approximates to those from the Cambridge Greensand, and therefore to *Ornithostoma* and to *Nyctosaurus*; but, if there two are exactly similar to those of the Cambridge Greensand, then *Ornithodesmus* differs from them in sundry particulars.

The Metacarpals.

The length of the wing-metacarpal is intermediate between the long- and short-tailed forms. In no other *Ornithosaurus* yet discovered has the branching-out process on the postaxial border of the proximal articulation, with its separate articulation, been noted. The different figures of the type-specimens seem to show, and the restorations by various authors do exhibit, the small metacarpals parallel one to the other, as in all vertebrates, and not dorsal to the wing-metacarpal. I am convinced that, eventually, it will be proved that the latter was their position in many of the forms restored in the former way. I have found on the distal carpal specimens in the Sedgwick Museum the same articular surface for the small metacarpals as in *Ornithodesmus latidens*.

The Wing-Phalanges.

The much-reduced dimensions of the third phalange, compared with the second and first seem to suggest that the shortening of the distal phalange was proceeding here, as in the American forms. The second wing-phalange has evidently been reduced in size to the limit of lightness, and the form is best fitted to combine this with strength. The small rod-like bone (Pl. XL, fig. 2, s.b.), which apparently articulated within the semicircular cavity on the proximal end of the first wing-phalange, may be a remnant of the fifth metacarpal. In fact, the wing-digit has been formed by the union of the fourth and fifth phalanges, and the thickening found at both the proximal and the distal ends of the wing-phalanges is the vestige of that union. It is at these extremities that this would be found, if anywhere: for the lessening in size of the bones for reduction of weight would take place in the middle of the shafts, after the ankylosis of the extremities. By this interpretation the structure of the manus of the Ornithosaurus becomes simpler.

The Ischium.

The separation ventrally of the ischium from the pubis by a deep notch is not found in *Dimorphodon*, *Ornithostoma*, or *Nyctosaurus*, but agrees with that observed in *Pterodactylus*.

The Femur.

The terminal head and neck, the straightness of the shaft, its attenuation in the median region, and its length, separate the femur of *Ornithodesmus* from those of *Ornithostoma* and *Nyctosaurus*. In the two last-named the head and neck are placed at a slight angle to the shaft, which is shorter, stouter, and more curved than in the first-named. In the high development of the great trochanter it resembles *Ornithostoma*. The femur of *Rhamphorhynchus* differs in the robustness of the neck (which is nearly the same size as the head), in the divergence of the neck from the shaft, in the comparatively-massive build of the proximal end, and in the shortness of the bone.

The femur of *Pterodactylus* resembles that of *Rhamphorhynchus* in the thick neck being set at an angle to the shaft, and in the undeveloped condition of the great trochanter; but it differs from that genus and approaches *Ornithodesmus* in the straightness and length of the shaft. The same thickness of the neck and inclination of the shaft are found in *Dorygnathus*, and apparently in *Dimorphodon* and *Scaphognathus*; although in *Dimorphodon* these characters are not well seen, for the head of the femur is lying within the acetabulum, and in *Scaphognathus* it is not well preserved enough to determine with accuracy. The femur of *Ornithodesmus* is separated by its terminal neck and head from any known genus of the Ornithosauria, and reveals a higher specialization.

V. Conclusions and Classification.

It is more than probable that, if the type-skulls of *Scaphognathus crassirostris* and *Dimorphodon* were not crushed, they would be found to possess the lizard-like occiput of *Ornithodesmus*.

Although the general outline of the skull remains one of *Pterodactylus*, its structure differs quite fundamentally, for it is essentially similar to the plan of *Scaphognathus* and *Dimorphodon*. The separation of the nares from the preorbital fossae is found in each. These skulls were increasing in lightness by the enlargement of the vacuities, and the reduction of their elements into thin bands and rods. The outcome of this adaptation was the severance of the jugal from the supra-temporal arcade, which in its genesis is seen in *Scaphognathus purdoni* and in its accomplishment in *Ornithodesmus latidens*. The triangular form of the jugal in the former had become an attenuated hollow rod in the latter, producing an incomplete orbit and an infra-orbital vacuity. The separation of the jugal, quadratojugal, and quadrate one from the other had also begun. The shape of the alveoli in *Sc. purdoni* proves that the teeth were semi-elliptical, thus approximating to the laterally-compressed form of *Ornithodesmus*. A vestige of the overlap of the teeth of *Sc. crassirostris* and *Dimorphodon* is found in *Ornithodesmus* in the last teeth of the upper jaw. The foregoing facts are strong evidence that the skull of *Ornithodesmus* is the highly modified skull of *Scaphognathus*.

The confluent nares and preorbital fossae of *Pterodactylus* caused by the degradation of the maxillo-nasal bar, and the reduction in dimensions of all the apertures of the skull in *Rhamphorhynchus*, show that their structure became modified in a direction opposite to that followed by *Ornithodesmus*. It is generally conceded that the skull of the recent *Sphenodon punctatus* is near the primitive type of the reptilian skull: *Scaphognathus*, *Dimorphodon*, and *Ornithodesmus* have retained its perforated character, *Pterodactylus* less so, and *Rhamphorhynchus* and *Ornithostoma* least. The modifications proceeding in these skulls were radically at variance. In *Pterodactylus* the maxillo-nasal bar had almost, if not entirely disappeared. It is said to exist in some examples of *Pt. elegans* (syn. *Pt. pulchellus*, according to Zittel), which demonstrates what had degenerated in the other species. How much significance can be attached to the small fragment of bone, hanging from the ventral surface of the posterior end of the premaxillary extension over the preorbital vacuities, cannot be decided. Hermann von Meyer thought it a prefrontal, which Dr. Plieninger⁴² considers an attractive theory, but one that has yet to be proved. It may or may not be the vestige of the arch, but certain it is that the bars have disappeared or contracted. *Ptenodracon brevirostris*, a genus which must be included within the sub-order Pterodactyloidea, also retains the maxillo-nasal bas.

In *Rhamphorhynchus* the apertures were gradually closing in. In *Rh. longiceps*⁴³ the skull retained more of the open character than in any other species of this genus. The obliteration of the fossae had proceeded farthest in the skull of *Ornithostoma* and *Nyctosaurus* (syn. *Nyctodactylus*). In the latter the antorbital fossae had become quite vestigial⁴⁴. The tendency of most forms through time has been to reduce the size of the teeth, and lose the posterior dentition. In some species of *Rhamphorhynchus* the loss is seen to be in the reverse direction, commencing from the tip of the beak backwards. In *Ornithostoma* and *Nyctosaurus* the edentulous jaws prove that a final stage had been reached. Although there are only small moieties of the jaws to reason upon, I consider that the genera of the Cambridge Greensand belong to the Rhamphorhynchidae. In some the teeth were retained, but the beaks were growing more attenuated and lance-like. In others the muzzle was retracting axially, causing the tip to deepen vertically and thicken laterally (This point has since been found to be otherwise). The bold convexity of the dorsal outline and the depth of the beaks may suggest origin from *Scaphognathus*; but the extremely-light build of that skull could not have supported at its extremity so heavy a weight as the obtuse ponderous tip, without buckling. All these genera can be dismissed, as having no near affinity to *Ornithodesmus*. The latter is quite outside the genus *Ornithocheirus*: for, according to Seeley's amended definition of the genus, the characters are (i) teeth prolonged anterior to the muzzle, (ii) a longitudinal ridge on the palate. The typical dentigerous premaxillae of the Cambridge Greensand in the Sedgwick Museum, although belonging to several genera, have been included in the genus *Ornithocheirus*, and endowed with the characters obtained from the fragments of bone; and also, on the discovery of the edentulous jaw, *Ornithostoma* with those pertaining to the American toothless forms. Thus Prof. Williston⁴⁵ remarks that not much remains to be known of the osteology of *Ornithocheirus*; whereas, in reality, nothing is known except the tip of the snout. Again, Dr. Plieninger⁴⁶, following Williston, gives this classification:-

Family:	Ornithocheiridae . Orbit, preorbital, and nasal opening completely separated. Early dorsal vertebrae blended into the so-called notarium.
Sub-family:	Ornithocheirinae . Scapulae in union with the notarium. Sagittal crest to skull. Genera: <i>Ornithocheirus</i> . Toothed. <i>Pteranodon</i> . Toothless.

