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Dr. A. Günther, M.D.,
from his friend,
the author.

MONOGRAPH

OF

THE FOSSIL REPTILIA

OF THE

LIASSIC FORMATIONS.

BY

PROFESSOR OWEN, F.R.S., D.C.L.,

FOREIGN ASSOCIATE OF THE INSTITUTE OF FRANCE,
ETC. ETC.

PART SECOND.

PTEROSAURIA.

Pages 41—81; Plates XVII—XX.

LONDON:
PRINTED FOR THE PALÆONTOGRAPHICAL SOCIETY.
1870.

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MONOGRAPH
OF
THE FOSSIL REPTILIA
OF THE
LIASSIC FORMATIONS.

ORDER—PTEROSAURIA, *Owen*.

Genus—DIMORPHODON, *Owen*.

Species—DIMORPHODON MACRONYX, *Buckland*.

REMAINS of volant Reptiles (*Pterosauria*) were later recognised, and, save in the instance about to be recorded, in a more fragmentary or scattered condition, in England than in Continental localities.

A single bone or tooth gives value to a slab of Stonesfield Slate, and the evidence of a Pterodactyle rarely goes beyond such specimen in that Oolitic deposit. A jaw with teeth, or a skull more or less entire, from the Chalk of Kent, or the Upper Green-sand of Cambridge, has been welcomed for the fuller information so yielded; and such fossils, with a few detached vertebræ and wing-bones, have expanded our conceptions of the bulk attained by some of the Flying-dragons at the decline of the Mesozoic period.

When the waters over which they flitted had a clayey or muddy bottom it afforded a quieter resting-place to the dead body of the Pterosaurian therein entombed. So the first discovered specimen of one of these in the upraised petrified ocean-bed now forming the Liassic cliffs of western Dorsetshire afforded BUCKLAND[1] subjects, in the compass of a slab about a foot square, for a description and figures of the leg and wing-bones, with part of the

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[1] "On the Discovery of a New Species of Pterodactyle in the Lias at Lyme Regis." By the Rev. W. Buckland, D.D., F.R.S., F.G.S. (Read Feb. 6, 1829.) 'Transactions of the Geological Society of London,' second series, 4to, vol. iii, 1835, p. 217, pl. xxvii.

vertebral column, of the species which he called *Pterodactylus macronyx*—the first evidence of the genus from deposits so low, or ancient, in the Oolitic series.

In 1858 I obtained the skull, with a few other parts of the skeleton of the same or a closely allied species, from the Lower Lias at Lyme Regis, and communicated a brief notice of it to the British Association, which that year met at Leeds.[1]

This specimen confirmed the accuracy of Buckland's conjecture, which I had doubted, viz., that the portion of lower jaw with the series of small lancet-shaped, close-set teeth,[2] in a second slab of Lias, belonged to the same Pterodactyle as the limb-bones he described; but it also showed that these teeth, so like those of some Fishes, were limited to the lower jaw, and were associated, in the same mouth, with long, slender, trenchant and sharp-pointed laniaries, projecting with wide intervals, and set in advance; which kind of teeth had, hitherto, alone been found in the different species of flying Reptiles.

The chief result of the study of the second discovery of a Pterosaurian in Lias, viz., its evidence of a new generic form (*Dimorphodon*) in the order of volant *Reptilia*, in addition to *Ramphorhynchus*, von Meyer, and *Pterodactylus* proper, was noted in the communication above cited.

The third specimen about to be described confirms that taxonomic deduction, showing a combination of the caudal character, mainly differentiating *Ramphorhynchus* from *Pterodactylus*, with the dental character above defined.

I propose first to describe and figure the two specimens yielding the cranial and dental characters of *Dimorphodon*, and then to attempt a restoration of the Liassic species, *D. macronyx*.

The first specimen with the skull is figured in Pl. XVII. It is on a slab of Lias, measuring 11 inches by 7 inches. The right side of the head is exposed:[3] it has been subject to pressure and some degree of dislocation. Certain bones of both wings, and a few other parts of the skeleton are preserved, pell-mell, in this slab, pressed amongst and upon the bones of the head, especially at the back part of the skull.

The right premaxillary (22), maxillary (21), and nasal (15), are almost in their natural positions, give the profile contour of that part of the skull, show most of the teeth of the right side upper jaw, and reveal the singular expansion of the nasal (*n*) and antorbital (*a*) vacuities. The alveolar part of the left maxillary (8′), with its ascending postnarial branch has been pushed obliquely downward, with fracture, but without much displacement, of the beginning of the alveolar ray, the inner surface of which is exposed.

The mandible (32) has been dislocated and pushed below the place of its articulation with the tympanic (28): the left ramus has also been subject to the same force which has

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[1] "On a New Genus (*Dimorphodon*) of *Pterosauria*, with Remarks on the Geological Distribution of Flying Reptiles;" in 'Reports (Sections) of the British Association,' 1858, p. 97.

[2] Buckland, loc. cit., pl. xxvii, fig. 3.

[3] The specimen has been drawn, in Pl. XVII, without reversing.

dislocated that side of the upper jaw; the hind part of this ramus is obliquely depressed, so as to expose the inner surface (32).

The anterior entire or undivided part of the premaxillary (22) is about 2 inches in length, and $1\frac{1}{4}$ inch in vertical height at its back part: it contains four pairs of teeth, which are the largest and longest of the series. The foremost tooth (1) is terminal, with a crown 5 lines in length, rather over 1 line in breadth (fore-and-aft) at its base; it is subcompressed, subrecurved, and sharp-pointed. An interval of 4 lines divides it from the second tooth (2), with a crown $5\frac{1}{2}$ lines long. After an interval of 7 lines projects the crown (3) of the third tooth, 7 lines in length and 2 lines in basal breadth, sharp-pointed like the first, but less bent. The socket and base (?) of the fourth tooth appear at an interval of 6 lines, and below is the entire and displaced homotypal tooth ($4'$) of the left side, showing the cavity on the inner side of its root which would have received the successional laniary. This tooth measures 1 inch 2 lines in total length, of which the exposed enamelled crown forms two-thirds. In advance of the foremost tooth (1) is seen part of its homotype ($1'$) of the left side, also displaced from the socket, and showing the depression and vacuity on the inside of the base, in relation to the succeeding tooth. Beyond the fourth alveolus the maxillary (21) appears, underlapping the part of the premaxillary ($22''$) which defines the lower and anterior part of the narial vacuity: the maxillary is continued straight backward, with feeble indications of two crushed alveoli (5, 6) for 1 inch 9 lines, when the seventh laniary (7) projects almost straight downward: the crown of this tooth is 5 lines long; the root, covered with rougher cement, slightly contracts to its implanted end, which has slipped a short way out of its socket. An interval of 4 lines divides this from the next laniary (8), which shows a crown of but 3 lines in length; this projects opposite the fore part of the lateral post-narial branch (21^{s}) of the maxillary. The base of the left homotypal tooth ($8'$) projects from the same part of the dislocated left alveolar branch of the maxillary; and above this, on the inner side of that bone, is exposed the coronal germ of a successor. In the right maxillary two other straight laniaries (9, 10) of rather decreasing length, project with similar or rather lessening intervals: then follows, after an interval of 3 lines, a pointed compressed crown $1\frac{1}{2}$ line in length (11); and, at shorter intervals, two smaller pointed compressed teeth (12 and 13).

These thirteen cuspidate teeth of the upper jaw are included in an extent of the alveolar border measuring 5 inches 2 lines. That border is continued backward, straight and edentulous, for 9 lines beyond the last tooth, when it is crossed by the large and long first phalanx (*rr* 1) of the wing-finger. This edentulous part of the maxillary forms the lower straight border or base of the large triangular antorbital vacuity (*a*), at the back part of which it is overlapped by the fore part of the slender malar (26). Above this vacuity are parts of the nasal (15) and prefrontal (14), both somewhat displaced in this crushed part of the skull. The arched part of the frontal forming the upper part of the rim of the orbit (*o*) is recognisable at (11) Pl. XVII. Above its hind part are indications of the post-frontal (12) and mastoid (8), with the process of the latter descending external to its articulation with the tympanic (28). The metacarpus and dislocated unguiculate digits of the wing-limb are confusedly interblended with the crushed and dislocated back part of this skull; three phalanges ($_{IV}1$, $_{IV}2$, $_{IV}3$) of the wing-finger are determinable.

The two anterior teeth (1', 2') of the mandible show longitudinal angular depressions at their base, indicating exposure of their inner side, and that they belong to the left ramus. The corresponding part of the right ramus may have been broken away: the third laniary (3') clearly belongs to this ramus, which is fractured beneath its socket. The point of this tooth is broken off: what remains of the body is curved, and is implanted more obliquely backward than the two preceding teeth. This at first led me to suspect it might be the foremost tooth of the mandible, and that the left ramus had been pushed in advance as well as downward: but my doubts on this point have been set at rest by the specimen (Pl. XVIII) next to be described, and I view the tooth in question as the third of the mandibular series: it is divided from the second by an interval of 6 lines, and the second stands at a rather shorter interval behind the first. Five lines behind the third tooth is the base of a fourth laniary (4'), and four lines further back is an indication of a fifth (5'). This is followed by the characteristic series of between thirty and forty very small, subcompressed cuspidate teeth, each less than a line in length, corresponding in extent with the maxillary part of the upper jaw. The entire series of mandibular teeth occupies an extent of alveolar border measuring 5 inches 1 line.

The depth of the right ramus gradually increases from 5 lines below the last laniary to 10 lines below the last denticle. The inner side of the dislocated ramus (32') shows a strong longitudinal ridge projecting inwards about 3 lines above the lower border. The outer surface of the ramus seems to have been strengthened near its lower border by a similar but lower ridge.

The distal ends of the antibrachial bones (54, 55) overlap the hind part of the mandible: that which shows the larger articular surface, opposite the three slender metacarpals, should be the radius. The base of the supplementary styloid bone appears near the distal end of the ulna, but is better shown in Buckland's original specimen.[1] Indications of two carpals intervene between these and the metacarpus. This overlies and conceals the articular pedicle of the mandible and contiguous parts (squamosal, malar, &c.) of the skull. The metacarpus includes the three slender supports of digits *I, II, and III*, and the strong and thick metacarpal of the wing-finger ($_{IV}$). This bone, being almost concealed by the first phalanx in Buckland's specimen, was overlooked, and that phalanx was described as the metacarpal of the wing-finger, which, accordingly, in the restoration, fig. 2, Pl. 27, of 'Buckland's Memoir,' is made three times the length of the other and more slender metacarpals (3'). I have, therefore, had that part of the original specimen, now in the British Museum, redrawn (Pl. XIX, fig. 1), the true metacarpal being shown at *m* 4. It corresponds with the same bone in previously described *Pterosauria* by surpassing in thickness, not in length, the other constituents of the metacarpus. In the specimen,

[1] As in the part re-drawn in fig. 1, Pl. XIX.

Pl. XVII, the metacarpal of one wing-finger is clearly shown at *IV m*. That of the other, lying upon the cranium, is more obscure. The thin compact wall of this pneumatic bone has been crushed in upon the wide air-cavity, as with most of the other long bones, so that it looks like two metacarpals. The proximal articular surface of *IV m* is partly concave and partly convex: the distal articulation is trochlear, moderately concave from side to side at the middle, convex from behind forward, with a depression behind, above the articulation, for securing the olecranoid process of the proximal phalanx. This phalanx (*IV*, 1), in one wing, is bent back upon the fore-arm, crosses the dislocated mandible, and has been pressed upon it, long and hard enough to leave a channel in the right ramus, where part of the phalanx has been removed: its length is 4 inches 6 lines.

The second, more slender and longer phalanx (*IV*, 2), is bent at nearly a right angle with the first, and lies below and parallel with the mandible: it is nearly 5 inches in length. The third phalanx (*IV*, 3) is bent upward in front of both lower and upper jaws: 4½ inches of its length is preserved in the slab: from the analogy of the better preserved specimens (Pl. XVIII, *IV*, 3), about 1 inch 3 lines are wanting from the distal end.

Of the three unguiculate digits the characteristic large claws are preserved: one (*II*) lies above the frontal (11) with the penultimate phalanx; the other two are between the upper and lower jaws, with some of the slender phalanges: all these parts of the ramus having been dislocated and scattered.

Parts of the distal ends of the radius and ulna (54′, 55′), the metacarpal of the wing-finger (*IV m′*), and the proximal end of its first phalanx (*IV r′*), of the opposite fore-limb, occupy a lower corner of the slab: carpal bones, one of the accessory styloid ossicles of the forearm, some of the slender metacarpals of the claw-fingers can be made out above these: and there are more obscure indications of vertebræ at that end of the slab, curving toward the cranium.

All the osseous and dental textures are black, as if charred by slow combustion of the animal matter.

Dimorphodon macronyx. Pl. XVIII.

In August, 1868, I was favoured by the Earl of Enniskillen, then at Lyme Regis, Dorsetshire, with a list of parts of a Pterodactyle, in a slab of Lias about 20 inches by 11 inches, and of other parts in detached portions of Lias, including the entire tail with its bone-tendons, which his Lordship had observed at Messrs. James and Henry Marder's, the judicious and persevering collectors of the fossils of that rich locality.

The result of this valuable and timely information was the securing for the British Museum the entire series of these Pterosaurian fossils.

They proved to be parts of the *Dimorphodon macronyx*, confirmed many of the observations made on previously acquired specimens, corrected others, and added almost all that was required for the restoration of the skeleton of this remarkable genus and species, which I have accordingly attempted in Pl. XX.

The slab of Lias with the second specimen, including the skull of *Dimorphodon macronyx*, is of larger size, shows more of the skeleton and in a more separated and definable state than in Pl. XVII. Nine dorsal vertebræ, third to eleventh inclusive, in natural juxtaposition, with the twelfth slightly dislocated, are preserved at the upper part of the slab (Pl. XVIII, D). The summits of the neural spines (*ns*) of most of these, and the disposition of many of the preserved ribs, show that they lie mainly with the dorsal aspect downward (as the specimen is figured). This explains and accords with the position of the parts of the pelvis, which lie a little way behind the dorsal vertebræ. The comparatively slender ilium (62, 62) is downward; the broad ischium (63), and the pair of spatulate pubic bones (64), are turned, like most of the ribs, upward, as I conclude the abdominal or ventral surface of the trunk was directed as the fossil lies in the figured slab. The bones of the hind-limb, in connection with the acetabulum, are turned outward, with their inner surface exposed. The projections of the trochlear terminations of the metatarsals (*i*, *iv*, 65), show that the sole of the foot is turned to view. Accordingly, we have here the bones of the left hind limb. On the hypothesis that the femur and tibia are seen from the outside, which at first suggests itself, they would belong to the right limb, viewed in profile. But then, the broad thin plate of bone contributing to the acetabulum, would represent the ilium, and the indications of the pelvis below the acetabulum and head of the femur would represent ischium and pubis. This interpretation, however, gives to *Dimorphodon* proportions of pelvic bones very different from those determined by Wagner in *Pterodactylus Kochii*,[1] and by Quenstedt[2] in *Pterodactylus suevicus*; and, besides, it leaves undetermined the pair of bones (64, Pl. XVIII) which closely resemble in form and proportion the 'pubic bones' (*u*, *u*) in Quenstedt's instructive plate.[3] In this plate the ilia (*s*, *s*) are represented as long slender bones, contributing the upper but smaller proportion of the acetabulum, and extending horizontally beyond it both forward and backward. The pelvis, in the position in which I conclude it to lie in the slab figured in Pl. XVIII, might well afford such indications of the pre- and post-acetabular productions of the ilium as are there shown at 62, 62. In *Pterodactylus suevicus* the ischium contributes the lower and major half of the acetabulum (*tr*, loc. cit.), and expands into a broad thin plate (*s*, ib.), having the proportions to that of the spatulate pubis, which the bone 63 bears to 64 in Pl. XVIII. The portion of the pelvis in the original specimen being preserved in natural connection with

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[1] "Ueber *Ornithocephalus Kochii*," in 'Abhandl. d. math.-phys. Klasse der Bayerischen Akad.,' ii, 4to, München, 1837.

[2] 'Ueber *Pterodactylus suevicus*,' &c., 4to, Tübingen, 1855.

[3] In the Memoir above cited.

the sacrum and contiguous vertebræ is figured in Pl. XIX, fig. 2; and the constituent bones are rightly recognised by Buckland (op. cit., p. 222).

It is interesting to note, that the pelvis of *Pterosauria*, so determined, resembles more closely that of the existing representatives of the section of *Reptilia* with the 4-chambered heart and double-jointed ribs, viz., *Crocodilia*, than it does the pelvis in *Chelonia* and *Lacertia*. The ischium in *Crocodilia*, *e. g.*, surpasses the pubis in size, and excludes that hæmapophysis from the acetabulum.[1] The ischium seems to contribute the larger share of the acetabulum in *Dimorphodon*, Pl. XVIII, *a*. In Birds, as in Lizards, the pubis forms part of the acetabular cavity.[2]

In the specimen, Pl. XVIII, a portion, *cd*, of a long tail, of which the vertebræ were surrounded by numerous slender bone-tendons, extends backward and downward beyond the pelvis: a better preserved portion with three caudal vertebræ (*c d'*) is preserved in a detached part of the matrix found in the vicinity of the larger slab. But to this part of the vertebral column I shall return in describing the more perfect specimen of the tail of *Dimorphodon*, from another individual (Pl. XIX, fig. 4).

Behind the skull are four cervical vertebræ (Pl. XVIII, c), and part of a fifth in natural juxtaposition, or perhaps a little separated at the articular surfaces. The under surface of the centrums and articular processes of the neural arches are exposed. The sides of the centrums show a slight concavity, but their crushed state obscures the natural contour of the under surface. The hind part of the under surface, in the last two of these vertebræ, shows a pair of low obtuse processes, with an indication of a convex terminal articular surface. The centrum expands in breadth as it advances, and sends out a short thick process (parapophysis) from each side of the fore part; to which, in the last three vertebræ, are indications of attachment, or parts, of a backwardly produced styliform rib. At the midline of the fore part of the last two of these vertebræ a fracture indicates a ridge or process there to have been broken off. The pre-zygapophyses are thick, and project far in advance of the concave anterior articular surface of the centrum: the convex posterior articular surface of the centrum projects as far beyond the post-zygapophyses. Their joints are more vertical than horizontal: the posterior surfaces looking slightly outward and downward.

The superior breadth of the neural arch, as compared with that of the centrum, brings its articular processes into view, along each side of the vertebral bodies, in the degree shown in Pl. XVIII, c. The character of the articulations indicate less extent and freedom of movement of the cervical vertebræ than in Birds, and more restriction in the lateral than in the vertical directions. The interlocking joints resulting from the different lengths of the fore and hind articular processes add strength to the part of the spine supporting the head.

The cervical vertebræ of *Dimorphodon*, so far as their structure is exemplified in the

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[1] 'Anatomy of Vertebrates,' vol. v, p. 188, fig. 119.

[2] Ib., p. 190.

present specimen, conform to the pterosaurian characteristics of these vertebræ, as shown in those of *Pterodactylus Sedgwickii*, described and figured in the 'Monograph on the Fossil Reptilia of the Cretaceous Formations,' Supplement No. I (1859), pp. 7—10, Pl. II, figs. 7—18; and in those of *Pterodactylus simus*, ib. Supplement No. III (1861), p. 7, Pl. II, figs. 1—5.

The skull preserved in the present specimen agrees in size with that in the slab previously received (Pl. XVII), repeats the characteristics of the genus *Dimorphodon*, and shows no differences of greater degree or value than may be set down to individual modifications. The part defective and partly obscured by intrusive bones from other parts of the skeleton is unfortunately that which leaves the precise determination of structure unsatisfactory in the previously described specimen. A trace only of tympanic remains at 28, and of the descending styloid process of the mastoid at 8: the thick metacarpal of the wing-finger (*iv, m*), intrudes into the orbit, and overlaps the upper end of the malar (26). More of the part of the frontal forming the superorbital arch (11) is shown than in Pl. XVII. Part of the concave surface of the orbital cavity beneath the superciliary ridge is here seen. The lacrymal (23) or descending branch of the prefrontal (14) meets the ascending process from the combined malar and maxillary, dividing the orbital from the antorbital cavity. The true size and shape of the latter vacuity (*o*) is here well displayed. The maxillary styloid process (21′) rises, at the same angle backward as in Pl. XVII, to join the nasal (15). The medial branch or ray of the premaxillary (22′), the end of which is depressed below the prefrontal in Pl. XVII, preserves its position in the present specimen, and yields the true arched contour of the profile of this remarkable skull.

The entire vertical extent of the vast narial vacuity, *n*, is here given, the longitudinal one, 3½ inches, precisely agreeing with that in the first-described skull. The anterior part of the premaxillary (22) shows, also, the same proportions and shape, viewed sideways, as in the first specimen. The conformity is instructively continued in the characters of the dental system. The apex of the crown of the laniary (Pl. XVIII, 1) from the fore end of the premaxillary shows the same curvature and proportions as in Pl. XVII; the same interval divides it from the second laniary (2); the longer interval, again, occurs between the second and the third laniary, with a longer and less curved crown. After an interval of seven lines comes the fourth tooth (4), corresponding in size and shape with the one which is displaced in Pl. XVII, 4′. After an interval of nine lines the apex of the crown of, seemingly, the successor of the fifth laniary (5) appears. It may be, normally, smaller than the rest; the socket of this tooth is feebly indicated in the subject of Pl. XVII. The sixth laniary (6) shows the same size and relative position as in that subject, and the same may be said of the five succeeding teeth, save that the last is rather larger than in Pl. XVII, which also shows an additional small hind cuspidate tooth. The suture between the premaxillary (22″) and the maxillary (21) is more plainly discernible in the present specimen.

The extent of alveolar surface of the left upper jaw occupied by the above-described dental series is 5 inches 3 lines.

In the left ramus of the mandible two of the large anterior laniaries are in place; one, answering to the second in Pl. XVII, 2', projects across the diastema between the second and third tooth above; in size, shape, and curvature, it resembles the second upper laniary, close to which it terminates. The next mandibular tooth is larger, less curved, and crosses the middle of the interval between the third and fourth upper laniaries. The tooth (1') displaced beneath the mutilated fore part of the mandible, I take to be the foremost of the mandibular series and suppose that its point would naturally project across the interval between the first and second of the upper teeth. The fourth laniary appears to be more displaced: its base or root, with a lateral depression, is shown behind the fifth tooth of the minute serial teeth, and the crown passes obliquely backward on the inner side of that of the sixth upper laniary, by which it is concealed. Of the serial teeth, with pointed crowns from half a line to a line in length, about thirty may be reckoned occupying an alveolar extent of 2 inches, 9 lines.

At the hind part of the left mandibular ramus, here exposed, three longitudinal ridges define two vacuities, of which the inferior may be natural. The upper one seems more plainly due to loss of the thin outer plate of bone extended between the upper two ridges. The proportions of the ramus closely accord with those of the first-described specimen. The fore part of the mandible is too much mutilated for useful comparison.

The dentition of *Dimorphodon*, as displayed by the second specimen of skull, consists, in the upper jaw, of laniaries with wide intervals, eleven in number on each side; in the lower jaw, of four, if not five, laniaries implanted at the fore part of each ramus of the mandible at intervals corresponding with three of the four anterior laniaries above; then follows the long series of close-set and minute pointed teeth. The difference of dentition as compared with the first specimen (Pl. XVII) is, in the upper jaw, in the additional small laniary or cuspidate tooth at the back part of the series in that specimen. In the lower jaw there does not seem to be any noteworthy difference in the number, kinds, and position of the teeth. The longest laniaries are included between the second and fifth in both jaws: the upper laniaries after the fourth become small and straight.

At the first view of the framework of the huge head of our Liassic dragon one is struck with the economy of bony material and the purposive skill with which it has been applied or disposed, so as to give strength where resisting power was most required.

The lodgment of the poorly developed brain enlists a miserably small proportion of the skull: the cranium proper, or brain-case, is relegated to an out-of-the-way corner, so to speak, and there it is almost concealed by the projections for joints or muscular attachments. The orbits accord with the large eyes given to this volant and swift-moving Reptile.

One can conceive no necessary interdependent relation between the wide external bony nostril (n) and the organ of smell, nor be led to conjecture that the tegumentary inlets to the nasal chamber were larger than is usual in Reptiles.

The main purpose of the head is for prehension of prey. The jaws are produced far forward to form a wide-gaping mouth, and are formidably armed. We may conceive, therefore, that the dragon may have occasionally seized an animal of such size as to require considerable force of jaw for overcoming its struggles. The means of resistance were afforded to the upper or fixed maxilla, not by a continuous wall of bone, but by curved columns or abutments. The chief of these is the upper medial arch of bone which overspans the skull lengthwise, from the short roof of the cranium to the fore part of the premaxillary (22); the frontals (11) and nasals (15) combining with the mid-fork or branch of the premaxillary (22',) to constitute this arched key-ridge of the roof of the head.

From it two piers or buttresses out-span on each side, to give strength and resistance to the upper jaw, and especially its alveolar tracts. One, proceeding from the nasal, meets the uprising process of the maxillary (21); this abutment, curving from above outward and obliquely forward, expands and backs the part of the jaw where the second group of large laniaries project. The second buttress is continued from the prefrontal (14), and arches more directly outward to meet the uprising process of the malo-maxillary. A third arch, due to the post-frontal (12) and malar (26), expands to abut upon the hind end of the maxillary arch, and gives support to the part of the skull which the temporal muscles tended to pull downward when they were giving to the mandible the power of a strong bite or grip. Finally, comes the strongest of the four piers, due to the mastoid (8) and tympanic (28), for giving articular attachments to the rami of the lower jaw.

Thus, four vacuities appear in the side-walls of the skull: the first ($_n$) is the largest, between the small consolidated or continuous fore part of the skull (22), and the naso-maxillary pillar (21^x, 15). This vacuity answers to the external bony nostril of the same side, in the Lizard's skull (Pl. XX, fig. 3, $_n$), where the nostrils are divided and more or less lateral. The second vacuity ($_a$) is somewhat less, of a triangular form, with the base downward: it answers to the antorbital vacuity in *Lyriocephalus* (ib., $_a$) and a few other Lizards, and to that in *Teleosaurus*, where, however, it is very small. The third vacuity ($_o$) still decreasing, is oval, with the narrow end or apex downward: it answers to the orbit, but is of large size compared with most Saurians; it is, however, exceeded in relative expanse by the orbit in *Lyriocephalus* (ib., $_o$).

The fourth vacuity is the narrowest: it answers to the so-called 'temporal fossa' and was occupied by the muscles of the same name. Extension of surface, for their origin, and additional strengthening of this back part of the skull are gained by laying horizontally across the temporal fossa the bony beams called 'upper and lower zygomata,' arching from the postfronto-malar to the masto-tympanic vertical columns. The heavy phosphate of lime, thus singularly economised by the disposition of the bones on mechanical principles plainly to that end, is made to go still further by the arrangement of the osseous tissue. Every bone is pneumatic, the abundant, open, cancellous structure being included in a very thin layer of compact osteine.

The bones of the limbs are dislocated and dispersed in the way and degree common to the specimens of this animal hitherto discovered (Buckland, loc. cit., pl. xxvii; and pls. XVII and XVIII of the present Monograph). The scapula (Pl. XVII, 51) and coracoid (ib., 52) in the same anchylosed condition as in the first-described specimen, are at the end of the slab opposite to that with the head. The corresponding humerus (53), preserved in a separate portion of the block of Lias, shows the entire contour of the pectoral process (*b*). The right humerus (53′) lies below the dorsal vertebræ (D); the upper part of the pectoral process (*b*) is wanting, but the obtuse thickening of the end of that remarkable production is well shown. The ridge (*c*) called 'ulnar,'[1] descending from the 'lesser tuberosity,' appears in this view of the 'palmar' surface of the bone.[2] The sigmoid flexure of the shaft is much better marked than in the humerus of *Pterodactylus suevicus*.[3] The stronger walls of the humerus have resisted the pressure better than those of most of the other long bones.