The only character obtained from the genus *Ornithocheirus* is 'toothed,' the family and sub-family characters are those of the genus *Ornithostoma* (*Pteranodon*).

Ornithodesmus is also generically distinct from *Ornithocheirus sagittirostris* (Owen)⁴⁷. The form of the teeth, the interspaces between them, their insertion in distinct alveoli with highly-raised rims, the length of the alveolar teeth, and the form of the rami, are quite different.

Ornithodesmus appears to have descended from a sub-order which should include *Scaphognathus* and *Dimorphodon*, necessitating the withdrawal of these two genera from the Rhamphorhynchidae, and the formation of a new sub-order.

The three entirely varied phases of development in the skulls of Ornithosauria give a ready means of division into three sub-orders, as follows:-

- Sub-Order: **Scaphognathoides.**
Skull an open framework of bone, all fossae very large. Nasal and preorbital vacuities separated. Concave lizard-like occiput.
- Sub-Order: **Pterodactyloidea.**
Half the area of the skull encased in bone, all fossae moderately large. Nasal and preorbital vacuities confluent. Convex bird-like occiput.
- Sub-Order: **Rhamphorhynchoidea.**
Skull nearly encased in bone, all fossae considerably reduced. Nasal and preorbital vacuities separated. Flat occiput.

In regard to the remainder of the axial and appendicular skeleton, the type-specimens are mostly crushed, fragmentary and so diversified in their nature, that the diagnosis of constant characters is rendered extremely difficult. The fusion of the dorsal vertebrae into a notarium is *Ornithostoma* and *Ornithodesmus* is absent in *Rhamphorhynchus*, *Pterodactylus* and all other known types. The anchylosed shield-shaped sacrum is permanent throughout the sub-order Rhamphorhynchoidea, *Ornithostoma* and *Nyctosaurus* being of this type. In many of the examples of *Pterodactylus* the form of the sacrum is not definitely determinable. If all follow the type of *Pt. suevicus*, they possess a sacrum approaching the fused shield-like sacrum of the Rhamphorhynchoidea. Whether the sacral ribs in *Scaphognathus*, *Dimorphodon*, and *Ornithodesmus* are free or blended is yet obscure. The number of vertebrae comprising the sacrum is variable. In the Rhamphorhynchoidea the sacrum is avian, shield-shaped, with anchylosed ribs; and in the Pterodactyloidea it is avian or reptilian, with ribs either free or anchylosed.

As fresh discoveries arise, we find that the division into long- and short-tailed groups is not a good one. *Scaphognathus crassirostris* has been placed in the long-tailed group by authors, as the wing-metacarpal is half the length of the antebrachium, and therefore *Sc. purdoni* has followed; but in neither is the tail known. Goldfuss restored the former with a short tail, and Zittel thought this correct. To the same sub-order Scaphognathoidea belong *Scaphognathus* with a short tail and *Dimorphodon* with a long; and to the Rhamphorhynchoidea, *Ornithostoma* and *Nyctosaurus* with a short tail, and *Rhamphorhynchus* with a long. In the Pterodactyloidea only short-tailed forms occur.

The form of the sternum in *Scaphognathus crassirostris* is uncertain, on account of the position and state of its preservation; and this element in *Sc. purdoni* and *Dimorphodon* is undiscovered. The sternum of *Ornithodesmus* is too highly specialized to provide any safe guide to the probable form of that bone in the two first-named genera.

The type of sternum of *Rhamphorhynchus*, with its strong anterior styliiform process possessing no true keel, and the sternal plate a broadly-expanded shield with square anterior borders, is not only common to this long-tailed genus, but also to the short-tailed *Ornithostoma* and *Nyctosaurus*, therefore invalidating this type of sternum as a peculiar feature of the long-tailed group. In *Pterodactylus*, as exemplified by *Pt. suevicus*, there is an anterior spine, but no true keel; and the sternal plate is semi-elliptical, with its anterior borders rounded.

The scapula and coracoid in the early genera of the Scaphognathoidea were not fused; but later they became so, as shown by *Ornithodesmus*, and in the Rhamphorhynchoidea by *Ornithostoma*. In the Pterodactyloidea no genus is known in which these bones are anchylosed.

The humerus is crushed in all type-specimens, and this may have had some effect in splaying out the deltoid crest: for probably in all it had originally a slightly inward curve. Such a curve is seen in a left humerus of *Ornithostoma* (*Pteranodon*)⁴⁸. In *Scaphognathus*, *Dimorphodon*, *Dorygnathus*, and *Pterodactylus* it spreads out as a wing from near the head of the bone. The two first-named have the superior border concave, and the two last-named convex and the wing deeper. In *Rhamphorhynchus*, *Ornithostoma*, and *Nyctosaurus*, the deltoid crest is placed near the proximal end of the humerus; it rapidly constricts, and broadens at the tip into a deeply-obtuse extremity. In *Ornithodesmus* it arises from below, and curves spirally downwards. We have thus four well-marked types. The species which come within these types are:-

Type of Scaphognathus:	Type of Pterodactylus :	Type of Rhamphorhynchus :	Type of Ornithodesmus :
<i>Sc. purdoni</i> (?) <i>Dimorphodon maxronyx</i> .	<i>Pt. antiquus</i> . <i>Pt. suevicus</i> . <i>Pt. longicollum</i> . <i>Pt. elegans</i> (syn <i>Pt. pulchellus</i>). <i>Pt. spectabilis</i> . <i>Pt. medius</i> . <i>Campylognathoides zitteli</i> . <i>Dorygnathus banthensis</i> . <i>Ptenodracon brevirostris</i> (?)	<i>Rh. gemmingi</i> . <i>Rh. muensteri</i> . <i>Rh. kokeni</i> . <i>Ornithostoma ingens</i> . <i>Nyctosaurus gracilis</i> .	<i>O. latidens</i> . <i>O. clunicultus</i> (?). Humeri from the Lower Chalk of Burham (Kent) in the British Museum (Natural History).

The *Scaphognathus* type differs from the *Ornithodesmus* type: for the reason that we behold in *Scaphognathus* the beginning, and in *Ornithodesmus* the end, of a high specialization; to the same cause is probably due the fact that the deltoid crest of the humerus of *Campylognathoides* and *Dorygnathus* are closer to the *Pterodactylus* than to the *Rhamphorhynchus* type.