Of the antibrachial bones parts of the shafts, crushed, are seen at 54, 55, apparently of the right wing. With the distal ends of these, the right carpus (56) and metacarpus (57) appear to have retained their natural connections. The slender metacarpals of the first (I), second (II), and third (III) digits appear emerging from beneath the left hind foot which overlies their proximal ends. The phalanges of the first digit (I), two in number, preserve their natural articulations. As are also those of the second digit, three in number. The metacarpal of this digit is longer by 2½ lines than that of the first. The additional phalanx would seem to be the proximal one, by its shortness: the second phalanx more nearly agrees in length with that supporting the claw-phalanx in the first digit; but it is thicker and a little longer. The four phalanges of the third digit (III) are dislocated; but the penultimate, which is the longest, retains its connection with the ungual phalanx. The proximal phalanx is longer than the second, which resembles in length, and seems homotypal with, the proximal phalanx of the second digit. It may be concluded, therefore, that the additional phalanx to II and III was developed at the attachment of the digit to the metacarpus. The largely and abruptly expanded metacarpal of the fourth digit is in great part covered by the correspondingly thickened and much elongated phalanx (*IV*, 1) therewith articulated. The olecranoid process of this phalanx is well shown, and the entire bone is preserved: its length is 4 inches 2 lines: it is bent directly and abruptly back upon its metacarpal. To the distal end is attached part of the second phalanx (*IV*, 2).

The proximal phalanx of the left wing-finger is preserved in a detached (*IV*, 1) part of the slab (Pl. XVIII) containing the major part of the skeleton. The second phalanx (*IV*, 2) of the left wing-finger lies in that slab, is entire, and yields a length of 4 inches 9 lines. The third

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[1] 'Monograph on Fossil Reptilia of Cretaceous Formations,' Suppl. No. iii, 1860, p. 14, pl. iii, fig. 1, c.

[2] Op. cit., 190.

[3] Quenstedt, op. cit., *c l*, *c r*.

phalanx ($_{IV,\,3}$) is 5 inches 6 lines in length; near its distal end is part of the slender terminal phalanx of this digit ($_{IV,\,4}$). There is no trace of a fourth unguiculate digit, and I return to Cuvier's view of the structure and homologies of the hand of the Petrodactyle,[1] which I had abandoned in favour of the seemingly more perfect evidence supporting Professor Goldfuss' restoration of *Pterodactylus crassirostris*,[2] adopted by Buckland[3] and myself.[4]

The metacarpal of the left wing-finger ($_{IV,\,m'}$, Pl. XVIII) lies beneath the back part of the skull, and is over-lapped by the superorbital part of the frontal. Portions of two of the unguiculate digits of the same fore-paw ($_{I,\,II}$) are seen in the wide narial vacuity.

The definition and finish, so to speak, of the joints of the wing-finger are worthy of note, especially of that between the metacarpal bone and proximal phalanx. In Reptiles generally the articular extremities of the long bones are not very definitely sculptured, and do not manifest that reciprocal adaptation of their inequalities which are observed in the joints of Mammals and Birds. The difficulty of determining the coadapted extremities of detached bones of Reptiles is increased by the great thickness of the cartilage which covers them and renders their mutual contact more intimate, and which is always wanting in fossil bones. The Pterosaurian modification is, however, purely adaptive; and the relation to Warm-blooded Vertebrates in this respect is one of analogy. An argument in favour of avian affinity from the joint-structures could only be propounded by one not gifted with the judgment needed to deal with problems of this nature.

The left femur (65') preserves its natural articulation with the acetabulum; the head is bent forward from the line of the shaft for an extent like that at which the condyles are produced backward; the shaft is straight, the great trochanter is feebly developed. There is no evidence of a modification of the distal condyle for the interlocking articulation with the fibula, which in Birds relates to their bipedal station and walk. The length of this femur is 3 inches 4 lines

The left tibia (66'), bent back at an acute angle upon the femur, measures 4 inches 10 lines in length. There is no trace of patella, nor has this sesamoid bone been found in any Pterosaur. The inner side of the bone being exposed, the styliform rudiment of the fibula is hidden from view. The trochlear termination of the distal end of the tibia is better marked than in *Crocodilus*, or even than in *Scelidosaurus* ('Monograph on Oolitic Reptilia,' Part II (1863), p. 16, Pl. X, 66), and consequently approaches more nearly to the characteristic form of the joint in Birds. The resemblance to the bicondyloid termination of the femur is instructively shown in the distal portion of the Pterosaurian tibia figured in Pl. XIX, figs. 8 and 9, and in the distal half of the right tibia of *Dimorphodon*

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[1] 'Ossemens Fossiles,' 4to, v, pt. ii, p. 371.

[2] Beiträge zur Kentniss verschiedener Reptilien der Vorwelt, in 'Nova Acta Acad. Natur. Curios.,' Leopold Carol., &c., 4to, tom. xv. "Reptilien aus dem lithographischen Schiefer, *Pterodactylus crassirostris*, nobis, tabs. VII—X."

[3] 'Bridgewater Treatise,' 8vo, 1836, pl. 22.

[4] Owen's 'Palæontology,' 8vo, 1861, fig. 97.

in the slab, Pl. XVIII, at 66, which crosses the right antibrachium (54, 55). The deflected posterior ends of the condyles are here shown, and beneath them three tarsal bones (*o*, *l*, *b*), with the characteristic short and thick metatarsal of the fifth toe (*m*, *v*).[1]

The tarsal bone between the tibial trochlea and the three metatarsals (*i*, *ii*, *iii*), answers to the astragalus, marked *a*, in *Scelidosaurus* and *Crocodilus* (Monograph and Plate above cited); two tarsals, of which the one representing the second row is the smallest, intervene between the tibia and the fifth metatarsal; the larger of these ossicles answers to the calcaneum (*l* in *Scelidosaurus* and *Crocodilus*, Monograph, *ut suprà*), the smaller and distal one to the cuboides (*b*, *ib.*).

The bony frame-work of the left foot (69′) is instructively preserved; the first four metatarsals are, as usual, long and slender, and resemble those in previously described *Pterosauria;* their under or plantar surface is exposed. The metatarsal of the first or innermost toe (*i*) is the shortest, that of the fourth toe (*iv*) is next in length; the third (*iii*) is the longest, but there is little difference in this respect; their distal condyles project toward the sole, and are made trochlear by a mid-groove.

The innermost digit shows the proximal and ungual phalanges in natural connection with each other and with the metatarsal: the ungual phalanx (*i*) is scarcely half the size of that of the corresponding digit (*1*) of the fore-foot. The ungual phalanges of the three other toes (*ii*, *iii*, *iv*) are preserved, showing the usual uniformity of size in the hind-foot of *Pterosauria:* the number and disposition of the contiguous but scattered phalanges best accord with the phalangeal formula (3, 4, 5) presented by the second, third, and fourth toes respectively, in better preserved feet of other *Pterosauria* (Pl. XIX, fig. 5). There is, however, here unequivocal evidence of a fifth toe, and that not merely rudimental but recognisably functional though without a claw. The tarsal bones (*b*, *b*) support a metatarsal (*m*, *v*) directed parallel with the metatarsals (*i*—*iv*), but much shorter and also thicker: it is 6 lines in length, and expanded at both ends, the proximal one being 2½ lines in breadth, the distal one 2 lines, and the middle of the shaft 1½ line. The under or plantar side of the bone is exposed, as in the others, and shows a shallow oblique channel passing from the proximal end obliquely to the inner side of the shaft, dividing two elevations at that aspect of the proximal end. The distal end is a moderately convex condyle, the outer and plantar prominence of which is broken off. I regard this bone as the fifth metatarsal. It supports a digit of two phalanges: the first (1, *v*) is slightly dislocated, so as to show the concavity of its proximal joint close to the condyle to which it was articulated: it is 1 inch 3 lines in length, and is thicker as well as much longer than the corresponding phalanx of the other toes. The second phalanx (2, *v*) is 1 inch in length: it is bent back upon the first, and gradually tapers to a point. Both phalanges,

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[1] This throws expository light on the idea, revived by Gegenbaur ('Vergleichend-anatomische Bemerkungen über das Fusskelet der Vögel,' in Reichert's 'Archiv für Anatomie, Physiologie, und wissensch. Medicin,' 1863, p. 445), viz., that the distal trochlear epiphysis of the Bird's tibia represents its proximal tarsal series, or astragalus.

in the specimen described, pass obliquely across and beneath the four long metatarsals supporting the unguiculate claws.[1]

From the position of this exunguiculate long and slender toe, as well as from its difference of structure, we may infer its application to a different office from that of the other toes. These obviously subserve the purposes of terrestrial locomotion, and perhaps of suspension: the fifth toe I infer to have helped to support, like the similarly shaped production of the calcaneum in certain Bats, the interfemoral expansion of alar integument, in the way indicated in the restoration (fig. 2, Pl. XX) of *Dimorphodon macronyx*. In the habitual mode of locomotion by vigorous act of flight this toe would be in action while the other four were at rest; hence the necessity for greater thickness and strength of its bones, and the size of one of the tendons, as indicated by the groove in the metatarsal. Interesting, also, is it to note the analogy of this 'wing-toe' with the 'wing-finger,' though they be not homotypes, as shown in the shortness as well as thickness of the metapodial bone and the length of the pointed, clawless, terminal phalanx.

The fourth slab of Lias adding to our means of reconstruction of *Dimorphodon*, was observed by the Earl of Enniskillen in the collection of Henry Marder, Esq., M.R.C.S., of Lyme Regis. It had been quarried from the same cliff as the preceding specimen (Pl. XVIII), and displayed the vertebræ and bone-tendons of a long and stiff tail (Pl. XIX, fig. 4).

Indications of such a tail, in which the vertebræ were associated with ossified tendons, were apparent, and have been noted in the description in the second specimen with the skull (Pl. XVIII, CD); whereby one was able to show that the vertebræ in the originally described specimen supposed to be cervical (Buckland, loc. cit., pl. xxvii, *a*, *a'*) were truly caudal, with similarly associated bone-tendons, as, indeed, *Von Meyer* had recognised after the discovery of the caudal structure of his *Ramphorhynchus*.[2] The specimen now to be described of the entire tail, as represented by its petrifiable parts (Pl. XIX, fig. 4)[3] I conclude, from the identity of character of some of its vertebræ with the three shown in Pl. XVIII, *c d'*, and from the discovery of this specimen in the same formation and locality, to belong to *Dimorphodon macronyx*.

The series of caudal vertebræ, to judge from the size of the anterior ones, comes from an individual as large as that represented by the fossils in Pls. XVII and XVIII, and, no doubt, from an adult or full grown one. This series is 1 foot 9 inches in length, following the curve,

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[1] "Cuvier, Wagler, und Goldfuss lassen den Fuss aus fünf ausgebildeten Zehen bestehen; in allen Pterodactyln habe ich aber nie mehr als vier solchen Zehen und höchstens noch einen Stummel vorgefunden." Von Meyer, op. cit., p. 20. But see 'Ossemens fossiles,' 4to, tom. v, pt. ii, p. 374—"Le cinquième réduit à un léger vestige," &c.

[2] "Beiträge zur näheren Kenntniss fossiler Reptilien," in Leonhard und Bronn's 'Neues Jahrbuch für Mineralogie,' &c., 8vo, 1857, p. 536.

[3] It has been drawn with the neural aspect downward.

which is single and slight; and it includes upwards of thirty vertebræ. These vertebræ, 3 lines in length of centrum in the first five, progressively increase to a length of 1 inch at the twelfth, begin to shorten gradually after the fifteenth, the twenty-first being 11 lines, the twenty-fourth 9 lines, the twenty-eighth 6 lines, and the thirtieth 5 lines in length. In breadth or thickness the vertebræ decrease from the first to the tenth; and then again gradually from the fifteenth to the last, which is filiform.

The first caudal, or the first of the series here preserved, has the anterior articular surface of the centrum subconcave. The inferior surface describes a slight concavity lengthwise; the upper part of the anterior half projects as a parapophysis, the end of which has been broken off, showing the open cancellous structure. A ridge from its upper part was continued to the fore part of the anchylosed neural arch. This arch developed zygapophyses, of which the anterior extend beyond the centrum; but they are better shown in succeeding vertebræ.

In the second caudal the base of the parapophysis has receded and now projects from the upper part of the side of the centrum, occupying more than its middle third. Part of a quadrate spinous process is here preserved, projecting above the centrum as far as the vertical diameter of that element.

In the third caudal the base of the parapophysis, reduced in vertical thickness, occupies the same positions and longitudinal extent. The postzygapophysis, after a deep hind notch of the neurapophysis, curves over the prezygapophysis of the succeeding vertebra, which enters that notch.

In the fourth caudal the base of the parapophysis has lost in longitudinal as well as vertical extent, and is more posterior in position. The subconvexity of the hind articulation of the centrum is here well shown. The confluent neural arch is low, attached to rather more than the fore half of the centrum. The postzygapophysis does not extend back beyond the centrum; the prezygapophysis is continued beyond the front or concave surface of the centrum into the neural notch of the preceding vertebra.

In the fifth caudal the parapophysis is smaller and more posterior. The neurapophysis rises from the anterior half of the side of the centrum and continues to show the zygapophysis, though reduced in size. Between the fifth and sixth caudals a small, slender hæmapophysis (*h*) has been articulated to the under part of the intervertebral space.

The reduced parapophysis is continued from the sixth caudal; this vertebra shows a much reduced indication of neurapophysis. The base of a hæmapophysis crosses the lower part of the space or joint between it and the seventh caudal, then expands both forward and backward, and more so in the latter direction; the inferior border of this expansion is straight.

In the seventh caudal the prezygapophysis is still indicated, though much reduced in size. The hæmapophysis, similar in shape to the preceding one, is longer; and three bone-tendons rise from the side of the hind projection of this hæmal arch.

In the eighth caudal the base of a reduced parapophysis projects from the side of the centrum behind its middle; a low prezygapophysis projects from the neural arch: but beyond this vertebra all trace of that arch disappears, or is indicated by feeble prominences in the fasciculus of bone-tendons which seem to be attached to neural processes of the non-elongated centrums. Six or seven filamentary bone-tendons, one thicker than the rest, extend lengthwise above the centrum. Some of these may be traced over two centrums, then end in a point, their place being taken by another bone-tendon beginning by a similar pointed end. The parapophysis disappears in the tenth vertebra.

The caudal vertebræ in the first discovered specimen of *Dimorphodon*[1] answer to the eighth—eleventh in the present series. The elongate centrums of the tenth and succeeding caudals, usually more or less uncovered by the bone-tendons, show a low lateral ridge, and a slight expansion at the ends. The hæmapophyses are traceable, much reduced in size, to the fifteenth—sixteenth vertebræ. The bone-tendons are in two fasciculi, one neural, the other hæmal, in position. From five to eight may be counted in the side view given of each of these fasciculi. The seeming increase of thickness of some, usually the more peripheral of the filaments, may be due to this flattened form, and to more or less of the side coming into view, instead of the edge. Five or six may be counted in each fascicule, even beyond the twentieth caudal; the number varying at parts through the formation of the bundle by successive tendons, as above mentioned. They are reduced to two or three at the thirtieth vertebra. The terminal joints of the elongate centrums appear to be flattened and closely adapted, allowing of very little motion. It is evident that, as in *Ramphorhynchus*, the tail was stiff as well as long, and doubtless served as a sustaining ray of the parachute of membrane continued backwards from the wings and hind limbs.

The vertical diameter of the second caudal showing its neural spine is five lines. The diameter of the ninth vertebra, including the neural and hæmal fasciculi of bone-tendons, is the same; and beyond this the vertebræ and their surroundings gradually diminish to the pointed end of the tail.

§ RESTORATION OF DIMORPHODON. Plate XX.

The several parts of the skeleton of *Dimorphodon* preserved in the slabs of Lias described and referred to in the foregoing pages have ultimately yielded the desired result of their scrutiny and comparison, viz., a restoration of the extinct animal, such as I have endeavoured to exemplify in Plate XX; and I propose to apply that plate in illustration of a summary of the osteology and dentition of *Dimorphodon*, comparing therewith the

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[1] Buckland, loc. cit., pl. 29, *a*, *a*. I have had these vertebræ carefully redrawn, from the specimen, in Pl. XIX, fig. 3.

previously known *Pterosauria*, and adding such deductions as to the status and affinities of the order as seem legitimately to flow from the facts.

The first distinguishing feature of *Dimorphodon*, or of the present liassic type of the genus, is the disproportionate magnitude of the head—the more strangely disproportionate, as it seems, in an animal of flight.

The head is large in proportion to the trunk, not only in respect of length but of depth, and probably, also, breadth; nevertheless, the shape and disposition of the constituent bones are such that, perhaps, no other known skull of a vertebrate is constructed with more economy of material—with an arrangement and connection of bones more completely adapted to combine lightness with strength.

So far as the skulls of *Pterosauria* have been sufficiently entire to show the shape of the head, no other known species resembles *Dimorphodon*. The cranial part is singularly small: the rest is mainly devoted to the formation of the large, long, and powerful prehensile and manducatory jaws. Among the débris of the cranial bones, in specimens Pls. XVII and XVIII, the mastoid (8), parts of the occipital (paroccipital, 4), the parietal (7), post-frontal (12), frontal (11), prefrontal (14), and nasal (15), are recognisable: the last two bones, however, are concerned more with the scaffolding or buttressing of the upper jaw than with the protection of the brain or formation of its case. Though contributing their shares to the otocrane, the chief developments of the paroccipital (Pl. XX, 4) and mastoid (ib. 8) relate to the muscular connections of the head with the trunk: the mastoid joins the postfrontal to form an upper zygoma, giving origin to part of the temporal muscles; it also affords a fixed articulation to the tympanic, and sends down a pointed process external to the masto-tympanic articulation. The parietals (Pl. XX, 7), confluent at the mid line, where they develop a low crest, swell out slightly at the temporal fossa, indicative of the size and saurian position of the mesencephalon. The frontal (11) is narrow and flat between the orbits, of which it contributes most of the upper part of the rim. This is continued by the postfrontal (12) behind, which sends down a long pointed process to unite with the malar (26), and a shorter and thicker one to join the mastoid (8). The prefrontal (14), of a triangular form, contributes to the upper and fore part of the orbit, and, either directly or by a connate lacrymal, unites with the ascending malo-maxillary process (21, 26), and the base of the prefrontal articulates with the frontal and the nasal. The nasals (15), to the usual connections with the frontal, prefrontal, and medial process of the premaxillary ($22'$), superadd a union with the lateral ascending process of the maxillary (21^{s}), completing the bar between the nostril (*n*) and the antorbital vacuity (*a*). The nasal bone forms the upper part of the nostril; the rest of the boundary of that singularly wide aperture is formed by the premaxillary and maxillary. Of the basis cranii and palate there do not appear to be any recognisable parts preserved. The maxillary is overlapped by the hind alveolar part of the premaxillary, and unites therewith by a long oblique suture ($21''$). The maxillary, receding, expands and sends upward a long slender pointed process to articulate with the nasal; it then joins the malar and the prefronto-lacrymal, and descends internal to the mandible to join the palatine.[1] Each maxillary (21, 21′) affords alveoli for eight or nine teeth.

The premaxillary is the largest of the bones of the head. The pair, by confluence or connation, constitute the fore part of the upper jaw (22), expanding from a sub-obtuse apex as it recedes, and preserving its entireness for an extent of about two inches. This tract seems to be arched above transversely, with a slightly convex upper longitudinal contour continued along the medial ray or process (22′). Of the configuration of the palatal surface the specimens give no evidence. From the analogy of *Pterodactylus Cuvieri* and *Pt. Sedgwickii*,[2] we may infer that this (premaxillary) part of the bony roof of the mouth was entire, and strengthened by a median ridge. The lateral or alveolar borders formed alveoli for four teeth on each side. Thus the hind expansion of the premaxillary divides into three rays or processes. The upper medial or nasal ray is the longest: it is continued backward, continuing the initial curve of the upper contour of the face as far as the nasals, the mid suture or confluence of which bones it overlaps, and joins suturally to an extent precluding any movement of the upper jaw on that part of the head. The length of this ray is about 3½ inches. The pair of lower or alveolar rays extend back for about 1½ inches.

The malar (26) forms the lower narrower end of the oval orbit, sending up one pointed process (united with that of the maxillary ?) toward the prefrontal, and a longer and stronger one to join the postfrontal. The squamosal (27) continues the zygomatic bar backward to abut against the tympanic. Its precise position and direction are left doubtful in the specimens hitherto obtained, but it is unquestionably present, and contributes to the fixation of the tympanic.

This (28) is a moderately long and strong pedicle, immovably articulated to the mastoid, paroccipital, and squamosal; thickest posteriorly, where it is strengthened by an outer marginal ridge, sending forward and inward a process which may articulate with the pterygoid (but of this I could not get clear evidence), expanding at its distal end to receive the abutment of the squamosal or lower zygoma, and to form the convex condyle for the articular element of the mandible.

The dentary parts of the mandible are confluent at the symphysis, which is as long as the undivided fore part of the premaxillary. The ramal part of the dentary is compressed, and gains a depth of about 10 lines before it bifurcates. The alveolar border of the dentary extends as far as that of the maxillary, viz. about 5 inches, beyond which the upper prong (Pl. XX, 32′) is continued above the mandibular vacuity, underlapping the surangular (29) and terminating in a point. The lower prong (ib. 32″) terminates in a point before attaining the vacuity; it is underlapped by the fore part of the angular (30), with which it articulates.

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[1] This description is on a homological hypothesis, subsequently discussed (p. 64).

[2] 'Monograph on Cretaceous Pterosauria,' Suppl. 1, 4to, 1859, Pl. I, fig. 1, *b*.

The divergence of the hinder prongs of the dentary exposes a small part of the splenial (31). The vacuity, if it be natural and not due to abrasion of a thin outer wall, is a long and narrow oval, 1 inch 8 lines in length, 6 lines in breadth. It is circumscribed behind by the confluent angular and surangular elements (29). The angular (30) forms a slight projection behind the articular concavity; it expands vertically, and contracts transversely as it advances, contributing a small share to the lower border of the vacuity, and contracting to a point below the dentary, about 5 inches from the angular process.

The range of variety shown by the skull is considerable in the order *Pterosauria*. In relative size, as in the expanse of the antorbital vacuity, *Pterodactylus crassirostris*[1] comes nearest to *Dimorphodon*; but the orbit is relatively larger, and the nostril much smaller. In *Rhamphorhynchus Gemmingi* the nostril and antorbital vacuity are of equal size, and each is about one eighth the size of the orbit, which is proportionally larger than in *Dimorphodon*. In *Pterodactylus longirostris*[2] the nostril is larger than the orbit; the antorbital vacuity is not half the size of the orbit. In *Pterodactylus suevicus*[3] the antorbital vacuity is still smaller. In *Pterodactylus Kochii*[4] that vacuity is limited, as in *Chlamydosaurus*, to the upper part of the boundary between the large orbit and the long and large nostril. In *Pterodactylus longicollum*[5] it appears to be wanting.

The shape of the skull offers many modifications in the several species, from the long and slender type of that of *Pterodactylus scolopaciceps* and *Pt. longirostris* to the shorter and deeper cone indicated by *Pt. conirostris*,[6] and to the inflated and more or less anteriorly obtuse form exhibited by *Dimorphodon* and the more gigantic *Pterodactylus simus*.[7]

The position of the tympanic pedicle varies from the almost vertical one in *Dimorphodon* to the almost horizontal one in *Pterodactylus longirostris* and *Pt. Kochii*. In *Pt. crassirostris* it shows an intermediate slope or position.

The mandible, conforming in relative depth and length to the general shape of the skull, has the symphysis longest in those species with long and slender jaws. In *Pterodactylus suevicus* the symphysis extends along the anterior third part of the mandible. In *Pt. crassirostris* it is shorter, and still shorter in *Dimorphodon*. The depth of the rami decreases behind the dentigerous part in *Pterodactylus longirostris*.

The generic dental character of *Dimorphodon* has been given in detail in the special descriptions of the specimens figured in Pls. XVII and XVIII. The range of variety mani-

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[1] 'Monograph on Fossil Reptilia of the Cretaceous Formations' (1851), *Pterosauria*, Pl. XXVII, figs. 2—4.

[2] Ib., ib., fig. 1.

[3] QUENSTEDT, op. cit.

[4] VON MEYER, op. cit., tab. i, fig. 2.

[5] Ib., ib., tab. vii, figs. 1—4.

[6] Dixon's 'Geology and Fossils of the Tertiary and Cretaceous Formations of Sussex, 4to, 1846, Pl. 38.

[7] 'Monograph on Fossil Reptilia of the Cretaceous Formations' (*Pterosauria*), Suppl. No. 3 (1861), Pl. I, figs. 1—3.

fested in this character is considerable in the present order, although in no species has any departure been observed from the predatory zoophagous condition. The teeth, always simple and pointed, vary in shape, in number, in position, in relative size. *Pterodactylus crassirostris* exemplifies the laniariform type of teeth, more or less elongate, and separated by intervals of varying extent. In this not uncommon condition the teeth are longest in the upper jaw, as offering more resistance than does the lower jaw in aid of the weapons most deeply implanted in the struggling prey.

In *Pterodactylus longirostris* the teeth are rather small, subequal, with short intervals, a little widening toward the hind end of the series, which is restricted to the anterior half of the jaw, both above and below.

In some *Pterosauria* a certain extent of the fore part of both upper and under jaws is edentulous, and from its shape has been inferred to have supported a horny sheath. The teeth are long slender canines, with wide intervals. They number from about 8 to 10 on each side of the upper jaw, and from 7 to 8 in each ramus of the mandible. Von Meyer proposed for this modification of mouth the generic name *Rhamphorhynchus*.

Dimorphodon shows the combination of scattered laniaries, with small, more closely set serial teeth in the lower jaw; it has more numerous teeth, occupying a greater extent of the alveolar margins of the jaws, than in any other Pterosaurian.

The very small teeth which have been observed in the short jaws of the little *Pterodactylus brevirostris*[1] are most probably characters of immaturity, not of species.

In regard to the bony structure of the head and the dentition, the general result of observation and comparison of Pterosaurian fossils, and common consent of competent investigators, having excluded the volant Mammals from the claim of affinity, the question becomes narrowed to whether the skull in *Pterosauria* more resembles that in the cold-blooded or the warm-blooded oviparous air-breathing Vertebrates.

Hermann von Meyer, who has contributed a great and valuable share to our knowledge of the Pterosaurian order,[2] quoting Oken's opinion, "that the skull is intermediate in character between that of the Chameleon and Crocodile," sums up his own conclusions on that head in the following terms :—"The skull of *Pterodactylus* is essentially comparable only with that of Birds and Saurians. The preponderating resemblance with the Bird's skull cannot be contested. Against this, however, is a remarkable dissimilarity in certain parts which, on the other hand, approximates it to the type of Saurians."[3]

The term *Sauria* is here used in the sense of Brongniart and Cuvier, and it is open

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[1] Goldfuss, loc. cit., tab. x, fig. 2.

[2] Especially in the admirable summary of his own and others' researches, in the part of his great work, 'Zur Fauna der Vorwelt' relating to "Reptilien aus dem lithographischen Schiefer," &c., fol., 1860.

[3] "Der Schädel der Pterodactyln, der nach Oken zwischen Chamäleon und Crocodil stehen würde, lässt sich eigentlich nur mit den Vögeln und den Sauriern vergleichen; die überwiegende Aehnlichkeit mit dem Vogelkopfe kann nicht bestritten werden; ihr gegenüber steht aber eine auffallende Unähnlichkeit in gewissen Theilen, die dafür zum Typus der Saurier hinneigen."—Op. cit., p. 15.

to the unbiassed investigator, and, indeed, becomes plainly his business, to determine, not merely whether Avian or Saurian characters predominate in the Pterosaurian skull, but to define the degree of affinity or correspondence of cranial structure therein traceable to such structures in *Enaliosauria*, *Dinosauria*, *Dicynodontia*, *Crocodilia*, *Lacertilia*, each of which may be a group, organically, of co-ordinate value with *Aves*.

Greater respect to the memory of so unbiassed a seeker after truth cannot be shown than by weighing with due care and what judgment one may be able to bring to the task the value and significance of each well-determined evidence of the cranial structure which Von Meyer has described and reasoned upon.