The bicapital crest of the early forms is prominently produced outwards, and in the later very much reduced: for example, in the Scaphognathoidea, *Scaphognathus* and *Ornithodesmus*; in the Rhamphorhynchoidea, *Rhamphorhynchus* and *Ornithostoma*.

All these genera, so far as can be discerned, possess trochlear joints at the distal articulation of the humerus, and nothing approaching the complicated specialization of this joint in *Ornithodesmus*.

The equal dimensions of the ulna and radius in the early examples did not persist; the radius gradually became smaller, especially in the central region of the shaft. The proximal articulatory surface of the radius evolved from a general flat area to two concavities divided by a ridge, for the trochlear surface of the humerus. The distal articulation remained a simple pulley.

The decussation to the ulna by the radius will probably prove to be common to more than one genus: for instance, in some of the Cambridge Greensand, Chalk, and American genera.

The foramen which pierces the ischio-pubic plate of most species does not occur in *Ornithodesmus*.

The pre-pubic bones of *Scaphognathus* and *Ornithodesmus* were probably spatulate, as in *Dimorphodon*. If so, they differ from the fan-shaped form characteristic of *Pterodactylus*, and from the curved band-like form seen in *Rhamphorhynchus*, *Ornithostoma*, and *Nyctosaurus*.

The terminal head and neck of the femur and the straight shaft in *Ornithodesmus* separate it from all other genera, where the head and neck are more or less inclined away from the shaft, which was more or less curved. In late forms the greater trochanter became very robust.

The bones of the foot in most of the type-species are either imperfectly preserved, or not discovered.

The widely-divergent characters of *Ornithodesmus* from all known types make it necessary to form a new family, the Ornithodesmidae. I offer, as best denoting our present knowledge, the following classification:-

I. Sub-Order: Scaphognathoidea

Skull short, not produced into a rostrum. Jugal V-shaped, and united with the supratemporal arcade. Dorsal vertebrae not fused into a notarium. Sacral ribs not ankylosed. Long or short tail. Deltoid crest of humerus wing-like, with the superior border concave. Wing-metacarpal shorter than half of the forearm. ? Pre-pubic bones spatulate.

Sub-Family: Scaphognathinae.

Short tails.

Genus: *Scaphognathus*.

Sub-family: Dimorphodontinae.

Long tails.

Genus: *Dimorphodon*.

Family: Ornithodesmidae.

Skull elongated. Six lateral fossae present. Orbits incomplete. Jugal separated from the upper, and the jugal and quadratojugal from the lower, temporal arcades. Maxilla united with the quadrate, without the intervention of the jugal or the quadratojugal. The last tooth of the upper jaw overlaps the lower jaw, and the last two of the lower jaw fit into slots in the upper. Notarium present, consisting of six vertebrae. No supra-neural plate. The first and last pair of transverse processes are equal in length, the median pair shorter, all distally unanchylosed. Sternum with a large median keel, no anterior spine-like projection, a small lateral expansion of the sternal plate, coracoid articular end facets overlapping each other and prolonged on to the lateral surface of the keel. Deltoid crest of humerus spiral. Radius decussating the ulna distally. Wing-metacarpal equal in length to half of the forearm.

Genus *Ornithodesmus*.

Nares posterior to all teeth. Orbits far behind the quadrato-mandibular articulation. Teeth lancet-shaped, compressed laterally, vertically placed, set with great regularity in the alveolar border, showing little variation in size, interlocking. Six free dorsal vertebrae. Humeral articulation with the radius a well developed trochlear, with the ulna a highly-specialized hinge joint dorsal to the radius. Shaft of radius very attenuated. Small metacarpals articulating with the carpus dorsally to the wing metacarpal. Neck and head of femur terminal, shaft straight.

II. Sub-Order: **Pterodactyloidea**

Half the area of the skull encased in bone, all fossae moderately large. Nasal and preorbital vacuities confluent. Convex bird-like occiput.

Family: Pterodactylidae

Skull bird-like, with a long or short muzzle. Dorsal vertebrae not fused into a notarium. Sacral ribs free (*Pt. antiquus*) or anchylosed (*Pt. suevicus*). Tail short. Sternum semi-elliptical, with an anterior spine. Scapula and coracoid separate. Humeral crest wing-like, with the superior border convex. Wing-metacarpal greater than half the length of the ulna. Pre-pubis bones fan-shaped.

Genus: *Pterodactylus*.

Sub family: Ptenodraconinae

Skull short. Preorbital and nasal vacuities separate.

Genus: *Ptenodracon*.

III. Sub-Order: **Rhamphorhynchoidea**

Skull nearly encased in bone, all fossae considerably reduced. Nasal and preorbital vacuities separated. Occiput flat.

Family: Rhamphorhynchidae.

Skull without a supraoccipital crest. Jaws toothed. Dorsal vertebrae not fused into a notarium. Sacrum a shield-shaped anchylosed mass, with foramina. Long-tailed. Sternum rhomboidal, anterior spine, no keel. Deltoid crest of humerus constricted medially. Wing-metacarpal less than half the length of the ulna. Pre-pubic bones band-like and curved.

Genera: *Dorygnathus*

Campylognathoides

Rhamphocephalus

Rhamphorhynchus

Family: Ornithostomatae.

Skull with prominent supra-occipital crest. Jaws edentulous. Short-tailed. Scapula articulating with the notarium. Wing metacarpal longer than the ulna.

Genus: *Ornithostoma* (*Pteranodon*)

Sub-Family: Nyctosaurinae.

No supra-occipital crest to skull. Edentulous. Tail short. Scapula not articulating with the early dorsal vertebrae.

Genus: *Nyctosaurus* (*Nyctodactylus*) No antorbital vacuity.

Family: Ornithocheiridae.

Longitudinal ridge on the palate.

Sub-Family: Ornithocheirinae.

Teeth prolonged anterior to the palate.

Genus: *Ornithocheirus*.

Footnotes

1. 'Catal. Foss. Rept. & Amph. Brit. Mus.' Pt. 1 (1888) p. 24.
2. According to Owen's determination, the type-specimen of *Ornithocheirus nobilis* (*Pterodactylus* Owen) is a part of the second phalange of the wing-finger, but one of the specimens to be reviewed proves it to belong to the central region of the shaft of the ulna.
3. Phil. Trans. Roy. Soc. 1887 (1888) ser. B, vol. clxxix, pp. 510-11.
4. R. W. Hooley, Q. J. G. S. vol. lxiii (1907) pp. 50-63 & pls. ii-iv.
5. E. T. Newton, Phil. Trans. Roy. Soc. 1887, ser. B, vol. clxxix (1888) p. 506.
6. 'Dragons of the Air', 1902, fig. 66 & p. 173.
7. 'Dragons of the Air', 1902, fig. 67 & p. 175.
8. For the guidance of future students of this specimen, I may mention that this area of the right ulna was accidentally excavated too much when the bones which covered it were being freed from the matrix.
9. A before mentioned, the bones of the Atherfield specimens are equal in size.
10. S. W. Williston, 'Restoration of *Ornithostoma* (*Pteranodon*)' Kansas Univ. Quart. Ser. A, vol. vi (1897) p. 51.
11. G. F. Eaton, Mem. Connect. Acad. Arts & Sci. vol. ii (1910) p. 13.
12. W. Buckland, Bridgewater Treatise No. 6, vol. I, 3rd ed. (1858) p. 218.
13. C. E. H. von Meyer, 'Reptil. Aus dem Lithogr. Schiefer d. Jura' 1860, p. 17.
14. F. Plieninger, 'Die Pterosaurier der Jura Schwabens' Palaeontographica, vol. liii (1907) p. 208.
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Recent classification Compared.