It is to be regretted that not in any of the numerous figures of the skull of *Pterosauria*, original or copied, has Von Meyer indicated the bones which he describes. When he writes—"The temporal bone lies external to the parietal and principal frontal bones, and mainly forms the temporal fossa,"[1] one much wishes he had indicated his 'Schläfenbein' in the skull of *Rhamphorhynchus Gemmingi*, pl. iii, fig. 4; pl. ix; pl. x, fig. 1; or in the more instructive example of cranial structure which he has borrowed from Goldfuss for the subject of his pl. v (*Pterodactylus crassirostris*).

By 'Schläfenbein' Von Meyer may mean that element of the compound 'temporal bone' of anthropotomy which I have called 'squamosal.' No doubt in Man and most Mammals the squamosal does contribute a notable share to the formation of the temporal fossa, whence the name 'temporal' given to the incongruous group of cranial elements coalescing in such warm-blooded Vertebrates with the squamosal, so exceptionally expanded in the *Mammalia*. But as to the value of the bed of the temporal muscles in determining the homology of the bones forming it, I would refer to the remarks in my work on the 'Homologies of the Vertebrate Skeleton.'[2]

Some clue to the bone signified by Von Meyer may be got from the following remarks—"Anteriorly it seems not to take, as in Birds, a share in the formation of the orbital rim; here, much more as in Saurians, it is pushed aside or supplanted by the postfrontal."[3]

The term 'temporal bone' (Schläfenbein) has been used in various senses, but whether it be applied to that element which I, with Cuvier, call 'mastoid' in *Reptilia*, or to that which others,[4] with Cuvier, call 'temporal' (meaning squamosal) in Birds, there is no bone that Von Meyer can be supposed to mean by 'Schläfenbein' which forms any part of the rim of the orbit in Birds.

Von Meyer recognises a 'postfrontal' ('Hinterstirnbein') in *Pterosauria*, and states that it pushes away his temporal (Schläfenbein) from the orbit. In *Pterosauria* the post-

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[1] "Das Schläfenbein liegt aussen an dem Scheitelbein und Hauptstirnbein, und bildet hauptsächlich die Schläfengrube."—Op. cit., p. 15.

[2] 8vo, 1848, p. 33.

[3] "Vorn scheint es nicht wie in den Vögeln an der Bildung des Augenhöhlenrandes Theil zu nehmen, hier vielmehr wie in den Sauriern durch das Hinterstirnbein verdrängt zu werden."—Op. cit. p. 15.

[4] Hallman, "Die vergleichende Osteologie des Schläfenbeins," p. 8, pl. 1.

frontal (Pl. XX, 12) is undoubtedly interposed between the bone I determine as 'mastoid' (ib. 8) and the orbit (ib. *o*); and my 'mastoid' in *Pterosauria* answers to Cuvier's and Hallman's 'temporal,' *i.e.* squamosal, in Birds. We may conclude, therefore, that Von Meyer's 'Schläfenbein' in *Pterosauria* is that marked 8 in the skull of *Pterodactylus crassirostris*.[1]

Certain it is that no bone answering to 8 in Pls. XVII, XVIII, XX of the present Monograph contributes to the formation of the orbit in any Bird. In the great majority of that class, as is well known, the rim of the orbit is incomplete below; it is formed above by the frontal, before by the prefrontal and lacrymal ('antorbital' of ornithotomists), behind by the postfrontal ('postorbital,' ib.). Where, as in some *Psittacidæ*,[2] the orbital rim ('Augenhöhlenrandes') is complete, the lower complement is formed by an extension of ossification from the antorbital to the postorbital processes, independently of either Cuvier's temporal (8) or my squamosal (27) in Birds.

I confess that the foregoing result of the analysis of a main ground of VON MEYER's assertion as to the "incontestable similarity between the Pterosaurian and Avian types of cranial structure" has not a little tended to shake my confidence in the grounds on which he has pronounced definite judgment on the matter. So far as we have yet got evidence of the structure of the skull in *Pterosauria*, it seems that, contrary to the rule in Birds, the orbital rim is entire; and that its lower border is completed by the zygomatic arch, and chiefly, if not exclusively, by the malar element; whereas, such arch passes freely beneath the orbital rim in the few Birds with that rim entire. Now, in this part of the cranial structure the *Pterosauria* agree with the *Crocodilia*: as in them the malar (26) sends up a process to unite with one descending from the postfrontal (12) to complete the orbital rim behind.

In the small species of Pterodactyles (*Pt. longirostris*, *Pt. scolopaciceps*, and in the perhaps immature animal represented by *Pt. brevirostris*) the hind convexity of the cranial wall is not marked by the apophysiary developments of paroccipital and mastoid, and accordingly resembles that part of the cranium in Birds, especially the smaller *Grallæ*; but before this similarity of shape can be pressed into the argument for the Avian affinity of the *Pterosauria*, it should be shown to be common to or constant in the extinct volant order.

But this is far from being the case. When a Pterosaur has gained the size of *Pterodactylus crassirostris*[3] or *Pter. suevicus*,[4] the back of the skull shows no cerebral swelling, but only the crests and processes for muscular attachments, as in other *Reptilia*

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[1] 'Monograph on Fossil Reptilia of the Cretaceous Formations' (*Pterosauria*) (1851),' Pl. XXVII, figs. 3 and 4.

[2] 'On the Archetype and Homologies of the Vertebrate Skeleton,' 8vo, 1848, pl. i, fig. 1 (*Calyptorhynchus*); 'Anatomy of Vertebrates,' 8vo, vol. ii (1866), p. 51, fig. 30 (*Psittacus*), also p. 63.

[3] Goldfuss, op. cit., pl. vii.

[4] Quenstedt, op. cit.

of similar size. Even in *Rhamphorhynchus Gemmingi* the cranial convexity is not posterior, but is limited to the temporal fossæ behind the orbit, as in the specimen figured by Von Meyer in pl. ix, op. cit.; and this indication of the optic lobes is less conspicuous in the subject of pl. x, fig. 1. In *Dimorphodon* there is still less trace of this alleged Avian characteristic.

The bone which, in the Bird, as in the Pterosaur, forms part of the otocrane, articulates with the ex- and par-occipitals behind, with the alisphenoid in front, with the parietal above, and with the petrosal within, which contributes the articular surface to the tympanic and the upper rim to the meatus auditorius, also articulates in the Pterosaur, as in the Crocodile, with the postfrontal: and this character appears to be constant in the *Pterosauria* as in the *Crocodilia*, while it is exceptional in *Aves*. In the particulars in which the bone 8 differs in the *Pterosaurian* from that in the Bird, it agrees with 8 in *Crocodilia*; as *e.g.* in its high position in the cranium, owing to the low development of the cranial chamber; its greater degree of projection from the true cranial walls; the extensive and suturally fixed character of its articulation with the tympanic as compared with the more definite and restricted glenoidal movable articulation which the mastoid (8) affords to 28 in Birds. In all these circumstances, whether the bone 8 (Pl. XX, fig. 1) be called mastoid or squamosal, it is Reptilian, not Avian, in the Pterosaur.

Herr VON MEYER states, in another of his comparisons, that in the *Monitor*, *Iguana*, and *Stellio*, the prefrontal ('Vorderstirnbein') enters into the formation of the periphery of the external nostril (Nasenloch).[1] This is the case with *Varanus*,[2] not with true Monitors.[3] In *Tejus nigropunctatus* some extent of the suture between the nasal and the maxillary intervenes between the prefrontal and the nostril. The non-extension of the prefrontal to the external nostril shows no Avian affinity in *Pterosauria*; rather an agreement with the majority of *Reptilia*, as, for example, with the whole order of *Crocodilia*.

In some *Crocodilia* (*Teleosaurus*) and *Lacertilia* (*Chlamydosaurus*, *Lyriocephalus*) there is an antorbital vacuity, which, in the latter Lizard (Pl. XX, fig. 3, *a*), is equal in size with the nostril (ib., *n*) and intermediate in position between that cavity and the orbit (ib., *o*), which is large. A process of the maxillary rises obliquely backward to join the nasal, and to separate the intermediate vacuity from the external nostril. The lacrymal and prefrontal form the bar dividing the intermediate cavities from the orbit. In most Birds a small intermediate vacuity is partitioned off from the nostril by a process of the maxillary rising to join the nasal, and is similarly separated from the orbit by the lacrymal, which descends to join the malar. The great range of variety in the development of this 'intermediate' or 'antorbital vacuity,' in *Pterosauria*, has already been pointed out; but

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[1] 'Zur Fauna der Vorwelt,' fol., 1860, p. 16.

[2] See Cuvier, 'Ossemens fossiles,' v, pt. 2, pl. xvi, fig. 1 ('grand Monitor du Nil, *Lacerta nilotica*'), p. 259, the *Varanus Dracæna* of Merrem, *Varanus niloticus* of most modern erpetologists; also in pl. xvi, fig. 7, 'Monitor du Java,' p. 260; the *Varanus bivittatus*, of Merrem.

[3] As *e.g.* *Tupinambis teguixin*, 'Sauve-garde d'Amérique.' Cuvier, vol. cit., pl. xvi, figs. 10, 11, and *Thorictes Dracæna*, ib., figs. 12, 13; 'La Dragone,' ib., p. 263.

the comparable structure is by no means peculiar, as Von Meyer would lead one to infer, to the skulls of Birds.[1]

In no Pterosaurian has any obvious and unmistakeable suture been seen indicative of the respective shares taken by maxillary (21) and premaxillary (22) in the formation of the dentigerous part of the upper jaw: both bones combine to support the array of teeth; they have coalesced, at least at their external or faci-alveolar plates; as, likewise, have the right and left premaxillary portions forming the fore end of the upper jaw. The suture between this premaxillo-maxillary bone and the suborbital portion of the zygomatic arch remains. Accordingly, there is a choice of analogies in the interpretation of the observed facts: a proportion of the compound bone may be assigned to the premaxillary, according to the analogy of the Crocodile and Lizard; or the whole may be called premaxillary, according to the analogy of the Ichthyosaur.

Goldfuss, guided by the Lacertian analogy, limits the premaxillary to the anterior part of the upper jaw, and to the upper part of the external bony nostril (*n*); and he illustrates this view by a dotted line representing the assumed suture in his restoration of *Pterodactylus crassirostris*, in pl. ix (op. cit.).[2] Von Meyer assumes, as arbitrarily, the Ichthyosaurian analogy, but views it as a specially Avian one, and ascribes to the *Pterosauria* a bird-like premaxillary,[3] and this determination is indicated by the numerals on the restoration of the skull of *Pterodactylus compressirostris* in my Monograph of 1851, quoted below, Pl. XXVII, fig. 5.

Of the maxillary bone (my 21) Von Meyer merely remarks that "it does not follow the type of Birds" ("folgen nicht dem Typus der Vögel," ib., p. 15). And yet, if the Pterosaurian premaxillary be interpreted according to that type, forming so large a proportion of the upper jaw as to include all the teeth, the edentulous maxillary must have had a correspondingly Avian proportion and position. Only, whereas in most Birds the small and slender maxillary sends up a process helping to define the back part of the nostril and fore part of the antorbital vacuity, the corresponding process in *Pterosauria* would be (as indicated in my Pl. XVIII, 22'), part of the premaxillary.

I incline to believe, however, that it may prove to belong to the maxillary; that the dentigerous part of the upper jaw is due, in *Pterosauria*, to the combined maxillaries and premaxillaries, but that the latter take a larger share in the formation of the alveolar tract than Goldfuss conjectures. One ground of such opinion is this: the portion of upper jaw with six pairs of laniary teeth in the huge *Pterodactylus Sedgwickii*, in which the palatal surface could be clearly worked out,[4] showed that the anterior expansion, with the group of three pairs of teeth, could hardly have been

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[1] "Zwischen Nasenloch und Augenhöhle liegt eine dritte Oeffnung, die wiederum an den Vögelschädel erinnert."—Op. cit., p. 16.

[2] Copied in Pl. XXVII, fig. 4, of my Monograph above cited of 1851.

[3] "Ein Vögeln-ähnlichen Zwischenkiefers," v, p. 15, op. cit.

[4] Monograph, Suppl. No. 1 (1859), Pl. I, figs. 1, *a*, *b*.

separated by a suture, at the slight constriction suggesting that structure in *Pt. crassirostris*,[1] without leaving some indication of its original existence, especially on the palate.

In the anterior confluence of right and left premaxillaries, and the backward production from their upper part of a bony bar uniting with the nasals and dividing the nostrils, we have a character of the Dicynodonts and of some Lacertians (*Varanus*) as well as of Birds, and the Saurian affinity is shown to be the truer one by the firmness of the naso-premaxillary union and the absence of any power of, or provision for, that hinge-like movement of the upper mandible upon the cranium which is peculiar to, though not constant in, the Avian class. Moreover, the outer surface of the premaxillary shows none of that spongy porosity and rugosity which relates to the sheath or horny covering of the beak characteristic of the Bird. Such structure has not even been detected in the feeble trace of edentulous anterior production of the upper jaw in *Rhamphorhynchus*, Von Meyer. I cannot, therefore, see, with Von Meyer, the beak of the Bird in an animal with a fixed and toothed upper jaw;[2] for on every hypothesis of its bony structure it finds a closer resemblance among the toothed Reptiles than in the class of Birds.

The mandible, or lower jaw, is supported, as in all Vertebrates below Mammals, by the tympanic, viz. the bone (28, Pls. XVIII and XX) which is shown by its osseous connections, its relations to the 'facial nerve,'[3] or its equivalent the 'ramus opercularis,'[4] and by its mode of formation, to answer to that which in Mammals is mainly reduced to the function of supporting the ear-drum. In air-breathing Ovipara it superadds this function to its more constant and essential use in non-mammalian Vertebrates, of supporting the lower jaw.

In reference to the question of affinity before us, the tympanic gives valuable evidence by reason of the moveable articulation and peculiar connections with the upper mandible essentially correlated to a covering of feathers. In *Pterosauria* the tympanic at its proximal end resembles that of Lizards by its fixed sutural mode of union with the cranium, and it furthermore resembles that in Crocodiles by the abutment of the zygoma against its distal end, to which it is suturally attached.

In Birds the tympanic enjoys a synovial moveable articulation by a single or double condyle at its proximal or cranial end, and presents a synovial cavity to a condyloid convexity of the hind part of the zygoma. By this test, therefore, the *Pterosauria* are shown to be not only 'Saurian,' but to be nearest akin to the existing orders which possess double-jointed ribs and the correlated cardiac structure. The difference of shape between the tympanic of the Pterodactyle and that of the Bird is too strongly marked not to have attracted attention; but I do not find in that of the Chameleon the

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[1] Goldfuss, loc. cit.

[2] "Wir sehen also hier die Schnautze der Vögel auf ein Thier mit unbeweglicher und mit Zähnen bewaffneten Schnautze angewendet."—Op. cit., p. 15.

[3] 'Anatomy of Vertebrates,' vol. ii, 8vo, 1866, p. 124, vol. iii, p. 155.

[4] Ib., vol. i, p. 303.

most resemblance to the *Pterosaurian* tympanic.[1] For, besides the Lacertian freedom of the bone from zygomatic abutment, the tympanic in the Chameleon has not the longitudinal strengthening ridges, nor the process turned toward the pterygoid.

The dentigerous mandible, like the maxilla, speaks for the Reptilian affinity of *Pterosauria*; the distinct sockets for the teeth ally them to the higher forms of *Sauria*. In reference to the generic modification of dentition in *Dimorphodon*, it has been remarked that this early form of flying dragon seemed to have derived one feature or modification from the Fish, and the other from the Crocodile or Plesiosaur.[2]

The length of the neck, which is not always equal to that of the head, is due, in *Pterosauria*, rather to the length than the number of the vertebræ. Counting the axis with the small coalesced atlas[3] as one, I give seven cervical vertebræ to the *Dimorphodon macronyx* (Pl. XX, fig. 1, c). Of these a series of four are preserved in the specimen (Pl. XVIII, c), showing, as described, the characteristics of the Pterosaurian cervical vertebræ which had been determined and illustrated in a former Monograph.[4]

Cuvier,[5] in his searching analysis of the evidence at his command of the osseous structure of the *Pterodactylus longirostris*, concluded that the cervical vertebræ were not fewer than seven, as in *Crocodilia* and *Mammalia*, or not more than eight, as in *Chelonia*.

Goldfuss was able to demonstrate the vertebral formula in his famous specimen of *Pterodactylus crassirostris*.[6] The number, 'seven,' was, however, obtained by reckoning the atlas distinct from the axis, and the last cervical may have been relegated to the dorsal series.

Quenstedt[7] shows seven cervicals in his instructive example of *Pterodactylus suevicus*, reckoning the atlas and axis as one vertebra; and this analogy I have followed in the restoration of *Dimorphodon*.

Rhamphorhynchus Gemmingi has six cervicals, counting the coalesced atlas and axis as one; but in the specimen figured by Von Meyer in his pl. ix,[8] there seems to be the centrum of a short 'seventh' cervical between the longer 'sixth' and the first (dorsal) vertebra supporting a long free pointed rib. It is certain that the number of cervicals does not exceed the latter reckoning or fall short of the first. Thus it is plain that the *Pterosauria* exemplify the Crocodilian affinity in the cervical region of the vertebral column. Lacer-

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[1] "Dieser Knochen ist nicht wie in den Vögeln quadratisch, sondern cylindrisch stielförmig beschaffem.—Hierin, so wie in einingen andern Theilen, zeigt das Thier die meiste Aehnlichkeit mit *Chamaeleon*."—Von Meyer, op. cit., p. 16.

[2] 'Report (Sections) of the British Association for the Advancement of Science,' 8vo, 1858, p. 98.

[3] 'Monograph on the Fossil Reptilia of the Cretaceous Formations,' Supplement, No. I, *Pterosauria* (1859), pp. 7—8, Pl. I, figs. 11—14.

[4] Ib., p. 9—11, Pl. II. 'Monograph,' &c., Supplement, No. III (1860), p. 7, Pl. II, figs. 1, 2 and 4.

[5] 'Ossemens fossiles,' tom. cit., p. 367.

[6] "Man zählt 7 Halswirbel, 15 Rippenwirbel, 2 Lenden, and 2 Kreuzbeinwirbel," loc. cit., p. 79.

[7] Op. cit., figs. 1—7.

[8] Op. cit.

tians have fewer definite cervicals; Birds have more. I have not seen any Bird with fewer than eleven cervicals.[1] The length and flexibility of the neck is correlated with the covering necessitated by the high temperature of the Bird.[2] The cold-blooded flying Reptiles have a comparatively short and rigid neck, but of a thickness and strength proportionate to the size of the head, and adequate to the work to be performed by the jaws in overcoming and bearing away the prey they may have seized.

The chief variety manifested by the *Pterosauria* in the cervical region is in the relative length of the last six vertebræ; this is greatest in *Pterodactylus longicollum* and *Pt. longirostris*; it is least in *Pt. crassirostris* and *Dimorphodon macronyx*, and apparently also in *Pterodactylus simus*, if we may judge by the breadth, compared with the length, of the vertebra figured in Pl. XVIII, (figs. 1 and 2) of my Monograph, above cited, of 1860.

There seems to have prevailed a greater range of variety in the number of vertebræ between the cervical series and the sacrum. In *Pterodactylus longirostris*, Cuvier estimated at least twelve which supported moveable ribs,[3] and nineteen or twenty in the dorso-lumbar series. Von Meyer concluded that the number of dorsal vertebræ fell not below twelve in any species, nor exceeded fifteen or sixteen in *Pterosauria*. *Pterodactylus Kochii* shows fourteen dorsal vertebræ; *Pt. crassirostris* not more than twelve, reckoned by the number of pairs of free ribs, which can be satisfactorily discerned.

I have seen no specimen of *Dimorphodon* yielding definitely the number of the dorso-lumbar vertebræ, *i. e.* of the vertebræ between the cervical and sacral; it is from the best considerations I have been able to give to the analogies of these vertebral formulæ, in better preserved examples of other species of *Pterosauria*, that I assign thirteen to this series in my restoration of *Dimorphodon macronyx* (Pl. XX); and I conclude that the thirteenth was a true lumbar vertebra or without connection with a free pair of ribs. If there should prove to be error in this estimate I cannot think it will extend beyond one vertebra, or at most two, in excess of twelve dorsals.

The nine dorsal vertebræ, which have kept together, in almost a straight line, in the specimen (Pl. XVIII, D), testify to the strength and closeness of their reciprocal articulations, under disturbing influences which have affected so great and general a degree of dislocation of most other parts of the skeleton.

BUCKLAND seems first to have observed the convexity of one of the terminal articular surfaces of the centrum of a dorsal vertebra, and to have deduced an affinity therefrom;

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[1] The Sparrow (*Pyrgita domestica*) has twelve ('Osteol. Catal. Coll. of Surgeons,' No. 1571, vol. i, p. 297).

[2] "As the prehensile functions of the hand are transferred to the beak, so those of the arm are performed by the neck of the Bird; that portion of the spine is, therefore, composed of numerous, elongated, and freely moveable vertebræ, and is never so short or so rigid but that it can be made to apply the beak to the coccygeal oil-gland, and to every part of the body, for the purpose of oiling and cleansing the plumage." —'*Anat. of Vertebrates*,' ii, p. 39.

[3] Vol. cit., p. 368:—"Il semble qu'il en est resté au moins douze en place du coté gauche." The specimen figured by VON MEYER, op. cit. in pl. i, fig. 1, shows thirteen ribs on the left side of the trunk.

(the specimen is marked *d* in the Plate 27 of his Memoir, loc. cit.), and is described "as the body of a vertebra showing a convex articulating surface, as in the Crocodile" (p. 221). Quenstedt's *Pterodactylus suevicus* showed similar detached dorsals, in one of which it appeared that "the articular surfaces of the body were convex at the back end, and concave at the fore part."[1] Buckland's specimen serves to dissipate any doubt on the point so important in reference to the Crocodilian affinity. It might be assumed that the Author viewed the convexity as posterior by the expression "as in the Crocodile;" and in the last of the dorso-lumbar series, which I regard, with Buckland, as 'probably lumbar,' in the sense of not being costigerous, the position of "its concave articulating surface" is demonstrated by those of the articular processes (zygapophyses) at the same end of the vertebra, which prove them to be the anterior pair, slightly prominent, looking upward and inward. Buckland notes these as "two anterior spinous processes, an obvious typographical error for 'oblique' or 'articular,' venial in one not professedly an anatomist.[2]

With regard to the Crocodilian affinity inferred from this structure, it must be remembered that the procœlian stucture, though it has been observed in Crocodiles from the Greensand of New Jersey,[3] is characteristic of the Tertiary and existing species, rather than of the order at large, which had more abundant and diversified (amphicœlian and opisthocœlian) representatives in the Secondary ages of Geology. Moreover, the anterior concavity and posterior convexity of the vertebral body obtain in most recent, Tertiary, and Cretaceous *Lacertilia;* and finally, the cup- and ball-joints of the centrum appear in the dorsal vertebræ of at least one genus of Birds, though with the ball in front.[4]

In the series of nine dorsals, preserved in the subject of Pl. XVIII, D, the centrums slightly lose length as they recede in position from the neck; the anterior ones measure 0·009 mm. = 4½ lines; the posterior ones measure 0·008 mm. = 4 lines; the transverse diameter of the articular ends is 0·007 mm. = 3 lines. The dorsal vertebra in Buckland's specimen presents the same dimensions. These dimensions increase as the two or three anterior dorsals approach the neck, but the greater enlargement of the last cervical is somewhat abrupt.

For the shape and proportions of the ribs (in the Restoration, Pl. XX), I have those marked *b*, *c* in the original specimen,[5] and the more numerous and better preserved ones

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[1] "Die Gelenkfläche der Wirbelkörper war auf der Hinterseite convex, wie beim Crokodil, vorn dagegen concav. So scheint es wenigstens."—Quenstedt, Ueber *Pterodactylus suevicus* im lithographischen Schiefer Würtembergs. 4to, 1855, p. 45.

[2] Buckland, loc. cit., pl. 27. [This vertebra is shown in Pl. III, fig. 2, of the present Monograph.]

[3] "Notes on Remains of Fossil Reptiles discovered in the Greensand Formations of New Jersey," 'Quarterly Journal of the Geological Society,' vol. v, 1849, p. 388.

[4] As in *Aptenodytes;* "On the Vertebral Characters of the Order *Pterosauria,*" 'Phil. Trans.,' 1849, pl. x, fig. 22, p. 163.

[5] Buckland, loc. cit., pl. 27.

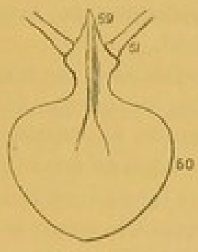
in the specimen figured in Pl. XVIII. Their articulations with the vertebræ have already been noticed. The ribs increase in length to the fifth or sixth, with some diminution of breadth after the third, and acquire a characteristic tenuity beyond the sixth pair. On the outer surface a groove extends from the neck, or interspace between the head and tubercle downward; the front border of the groove being somewhat prominent, but subsiding in the hinder ribs. Epipleural appendages are indicated in some specimens; but the indications are feeble, and, if rightly so interpreted, these appendages seem to have been but partially ossified.

The sternal ribs, beyond the sternum, unite below with the free ends of the abdominal V-shaped, intermuscular styles.

The irregular elongate mass (marked 18 in pl. xxviii of Buckland's Memoir) and conjectured to be "sternum—much broken, and its form indistinct" (loc. cit., p. 221) includes two crushed cervical vertebræ, and part of a third. Of the sternum I have not been able to discern a satisfactory trace in any of the specimens of *Dimorphodon;* its proportions and position are, therefore, indicated in the 'restoration' (Pl. XX) according to the analogy of that in *Pterodactylus suevicus*,[1] *Pt. simus*,[2] and in *Rhamphorhynchus*.[3]

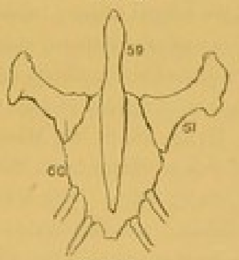
In the main, as regards breadth of the hind part and depth of the fore part, the breastbone of *Pterosauria* is formed on the Ornithic pattern; *i. e.* it is shield-shaped, and it has a keel. But the keel does not descend from the expanded portion; it is formed, as shown in a former Monograph (Suppl. No. III, p. 8), by the vertical development of the anterior production answering to the ossified sternum of Crocodiles and to the episternum of Lizards. I would recommend a comparison of the figures of the sternum in *Iguana* and *Notornis*, given at p. 21, vol. iii, of my 'Anatomy of Vertebrates,' to whosoever may desire to form an opinion of the evidence of affinity to Birds or to Reptiles, respectively, afforded by the Pterosaurian sternum, especially as this is illustrated in figures 7 to 12 of Pl. II of the Supplement No. III, above cited. No one desirous of simply getting at the

Fig. 1.



Pterosaur.

Fig. 2.



Crocodile.

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[1] Quenstedt, loc. cit. (1855).

[2] 'Monograph,' Suppl., No. III (1860), Pl. II, figs. 7—12.

[3] Von Meyer, op. cit. (1860), pl. vii, figs. 1 and 3, and pl. ix, fig. 1.

truth of the matter can put aside the 'post-coracoid lateral emarginations,' and other modifications defined in that Monograph as 'distinctive Pterosaurian characters.' No Bird has shown any approach to them. What modifications of the Pterosaurian sternum *Dimorphodon* may have presented, we have yet to learn.

In all cases in which it has been observed, the sternum in *Pterosauria* (fig. 1) resembles in essential characters that of *Crocodilia* (fig. 2); its chief part is a longitudinal, compressed, deep bar (59), expanding laterally, some way from the fore-end, for the articulation of the coracoids (51),[1] and having the posterior expansion (60), which remains cartilaginous in the *Crocodilia*, more or less ossified, in the form of a thin semicircular plate: but the whole bone, though adaptively modified for attachment of muscles of flight, preserves the characteristic shortness compared with the trunk, and offers a striking contrast to the long and large subabdominal plastron in most birds of flight. There is no distinct T-shaped episternum, such as exists in most *Lacertia*, and no trace of clavicles as in Lizards and Birds. Distinct lateral elements for articulation with sternal ribs I have not satisfactorily made out in any specimen.

The abdominal hæmal arches consist of slender hæmapophyses and of chevron-shaped hæmal spines.

There is evidence of one lumbar or ribless vertebra anterior to the sacrum, in *Dimorphodon;* and no Pterosaurian appears to have shown more than two such vertebræ: in this character we are again directed to the true Reptilian relation of *Pterosauria,* and warned off the beguiling marks of Avian affinity.