S. W. Williston ⁴⁹	Felix Plieninger ⁵⁰
Sub-Order: Pterodactyloidea.	Sub-Order: Pterodactyloidea.
Family: Ornithocheiridae.	Family: Pterodactylidae.
Sub-Family: Ornithocheirus.	Genus: <i>Pterodactylus</i> .
Genera: <i>Ornithocheirus</i> <i>Pteranodon</i> (<i>Ornithostoma</i>)	Family: Ornithocheiridae.
	Sub-Family: Ornithocheirinae.
	Genera: <i>Ornithocheirus</i> . <i>Pteranodon</i> .
	Sub-family: Nyctosaurinae.
	Genus: <i>Nyctosaurus</i> (<i>Nyctodactylus</i>).
	Sub-Order: Rhamphorhynchoidea.
	Family: Rhamphorhynchidae.
	Genera: <i>Dimorphodon</i> . <i>Campylognathoides</i> . <i>Dorygnathus</i> . <i>Scaphognathus</i> . <i>Rhamphorhynchus</i> .

R. W. Hooley.

Sub-Order: Scaphognathoida.	Sub-Order: Rhamphorhynchoidea.
Family: Scaphognathidae.	Family: Rhamphorhynchidae.
Genus: <i>Scaphognathus</i> (Wagner.)	Genera: <i>Campylognathus</i> (Plieninger.) <i>Dorygnathus</i> (Theodori.) <i>Rhamphorhynchus</i> (Meyer.) <i>Rhamphocephalus</i> (Seeley.)
Sub-Family: Dimorphodontidae.	
Genus: <i>Dimorphodon</i> (Owen.)	
Family: Ornithodesmidae.	Family: Ornithostomatidae.
Genus: <i>Ornithodesmus</i> (Seeley.)	Genus: <i>Ornithostoma</i> or <i>Pteranodon</i> (Seeley.) (Marsh.)
Sub-Order: Pterodactyloidea.	
Family: Pterodactylidae.	Sub-family: Nyctosaurinae.
Genus: <i>Pterodactylus</i> (Cuvier.)	Genus: Nyctosaurus or Nyctodactylus (Marsh.)
Sub-Family: Ptenodraconidae.	
Genus: <i>Ptenodracon</i> (Lydekker.)	Family: Ornithocheiridae.
	Sub-Family: Ornithocheirinae
	Genus: Ornithocheirus (Seeley.)

VI. Measurements in Millimetres.

Breadth of the muzzle 25 mm. from the tip	40
Depth of the same at the same point.....	40
Breadth of the skull at the centre of the upper border of the orbits.....	36
Breadth of the skull at the posterior end of the maxilla.....	99
Depth at the same point.....	83
Breadth of the cranial roof between the supra-temporal pits.....	16
Breadth of the skull between the centres of the squamosal bars.....	90
Greatest breadth of the brain -capsule.....	58
Depth of the supra-temporal pits from the cranial roof to the squamosal bar.....	35
Depth of the occiput, summit to lowest outer angle of quadrate.....	62
Width of the occiput across the foramen magnum.....	73
Commencement of anterior nares from the tip of the beak.....	95
Breadth at the same point.....	9
Breadth at 140 mm. from the tip of the muzzle (line of fracture).....	20
Vertical diameter of the orbits.....	30
Anterio-posterior diameter.....	38
Length of the infra -orbital vacuities.....	80
Greatest breadth of the same.....	12
Length of the infra-temporal vacuities.....	95
Breadth of the same.....	17
Distance of the quadrate articulation in front of the orbits.....	99
Depth of the same below the dorsal outline of the beak.....	89
Depth of the palate, below the dorsal outline of the beak, 51 mm. from the anterior border of the nares.....	28
Height above the ventral edge of the mandibles when the jaws are closed, 51 mm. from the anterior border of the nares.....	26
Length of the alveolar tract of the upper jaw.....	85
Length of the alveolar tract of the lower jaw.....	94
Length of the anterior teeth.....	8
Greatest breadth of the same.....	4
Length of the posterior teeth.....	7
Greatest breadth of the same.....	7
Length of the mandibular symphysis.....	70
Length of the centrum of the cervical vertebra.....	53
Width between the exterior borders of the prezygapophyses of the same.....	40
Width between the exterior borders of the postzygapophyses of the same.....	48
Length of the dorsal edge of the notarium.....	110
Length of the ventral edge of the same.....	105
Length of the centrum of the first dorsal vertebra.....	14
Length of the scapula, from the glenoid cavity.....	90
Depth of the distal end of the same.....	23
Pre-postaxial diameter of the scapula ; humeral end.....	40
Ditto: coracoid.....	33
Length of the coracoid.....	113
Antero-posterior diameter of the sternal end of the coracoid.....	27
Ditto: centre of shaft.....	6
Length of the humerus (proximal to distal condyle).....	220
Pre-postaxial diameter of the proximal end of the same.....	51
Ditto: centre of shaft.....	22
Ditto: of the distal end.....	64
Spiral curve of deltoid crest begins below the proximal articulation of humerus.....	40
Length of the same along its outer curve.....	75
Depth of the same from the distal point to the shaft of the humerus.....	27
Pre-postaxial diameter at the proximal end of the radius.....	30
The same at the distal end.....	38

The same at the centre of the shaft.....	7
Pre-postaxial diameter of the proximal end of the ulna.....	60
The same at the distal end.....	52
The same at the centre of the shaft.....	19
Length of the pteroid.....	96
Breadth of expansion at the proximal end of the pteroid.....	10
Length of the lateral carpal.....	25
Pre-postaxial diameter of the proximal carpal.....	49
Pre-postaxial diameter of the distal carpal.....	43
Length of the carpus.....	28
Pre-postaxial diameter of the proximal end of the wing-metacarpal.....	56
Length of portion of proximal end of the first wing-phalange, Atherfield specimen No.2...	318
Dorso-ventral diameter of the proximal end.....	54
Dorso-ventral diameter of the distal end.....	44
Dorso-ventral diameter of the proximal end of the second wing-phalange.....	44
Length of the portion of the third wing-phalange, Atherfield specimen No. 1.....	127
Length of the sternal plate.....	65
Breadth of the same.....	45
Length of the keel.....	70
Depth of the same.....	60
Depth of the ischium from the acetabulum to the anterior ventral angle.....	76
Length of the femur as preserved. (distal end slightly water worn, but showing thickening for the articulation.).....	200
Pre-postaxial diameter of the centre of the shaft of the femur.....	9
Dorso-ventral diameter of the same.....	12

The following measurements have been obtained by accepting 89 mm. as the length of the missing block from Atherfield specimen No. 1:-

Length of the skull.....	500
Length from the tip of the muzzle to the centre of the orbits.....	500
Length of the mandibles.....	423
Length of the radius.....	368
Length of the ulna.....	381
Length of the first wing-phalange.....	393
Length of the second wing-phalange.....	388

Estimated spread of wing, from tip to tip, and allowing for the natural curve.....about 5 metres.

I have much pleasure in acknowledging the ever-ready assistance in the preparation of this paper afforded to me by Dr. A. Smith-Woodward, F.R.S., and Dr. C. W. Andrews, F.R.S.

Bibliographies are to be found in:-

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K. A. Zittel, 'Traité de Paléontologie' vol. iii (1893).

F. Plieninger, 'Die Pterosaurier der Juraformation Schwabens' palaeontographica, vol. liii (1907) pp. 210-17.

Ptenodracon (Lydekker 1888) mentioned in the text has been reclassified as a juvenile Pterodactylus.

Explanation of plates XXXVI-XL.

Plate XXXVI

[The right-hand block in figs. 1 and 2 is here exhibited with the matrix removed at a different angle from the other block. This block requires a half-turn to put the proportions thereon in their true connexion with those on the other block.]

Fig. 1. Upper view of Atherfield specimen No.1, partly cleared matrix:

Sn., snout;
pr.b., premaxilla bar;
no., dorsal border of the notarium;
rb., rib;
hu.r., distal end of right humerus;
r.r., right radius;
u.r., right ulna;
hu.l., distal end of left humerus;
r.l., left radius;
u.l., left ulna;
p.cp., Proximal carpal;
pt., pteroid;
la.cp., lateral carpal;
w.mc., wing-metacarpal;
mc., portion of one of the small metacarpals;
1.w.ph., distal end of the first wing-phalange;
2.w.ph., second wing-phalange;
3.w.ph., proximal half of the third wing-phalange;
B.M. R/3877. x about 7/24.

Fig. 2. Nether view of Atherfield specimen. No. 1, partly cleared of matrix:

Sn., ventral view of snout;
mx.p., inner view of maxillo-nasal process;
mn., portion of the mandible;
Q.r., portion of right quadrate;
Q.l., portion of left quadrate;
c.v., cervical vertebrae;
no., notarium;
d.v., dorsal vertebrae;
h.r., right humerus;
u.r., right ulna;
hu.l., left humerus;
r.l., left radius;
u.l., left ulna;
sc. scapula;
p.cp., proximal carpal;
d.cp., distal carpal;
l.cp., lateral carpal;
w.mc., proximal end of wing-metacarpal;
Isch., Ischium;
f., femur;
ti., portion of tibia.
B.M. R/3877. x about 7/24.

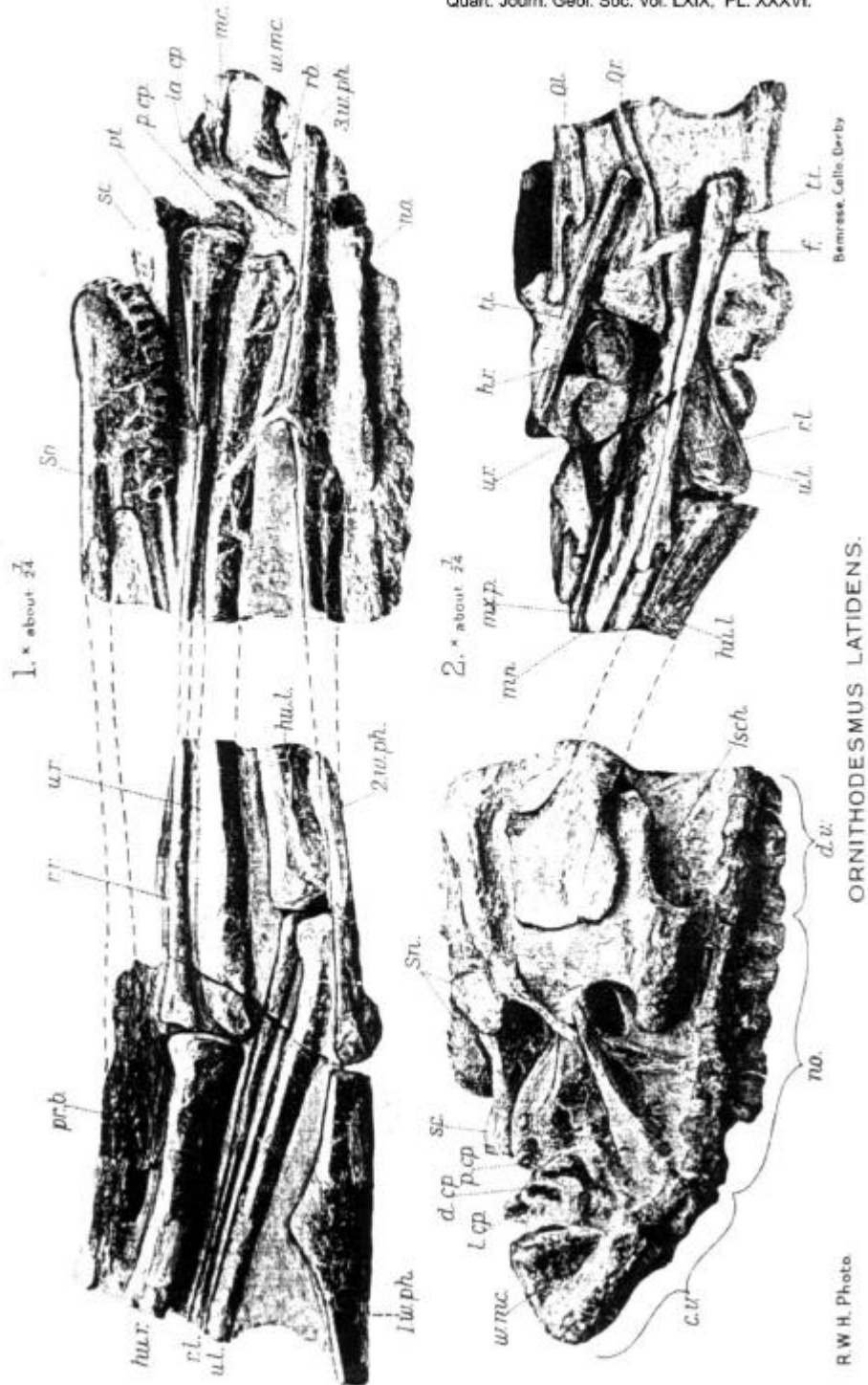
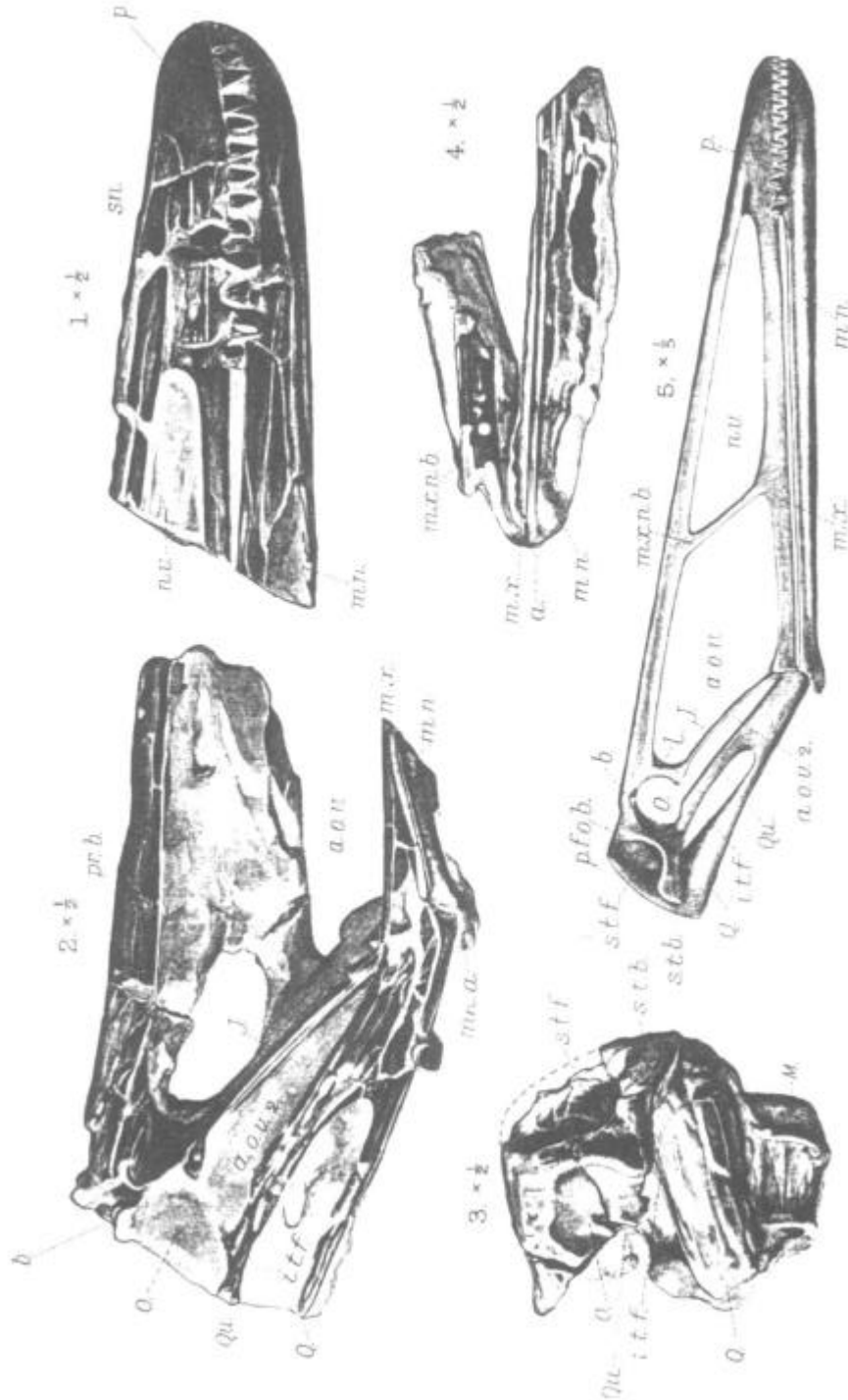