The indications of epipleural appendages of ribs, more or less bony, if rightly interpreted, answer to the gristly ones in *Crocodilia* and some *Lacertia*.[2] The restoration of the bony cage of the thoracic-abdominal cavity of *Dimorphodon* (Pl. XX) is based on the analogy of better preserved specimens of *Pterosauria* in regard to this part of the skeleton. Scattered elements of the hæmal arches, 'abdominal ribs,' &c., have alone been met with in the specimens of *Dimorphodon* hitherto obtained.

The sacrum, on the probable hypothesis of retention of the length of centrum shown in the lumbar vertebra, would include at least four vertebræ; if, as by the analogy of the sacrum (figured in Pl. II, fig. 26, of the Monograph, &c., Supplement No. 1, 1859), the vertebræ lost length at this confluent tract, there might be five or six sacrals articulating with the iliac bones in *Dimorphodon*. VON MEYER figures 5—6 anchylosed sacral vertebræ in his *Pterodactylus dubius;*[3] and the sacrum appears to consist of at least six confluent vertebræ in *Rhamphorhynchus grandipelvis*, Von Meyer.[4]

With all the evidence that the *Pterosauria*, like the *Dinosauria* and *Dicynodontia*,

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[1] 'Monograph on Cretaceous Reptilia,' Supplement, No. III (1860), Pl. II, figs. 7—12.

[2] As in *Hatteria*, see Günther's excellent Memoir, in 'Philos. Trans.,' Part II, 1867, p. 13, pl. ii, figs. 17, 24.

[3] Op. cit., p. 17, pl. vi, fig. 1.

[4] Op. cit., p. 53, pl. viii, fig. 1.

exceeded the sacral formula prevailing in existing *Crocodilia* and *Lacertilia*, we should gain no firm ground therefrom for predicating Avian affinity or for building thereon a derivative hypothesis of the class of Birds. Many existing Chelonian Reptiles have a sacrum composed of more than two vertebræ.[1]

The perfect specimen of tail-vertebræ and associated bone-tendons in the specimen (Pl. XIX, fig. 4) completes satisfactorily the restoration of this part of the vertebral column in *Dimorphodon*. Before the discovery of *Rhamphorhynchus*, the order *Pterosauria* was known only through species having the tail very short. Not only were the vertebræ comparatively few, estimated at twelve or thirteen in *Pterodactylus longirostris*,[2] at fourteen in *Pt. spectabilis*, at fifteen in *Pt. scolopaciceps*,[3] and as low as ten in *Pt. Meyeri*,[4] but they were very small and short. The great advocate of the Avian affinity of the Pterosaurs, SOEMMERRING, based his chief argument in this character. But CUVIER was able to adduce instances of *Reptilia* with tails as short; and he might now have cited a Bird with a tail-skeleton as long, as slender, and as many-jointed as in divers Saurians.[5] The earliest indication of a range of variety in this part of the bony framework of a Pterosaur was deduced, with his usual sagacity, by BUCKLAND.

In the original specimen of *Dimorphodon* are three caudal vertebræ at the base of the tail, marked K, in pl. xxvii of his Memoir, from the size of which vertebræ, together with the larger and longer legs, as compared with *Pterodactylus longirostris*, BUCKLAND inferred that the entire "tail was probably longer, and may have co-operated with the legs in expanding the membrane for flight."[6] "A long and powerful tail," he proceeds to remark, "is in strict conformity with the character of a Lizard" (ib.).[7]

BUCKLAND would have had further direct confirmation of the length and strength of the tail of his Lias Pterosaur, if he had recognised the series preserved at *a*, *a'*, in his pl. xxvii, as caudal vertebræ; but they were conceived to belong to the neck, notwithstanding their slenderness and length, and that around them were "small cylindrical bony tendons, resembling the soft tendons that run parallel to the vertebræ in the tails of Rats."[8] When the evidences of caudal structure were first recognised by Von Meyer, in *Rhamphorhynchus Gemmingi*, he detected the homologous structures in pl. xxvii of

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[1] 'Anat. of Vertebrates,' vol. i, p. 65.

[2] By Cuvier, vol. cit., p. 368.

[3] Von Meyer, op. cit., p. 17.

[4] Ib., p. 17.

[5] Owen "On the *Archæopteryx*," 'Philos. Trans.,' 1863, p. 33, pls. i—iv.

[6] Buckland, loc. cit., p. 221.

[7] *Archæopteryx* had not then been discovered; else, it might have been objected to the above hint of affinity, not only that there had been short-tailed Pterodactyles, but also long-tailed Birds.

[8] "Mr. Clift and Mr. Broderip have discovered that the remaining cervical vertebræ are surrounded with small cylindrical bony tendons of the size of a thread. These run parallel to the vertebræ, like the tendons that surround the tails of rats, and resemble the bony tendons that run along the back of the pigmy musk and of many birds" (loc. cit., p. 218).

Buckland's Memoir, and suggested that its subject might belong to the same section or genus.[1] The subsequent discovery of the skull and dentition has, however, shown that another generic section of *Pterosauria*, or at least one species thereof, had a similar long and stiff tail. The modification involving that quality does not, however, extend throughout; the anterior caudal vertebræ retain the more normal character, and the appendage would be most moveable at its base. No doubt a small degree of yielding at the many persistent vertebral joints—for complete anchylosis has not been observed—would allow a slight curvature to the extent to which the tail is represented as yielding to a lateral force in the restored figure (Pl. XX, fig. 2). The number of the caudal vertebræ in *Dimorphodon macronyx* was at least thirty; the termination of the specimen figured in Pl. XIX, fig. 4, does not indicate a loss there of as many centrums as would bring the number up to thirty-eight, which are assigned by Von Meyer to his *Rhamphorhynchus Gemmingi*.

As we cannot, therefore, with Soemmerring, insist on the shortness of the tail in some *Pterosauria* as proof that they were Birds, so neither can we conclude from the length of the tail in other *Pterosauria* that they were Reptiles. The legitimate taxonomic deduction from such caudal modifications is, that they are not of sufficient importance for determination of a class, and that they do not exclusively characterise the genus. They indicate adaptations in an extreme and variable part or appendage of the body to special powers or ways of movement, or sustentation, in air of the present group of volant animals.

So, likewise, it cannot be, as it has been, inferred from the length of tail in *Archæopteryx*, that it was a Reptile.[2] What we learn from that Avian fossil is akin to what we have learnt from Pterosaurian remains, viz., that the tail is a seat of extreme modification, in respect of length and number of joints, within the limits of the feathered class. Mammalogists, with a like drift, could add instructive evidence of corresponding caudal variability within the limits of the order, as in the volant *Cheiroptera*, and even within the bounds of the family (*Bradypus* and *Megatherium*, *e. g.*).

The value of the discovery of *Archæopteryx*, in relation to *Pterosauria*, is enhanced by the peculiar nature of the matrix, conservative of cutaneous as well as of osseous characters; showing casts of down and feathers,[3] impressions of the fine foldings or wrinkles of thin expansions of naked skin, as well as delicate tendons surrounding, working, strengthening, and stiffening the caudal framework.

With these parts the fine lithographic lime-marl should have preserved the plumose appendages of the long tail of *Rhamphorhynchus*, if that flying Reptile had possessed such; and, along with caudal plumes and vertebræ, should have been preserved the bone-tendons of the tail, if *Archæopteryx* had possessed that structure.

It is probable, from the constancy with which caudal vertebræ of long-tailed

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[1] In 'Leonhard und Bronn's Neues Jahrbuch für Mineralogie,' &c., Jahrgang, 1857, p. 536.

[2] *E. g.*, as the *Gryphosaurus* of Andreas Wagner.

[3] A few of the delicate, downy body-feathers of *Archæopteryx* are clearly indicated near one side of the trunk in the slab with most of the bones of the specimen of *Archæopteryx* in the British Museum.

Pterosaurs have been found associated with their tendons,[1] that detached caudal vertebræ of *Archæopteryx* might be recognised through the want of them.

We may confidently conclude that the Oolitic mud which has entombed the greatest number and variety of the flying reptiles of its period would have shown us, when petrified into lithographic slate, their feathers, if, as warm-blooded animals, they had needed such heat-conserving a covering. The plumose clothing of the long-tailed bird of the period proves its hæmatothermal character, as the want of it shows the long-tailed pterosaur to have been cold-blooded.

The tyro, fresh from the lecture-room of his physiological teacher, ambitious of soaring into higher regions of biology than were opened to him at the medical school, impressed with the relations of active locomotion to generation of animal heat, may be pardoned for inferring that the amount of work involved in sustaining a Pterodactyle in the air would make it, physiologically, highly probable that it was a hot-blooded animal. But a competent friend, finding him bent on rushing with such show of knowledge into print, would counsel him to provide himself with a thermometer adapted to the delicate testing of the internal heat of small animals. So provided, if he should chance to beat down a chafer in full flight, the experiment, made with due care and defence of the fingers guiding the instrument, would teach him how fallacious would be the inference that, because an animal can fly, it must, therefore, be hot-blooded. Unless he happen, in introducing the bulb by the widened vent into the abdomen, to plunge it into a mass of ova, he will find the heat of the beetle, notwithstanding the amount of work involved in sustaining and propelling itself in air, not to exceed by more than one degree that of the atmosphere. If he has knocked down a female cockchafer prior to oviposition, the ovarian masses may indicate half a degree, or even one degree, higher of temperature (Fahr.). With the cooling of the air in the summer night the temperature of the *Melolontha* concurrently falls. So, likewise, would that of the flying reptile, whatever "amount of oxidation and evolution of waste products in the form of carbonic acid"[2] might have attended their exercise of flight. The constant correlative structure with hot-bloodedness is a non-conducting covering of the body. We may with certainty infer that *Archæopteryx* was hot-blooded, because it had feathers, not because it could fly.

There is no ground, from observation of the Sharks and Porpoises that accompany swift-sailing vessels, maintaining themselves near the surface, exercising their several and characteristic evolutions in quest or capture of prey, for inferring that the amount or the energy of muscular action is very different in the two surface-swimmers.

Sharks have and, no doubt, work a greater proportion of muscle than Cetaceans; a less proportion of their body is excavated into visceral cavities. Yet the Shark is cold-blooded; its temperature rises and falls with that of its medium; it has no provision, by

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[1] As seen in Pl. II, at *cd*, and in Pl. III, figs. 3, 4, 5.

[2] 'Proceedings of the Zoological Society,' April, 1867, p. 417, Prof. Huxley "On the Classification of Birds."

a blanket of blubber or other superficial modification, in aid of the maintenance of a fixed and high degree of blood-heat.

There are conditions, it is true, in which a Reptile generates a higher degree of heat than is usual, but they are not those accompanying any unusual or excessive muscular work and waste; they are attended with rest, not locomotion. The incubating Boa gives to the hand that may be insinuated between the coils surrounding the eggs the sensation of a warm-blooded animal. VALENCIENNES[1] found, in the Reptile-house at the Jardin des Plantes, when its temperature, in the month of May, was 23° (Centigrade), that the heat of the *Python*, between the folds and upon the eggs, was 41·5° (ib.); so also the heat of the incubating surface of the Bird may rise to 10 degrees (Centigr.) above the ordinary temperature—higher in this passive state than it ever reaches during flight.

The organic condition which determines the hot-blooded or cold-blooded nature of a volant Vertebrate is the separation or the commingling of the arterial and venous bloods in the course of their respective circulations. From the demonstrated absence of any heat-retaining covering of the skin in *Pterosauria*—the kind and amount of negative evidence hereon being decisive—I infer that the black and red sanguineous streams were mixed by intercommunication of the aortic trunks of the right and left ventricles, as in the Crocodile.[2] The plumose integument of *Archæopteryx* bespeaks the separation, not only of the pulmonic and systemic ventricles, but of the arterial trunks thence arising; it was, consequently, hot-blooded, not because it could exert the muscular force required to sustain itself in the air. The all-important condition of the circulating system has wide correlations, not only with the extensive superficies acting upon the surrounding medium, and being reacted upon thereby, but with a rapid and uninterrupted respiration, with an advanced status of the nervous system, especially the brain, involving higher intelligence and more lively and varied instincts, especially the parental. In the organic character determining temperature, breathing, and higher phenomena of life, Birds agree with Mammals and differ from Reptiles.

Birds agree with Implacental Mammals (*Lyencephala*) in the development, by the embryo, of a vascular allantois devoid of villi for placental connection.[3] They agree with the same Mammals and differ from Reptiles in the transversely and deeply folded cerebellum, and in the larger proportion of that and of the cerebrum to the optic lobes. Birds resemble Reptiles in the absence, not only of a corpus callosum, but of a fornix and hippocampal commissure. The *Lyencephala* have the hippocampal commissure, but no

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[1] "Faites pendant l'incubation d'une femelle du Python à deux raies (*Python bivittatus*, Kuhl)," &c. 'Comptes rendus de l'Acad. des Sciences,' Paris, 19 Juillet, 1841.

[2] 'Anat. of Vertebrates,' *i*, pp. 510—512, figs. 339, 340.

[3] This character is affirmed to be "of extreme importance, and to define Birds and Reptiles, as a whole, very sharply from Mammals."—Prof. Huxley 'On the Classification of Birds,' loc. cit., p. 416. But, then, the emphatic assertion comes from a writer on Elementary Physiology, who infers the blood of the *Pterosauria* to have been hot because they were able to sustain themselves in air!

corpus callosum; this characterises the Placental Mammalia. Birds differ from other Oviparous Vertebrates in the chalaziferous ovum. The particulars in which Birds differ from all Mammals and agree with Reptiles are comparatively unimportant ones of the skeleton. The occipital condyles (*e.g.*) are more completely blended or unified than in Cetacea. The tympanic is interposed between the mandible and the mastoid, as in Reptiles.[1]

Two genera of Lyencephalous Mammals retain the osteological character common to Birds and Reptiles of the connection of the scapula with the sternum by the intermediation of a fully developed coracoid, and it is one of several and more important characters disproving any sharp definition of the higher warm-blooded Ovipara, at least, from the Ovo-viviparous or Implacental Mammalia.