Plate XXXVII

- Fig. 1.** Sn., the snout, freed from matrix:
p., Premaxilla;
n.v., nasal vacuity;
mn., mandible.
 B.M. R/3877. x ½.
- Fig. 2.** Portion of the skull near the orbit:
O., orbit;
a.o.v., antorbital vacuity;
a.o.v.2., antorbital vacuity No. 2;
i.t.f., infra-temporal fossa;
pr.b., premaxillar bar;
J., jugal; *Qu.*, quadratojugal;
Q., quadrate;
mx., maxilla;
mn., mandible; *mn.a.*, mandibular articulation;
b., rounded boss of bone;
 B.M. R/3877. x ½.
- Fig. 3.** Left lateral aspect of the hinder portion of the cranium, as preserved in B.M. R/176:
O., orbit;
s.t.f., supra-temporal fossa;
i.t.f., infra-temporal fossa;
s.t.b., supra-temporal bar;
Qu., quadratojugal; *Q.*, quadrate;
M., matrix with a fragment of limb bone. x ½.
- Fig. 4.** Interior view of the right maxillo-nasal process:
mx.n.b., part of the maxillo-nasal bar;
mx., maxilla;
a., line of division between the upper and the lower jaw;
 B.M. R/3877. x ½.
- Fig. 5.** Restoration of the skull, perspective lateral view:
n.v., nasal vacuity;
a.o.v., Antorbital vacuity;
a.o.v.2., antorbital vacuity No. 2;
o., orbit;
s.t.f., supra-temporal fossa;
i.t.f., infra-temporal fossa;
p., premaxilla;
mn., mandible;
mx., maxilla;
mx.n.b., maxillo-nasal bar;
J., jugal;
Qu., quadratojugal;
Q., quadrate;
s.t.b., supra-temporal bar;
p.f.o.b., post-fronto-orbital bar;
l. lachrymal;
b., rounded bass of bone; x. 1/5.



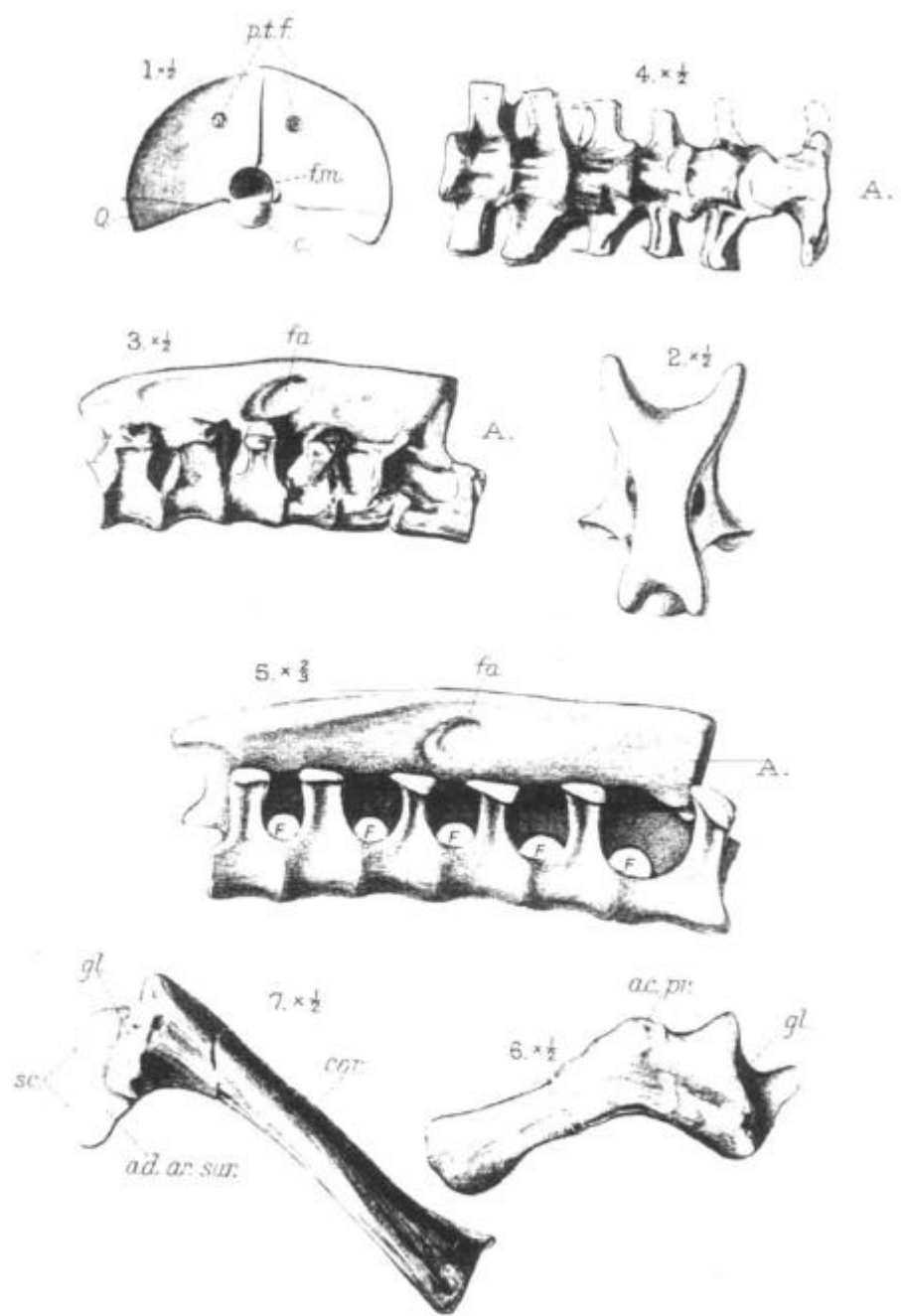
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Plate XXXVIII

- Fig. 1.** Restoration of the occiput:
p.t.f., Post-temporal fossa; *f.m.*, foramen magnum;
c., occipital condyle; *Q.*, quadrate; x ½.
- Fig. 2.** Restoration of a cervical vertebra, ventral view. x ½.
- Fig. 3.** Right lateral view of the notarium:
fa., the supposed articular facet for the scapula;
A., anterior end.
B.M. R/3877. x ½.
- Fig. 4.** Ventral view of the notarium:
A., anterior end; x ½.
- Fig. 5.** Restoration of the notarium, right lateral aspect:
F,F, foramina;
fa., facet for the scapula;
A., anterior end; x 2/3.
- Fig. 6.** Inner view of the left scapula, *minus* a moiety of the humeral end:
gl., glenoid cavity;
ac.pr., acromion process.
B.M. R/3877. x ½.
- Fig. 7.** Humeral end of the right scapula and perfect coracoid:
sc., proximal end of scapula;
cor., coracoid;
gl., glenoid cavity;
ad.ar.sur., additional articular surface, placed at right angles to the glenoid cavity.
B.M. R/3878. x ½.



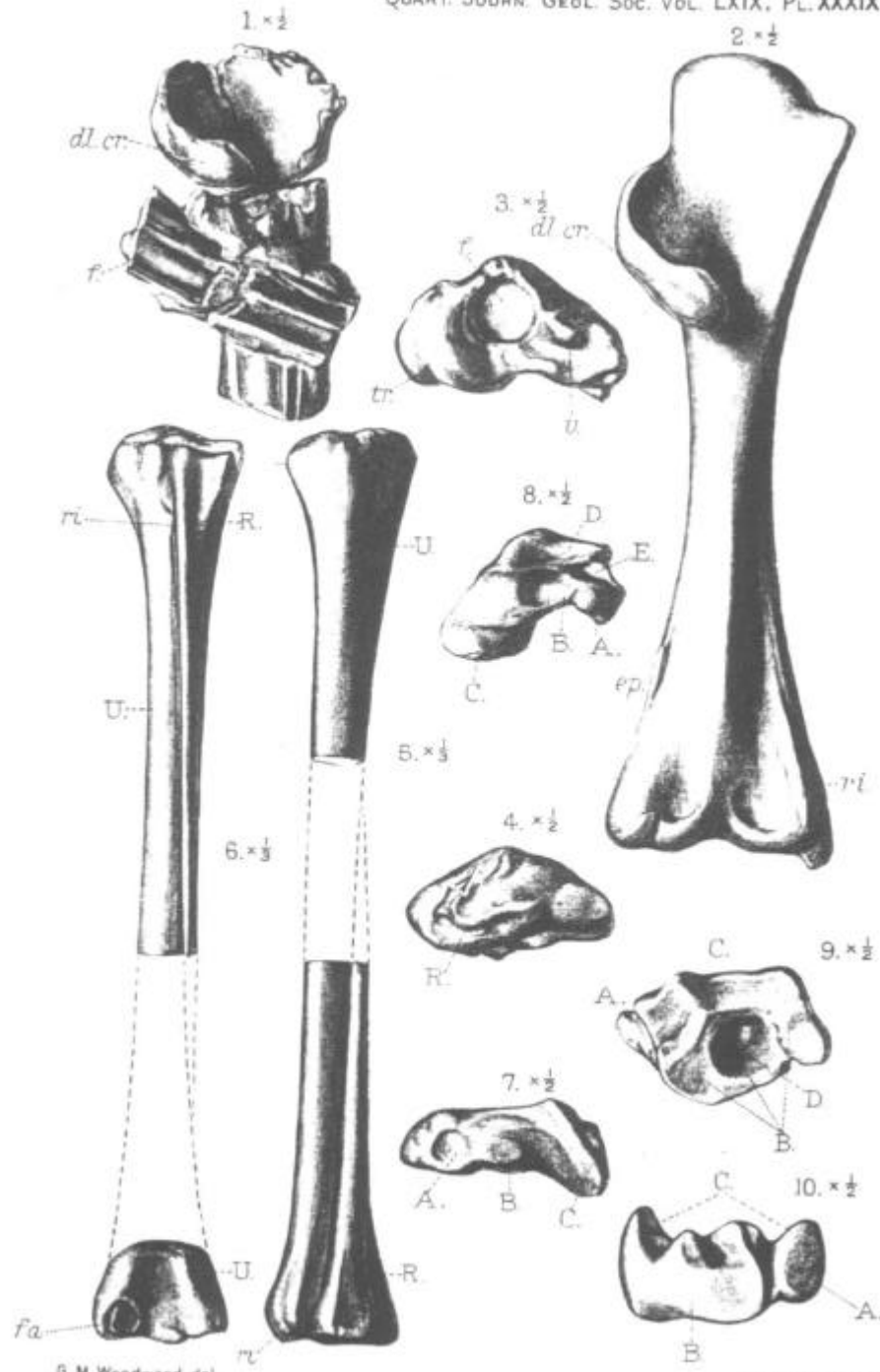
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Plate XXXIX

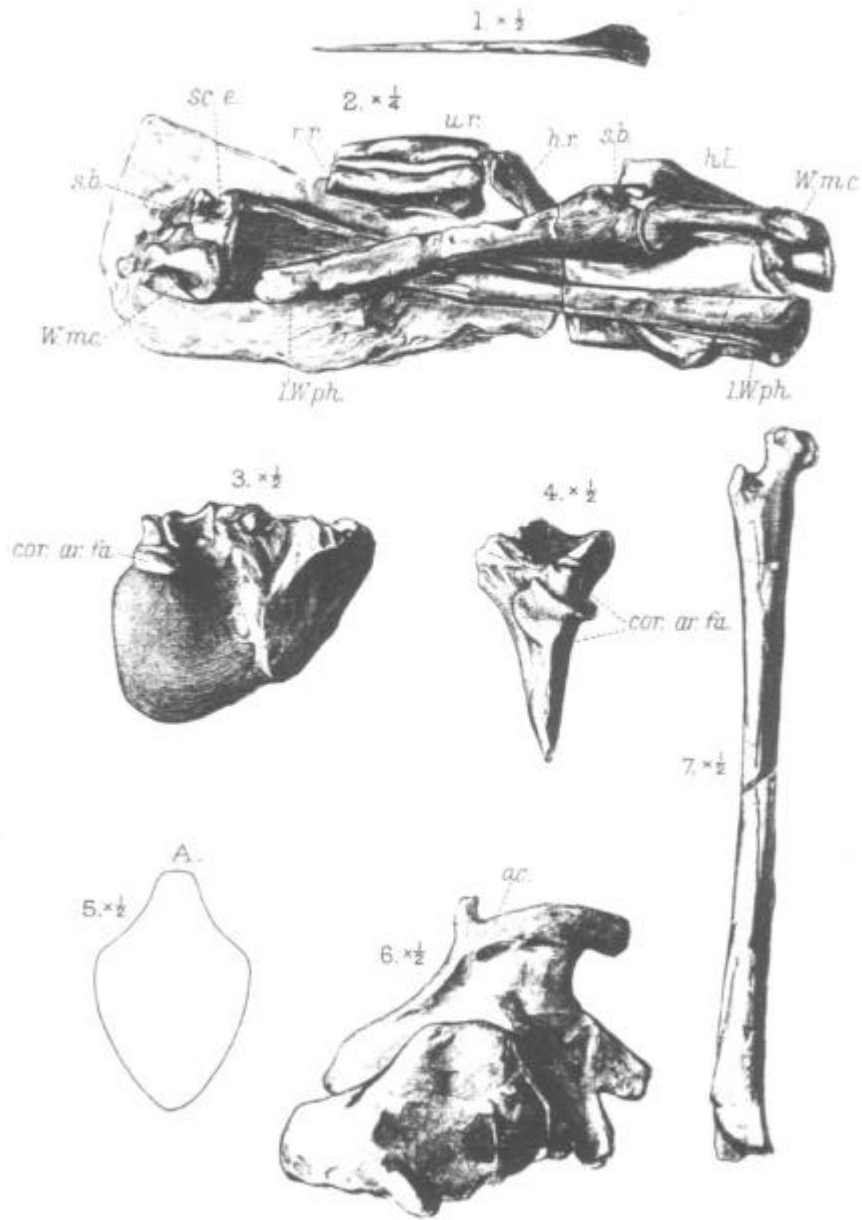
- Fig. 1. Portion of the right humerus, exhibiting the spiral curve of the deltoid crest:
dl.cr., deltoid crest;
f., fragment of bone attached to the humerus; B.M. R/176. x ½.
- Fig. 2. Restoration of the humerus:
dl.cr., deltoid crest;
ep., epiphysis overlapping the shaft;
ri., ridge for muscle attachment. x ½.
- Fig. 3. Distal articulation of the humerus:
f., circular foramen into shaft;
tr., trochlear for the radius;
v., valley for the ulna ridge. B.M. R/3877. x ½.
- Fig. 4. Proximal articulation of the left ulna:
R., transverse ridge for articulation in the valley on the distal articular surface of the humerus.
 B.M. R/3877. x ½.
- Fig. 5. Dorsal view of the right radius and ulna, showing decussation:
R., radius; *U.*, ulna; *ri.*, ridge;
 B.M. R/3877. x ½.
- Fig. 6. Ventral view of the left radius and ulna:
R., radius; *U.*, ulna; *ri.*, ridge;
fa., articular surface articulating with the proximal carpal;
 B.M. R/3877. x 1/3.
- Fig. 7. Distal articulation of the ulna:
A, circular pit; *B*, oval convex condyle;
C, articular surface on the shaft of the ulna.
 B.M. R/3877. x ½.
- Fig. 8. Proximal articulation of the proximal carpal:
A, hemispherical knob; *B*, oval cavity;
C, articular surface for articulation with that on the ulna marked C in fig. 7;
D, elongate cavity for the radius;
E, small concavity. B.M. R/3877. x ½.
- Fig. 9. Distal articulation of the distal carpal:
A, articular facet below the main articular surface;
B, main articular surface;
C, articular surface for small metacarpals;
D, deep circular cavity. B.M. R/3877. x ½.
- Fig. 10. Proximal articulation of the wing-metacarpal:
A, articular facet below the main articulation;
B, main articular surface;
C, the position of the small metacarpals in within this space.
 B.M. R/3877. x ½.



ORNITHODESMUS LATIDENS.

Plate XL

- Fig. 1. Right pteroid bone:
B.M. R/3877. x ½.
- Fig. 2. Upper view of Atherfield specimen No. 2:
h.r., distal end of the right humerus;
r.r., proximal end of the right radius;
u.r., proximal end of the right ulna;
h.l., distal end of the left humerus;
W.mc., distal end of the wing-metacarpal;
s.b., small bones, apparently articulating in semicircular emarginations (*s.c.e.*) on the first wing-phalange, *l.W.ph.* B.M. R/3878. x ½.
- Fig. 3. Left lateral view of the sternum:
cor.ar.fa., coracoid articular facets.
B.M. R/3877. x ½.
- Fig. 4. Slightly oblique anterior view of the sternum, to exhibit coracoid facets:
cor.ar.fa., coracoid articular facets.
B.M. R/3877. x ½.
- Fig. 5. Restoration of the dorsal outline of the sternum:
A, anterior end. x ½.
- Fig. 6. The right ischium:
ac., part of the acetabular rim.
B.M. R/3877. x ½.
- Fig. 7. The right femur, distal end partly destroyed:
B.M. R/3877. x ½.



G. M. Woodward, del.

ORNITHODESMUS LATIDENS.

Reynolds, G. C. Derby

Discussion

The president (Dr. A. Strahan) desired to emphasize the importance of the work which has been carried out by the Author for some years past. Not only had a large number of valuable fossils been rescued from destruction by his care and perseverance, but by his skill in interpreting them conclusions of much interest had been placed before the Society.

Dr. C. W. Andrews congratulates the Author on his success in collecting such beautifully preserved reptilian skeletons from the Wealden Beds of the Isle of Wight. He remarked that there was some doubt whether the generic name *Ornithodesmus* was applicable to the species now described, it having been applied originally to a number of fused vertebrae which differ materially from either of the two groups of fused vertebrae in the specimen now under consideration. The peculiarities in the arrangement of the temporal arcades and fossae he considered to be entirely due to the nearly antero-posterior direction of the elongated quadrate. The Author's interesting account of the mechanics of the wing-bones, particularly of the carpal region, could not be profitably discussed in the absence of specimens and diagrams.

Dr. A. Smith Woodward expressed his admiration of the Author's work and perseverance. He hoped that, as soon as the paper was published, the specimens described would be mounted and exhibited in the British Museum (Natural History).

The Author briefly replied. He thanked the Fellows for the kind way in which they had received his paper. He said that the lengthening of the muzzle, as an aid in procuring food, had undoubtedly drawn forward the bones below the orbits. The facial portion of the skull was about $5\frac{1}{2}$ times that of the cranial. The length of the skull was 560 millimetres, and the spread of the wings when curved in flight about 5 metres.