The scapular arch retains, in *Pterosauria,* its crocodilian simplicity, modified in shape and in the angle at which the scapula meets the coracoid adaptively for the function of flight in the limb suspended thereto. There is, consequently, a close similarity to the same elements in Birds of Flight,[2] but without any trace of the superadded furculum. The articular grooves on the sternum for the coracoids communicate or run into each other at the mid line. The articulation of the corresponding end of the coracoid must be as secure, and yet with as easy a motion, due to a well-turned synovial joint (shown first in *Pterodactylus Woodwardi* and *Pt. simus*),[3] as in any Bird. The confluence of the scapula with the coracoid seems not to be constant in the order *Pterosauria;* and where it has been found, as in *Dimorphodon* and *Pterodactylus Fittoni,* traces of the original suture are present, as represented in the large Neocomian *Pterosauria* in my Monograph of 1859.[4]

In some specimens of *Ramphorhynchus Gemmingi* and in *Ramphorhynchus longicaudus* the scapula and coracoid seemed not to have coalesced.[5] The coalescence is complete and constant (so far as may be inferred from two specimens) in *Dimorphodon.*

For the analysis of the characters of the humerus in *Pterosauria,* I may refer to my Monograph, Suppl. No. III (1861), pp. 13—17, Pl. III. The chief seat of variety is the "radial crest" (Pl. XVIII, 53, *b*, of present Monograph). In the shape and proportions of this extraordinary process *Dimorphodon* resembles *Pterodactylus* more than it does *Ramphorhynchus.* In the proportions of the humerus to the body there is little diversity in the several species.

The antibrachium is commonly two sevenths longer than the humerus. It consists

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[1] As a taxonomic character—whatever degree of value may be adjudged to it—this mode of connection of the lower jaw with the skull gains nothing by calling the tympanic 'quadrate bone,' or by affirming it to represent the '*incus*' or the '*malleus*' of Mammalia, whichever may happen to be the favourite fancy of the day.

[2] 'Monograph,' Suppl. No. I (1859), p. 13.

[3] 'Monograph,' Suppl. No. III (1861), p. 12, pl. ii, figs. 7—12.

[4] Suppl. No. I, Pl. III, figs. 1—5.

[5] Von Meyer, op. cit., p. 18.

of two equal-sized, closely and extensively united bones, with one or two slender styliform ossicles attached lengthwise, having the base a little below the distal ends of the radius and ulna. The latter bone shows no pits for the attachment of quill-feathers, as in the hot-blooded volant *Ovipara*. A carpus with one large and one small bone in a proximal row, and with a second large and at least one smaller bone in a distal row, is another character by which the *Pterosauria* manifest their closer affinity to Reptiles than to Birds. The remains of the gigantic species from the Cambridge Greensands have yielded the characters of the two larger carpal ossicles.[1]

Variation, as usual, begins to assert its sway as the segments of the limb recede from the trunk. This is mainly shown in the relative length of the metacarpus. In *Ramphorhynchus Gemmingi* it is to the antibrachium as 2 to 7, and to the first phalanx of the wing-finger as 1 to 5, or rather less. In *Dimorphodon* the metacarpus is to the antibrachium rather more than 2 to 6, and is little less than one half the length of the first phalanx of the wing-finger. In *Pterodactylus longirostris* the metacarpus is two thirds the length of the first phalanx. In *Pterodactylus longicollum* the metacarpus is almost four fifths the length of the first phalanx of the wing-finger. In *Pt. suevicus* the metacarpus is one eighth longer than the antibrachium.

There are diversities also in the relative length of the phalanges of the wing-finger. In *Dimorphodon* they increase in length from the first to the third. In *Ramphorynchus Gemmingi* the first and second phalanges are of equal length, and the third is shorter. In *Pterodactylus longirostris, Pt. scolopaciceps, Pt. Kochii,* they decrease in length from the first to the third, and in a greater degree in *Pt. suevicus*.

The most marked variety, however, if the structure has been rightly determined or be not due to some accidental mutilation of the individual, is that on which VON MEYER[2] has founded his genus *Ornithopterus*, viz. a reduction in the number of phalanges of the wing-finger from four to two, and the articulation of the proximal one to two large metacarpals. The last pointed phalanx of the wing-finger in *Ramphorhynchus* is rather longer than the penultimate one; in *Ornithopterus Lavateri* it is only one third the length of the penultimate phalanx.

The evidences of pelvic structure in other *Pterosauria*, already referred to, leaves no doubt as to that in *Dimorphodon*, as restored at *s*, 62, 63, 64, in Pl. XX. The expansion of the ischial and pubic elements and the direction of the latter are strong evidences of Reptilian affinity, and decisive differences in the comparison with Birds. Given the greatest number of vertebræ grasped by the ilia, it falls short of the least number presented in the class of Birds, as by certain *Natatores*, which concomitantly manifest a vacillating or waddling gait. Nothing in the structure, proportions, and connections of the pelvic arch squares with the notion of bipedal progression or erect sustentation of the body and wings of the *Pterosaur*. The share taken by the hind limbs

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[1] 'Monograph,' Suppl. No. III (1861), p. 17, Pl. II, fig. 6; Pl. IV, figs. 5—9.

[2] Op. cit., p. 25, pl. vi, fig. 5.

in resting or moving on dry ground was that indicated in the restoration of the skeleton in Pl. IV.

The hind limbs of *Dimorphodon* are, nevertheless, larger and stronger in proportion than in other *Pterosauria*. The femur, in most species, equals the humerus in length, and, in *Dimorphodon*, also in thickness. In *Pterodactylus longirostris* and *Pt. Kochii* the femur is the more slender bone; in *Ramphorhynchus* it is likewise shorter than the humerus.

The tibia, more slender than the antibrachial bones, in *Pterodactylus longirostris* and *Pt. Kochii*, is of equal length therewith. In *Dimorphodon* the tibia is less slender in proportion to the antibrachium, and is longer by one seventh. In *Ramphorhynchus* it is much more slender than the antibrachium, and is nearly one third shorter. The ankle-joint works between the tibia and tarsus, which, as in other Reptiles and Mammals, is distinct from the metatarsus. There is no calcaneal prominence, and the foot admits of easy rotation, as in the 'Restoration,' Pl. XX, fig. 2, where the inner toe is turned outward and the sole presented to view, to show the application of the wing-toe in flight to the interfemoral web.

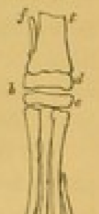
Whether the trochlear terminal joint of the tibia be ossified from a separate centre in the Pterodactyle as in the Bird requires a specimen of the requisite immaturity for determining. If the hind limbs and pelvis presented the structure for sustaining and moving the animal erect on land, an epiphysial state of the articular ends of the long bones might be physiologically inferred. I conclude, from the absence of the modifications essential to bipedal station and progression in *Pterosauria*, that the articular ends of both femur and tibia, including the distal condyles of the latter bone, were co-ossified with the shaft as in other Saurians.

When in warm-blooded Vertebrates, whether Birds or Mammals, the metapodial elements of different toes coalesce, the epiphyses of such coalesced series, or 'cannon bone,' are usually connate, forming a single bone. As, *e.g.*, at the proximal end of the Cow's and Bird's metatarsus (figs. 3 and 4, *c*),[1] and also even at the distal end of the cannon-bone in Ruminants (fig. 3, *d*). I demonstrated the fact in both the metacarpus and metatarsus of a young Giraffe, in my 'Hunterian Lectures' of 1851. The specimens are Nos. 3631 and 3635 in the Osteological Collection of the Royal College of Surgeons ('Catal.' 4to, 1853, p. 601).

Fig. 3.

Ruminant.

Fig. 4.



Bird.

The distal trochlear end of the Bird's tibia, in its epiphysial state (fig. 4, *d*), answers to the distal trochlear epiphysis of the Ruminant's tibia (fig. 3, *a*). In its anchylosed state the distal bicondylar trochlear joint or end of the Bird's tibia answers to the distal bicondylar trochlear joint or end of the Pterosaur's tibia. The proximal

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[1] "The upper articular surface is formed by a single broad piece. The original separation of the metatarsal bone below into three pieces is plainly indicated."—"On the Anatomy of the Southern Apteryx," 'Trans. Zool. Soc.,' ii (1838), p. 293.

epiphysis of the Bird's metatarsus (fig. 4, *c*) answers to the proximal epiphysis of the Ruminant's metatarsus (fig. 3, *c*).

The interspace between the leg and foot is the seat of variable and inconstant centres of ossification, from zero, as in *Proteus*, *Amphiuma*, *Aves*, to the four ossicles in *Crocodilus*, and the seven ossicles in *Chelone*.

The functions of the hind leg in Birds require peculiarly strong, firm, close-fitting, interlocking joints. Thus, the fibula articulates directly with the femur, and the metatarsus as directly with the tibia. No interposed ossicles are permitted to affect the simple efficiency of this tibio-metatarsal joint in the long-footed feathered bipeds. In quadrupeds and in the short- and broad-footed *Bimana* tarsal ossicles, interposed at the space *b* (fig. 3), have their use. But whether the tarsus exist or not, in the *Hæmatotherma* the articular ends of the long bones begin as 'epiphyses;' and when two or more metacarpals are to become massed into one bone, the epiphysis (*c*) is single—a very significant developmental guide to the homology in question.

The strangest aberrations in homological aims have arisen from a non-recognition of the distinction between teleological and homological centres of ossification.[1] Not only is a tibial epiphysis made into a tarsal bone—and why other epiphyses, such as the proximal one of the tibia, or the distal one of the femur, should be differently treated is not obvious—but new bones by the score are added to the cranial series. 'Basitemporals,' 'prevomers,' 'antorbitals,' 'perpendicular ethmoids,' 'ali-ethmoids,' &c. &c., have been heaped up to obstruct the comprehension of the plain and intelligible nature of the bird's skull.

The four unguiculate digits of the foot are of nearly equal length, but present a slight difference in their proportions[2] in the *Pterosauria*. Cuvier having determined the Lacertian character of the phalangial formula of these digits, viz. 2, 3, 4, 5, adds that, apparently, the fifth digit was reduced to a slight vestige of two pieces in *Pterodactylus longirostris*.[3] Subsequently discovered species have offered a like indication, to which Von Meyer alludes as a rudiment or stump ('stummel') of the fifth toe.[4] No other specimens, to my knowledge, save the third of *Dimorphodon* (Pl. XVIII) and the *Ramphorhynchus* (Pl. XIX, fig. 5) have shown the condition of the fifth digit as of three pieces, viz. a metatarsal (*m*, *v*) and two phalanges (*v*, 1 and 2).

The metatarsal of this toe shows an interesting affinity to that in the *Crocodilia* by its greater breadth and shortness in comparison to the other metatarsals. The two phalanges have proportions and forms which clearly show their adaptive relations as aids in sustaining the interfemoral or caudo-femoral parachute ('Restoration,' fig. 2, Pl. XX).

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[1] Owen, "Lectures on the Comp. Anat. of Vertebrate Animals," 8vo, 1846, p. 38.

[2] See Monograph, pl. xi, fig. 3.

[3] "Il paroit qu'ici le cinquième étoit réduit à un leger vestige de deux pièces."—'Oss. Foss.,' vol. cit., p. 374.

[4] "Cuvier, Wagler, und Goldfuss lassen den Fuss aus fünf ausgebilteten Zehen bestehen; in allen Pterodactyln habe ich aber nie mehr als vier solcher Zehen, und höchstens noch einen Stummel vorgefunden."—Op. cit., p. 20.

The crushed condition of most of the long bones in the specimens of *Dimorphodon* show the wall of the shaft to have been compact and thin, the cavity large. Although I have failed to detect such clear evidence of the foramen pneumaticum in these crushed bones as in some of the vertebræ, I cannot resist the inference from the structure of the long bones that they were filled with air in the living animal, as has been demonstrated in remains of the larger *Pterosauria* of the Cretaceous series.[1]

This general osteological character of the *Pterosauria* leads me to offer a few remarks on its relation to their peculiar power of locomotion among *Reptilia*, and to the affinity it may indicate to other groups of volant Vertebrates.

Weight is, of course, indispensable to directed motion through the air; but, given the weight requisite for the action against gravity resulting in flight, whatever structure tends to dispense with additional burthen enables the force to act with more avail—with less unnecessary resistance to overcome.

Where provision is made for unusual flying force, as by the enormous pectoral muscles and concomitant shape of wing in the Swift, the required weight of body called for heavier bones; hence the non-pneumaticity of the skeleton. Diminished flying force, especially with increased bulk of body, is attended with modifications of bony structure obviously adapted, and which have always been recognised in relation, to reduction of weight in the mass to be moved through the air. It is true that the mere quantity of air contained in bones would have an effect inappreciable in aid of the force raising a weight of 5 lb. or 10 lb. from the ground;[2] but the true view of the question is—given a bone of 1 foot in length and 3 inches in circumference, whether the restriction of bony matter to a thinness of $\frac{1}{2}$ a line at the circumference, and a substitution of air for the rest of the diameter throughout the shaft, be not a provision for diminution of weight and conservation of strength which does relate to facilitate locomotion through air?

If the humerus of the Ostrich (No. 1373, Osteological Collection in the Museum of the College of Surgeons, London, 'Catalogue' of do., 4to, 1853, p. 265) be compared, as to weight, with the similarly sized humerus of the Argala Crane (No. 1107, ib., 'Catal.,' p. 214), the difference is striking and suggestive; the latter bone being "remarkable for its lightness, as compared with its bulk and seeming solidity" (ib., 'Catal.' ib.). I demonstrated the cause of the difference by a longitudinal section of

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[1] 'Monograph on the Fossil Reptilia of the Cretaceous Formations (Order *Pterosauria*),' ('Pal. Soc. Mon.', vol. v), 4to, 1851, pp. 80, 98, 101.

[2] A writer impugning the physiological inferences of Hunter and Camper, the discoverers of the pneumaticity of the bird's skeleton, remarks:—"A living bird weighing 10 lb. weighs the same when dead, plus a very few grains; and all know what effect a few grains of heated air would have in raising a weight of 10 lbs. from the ground. The quantity of air imprisoned is, to begin with, so infinitesimally small, and the difference in weight which it experiences by increase of temperature so inappreciable, that it ought not to be taken into account by any one endeavouring to solve the difficult and important problem of flight."—Pettigrew, "On the Mechanism of Flight," 'Linnean Transactions,' vol. xxvi, p. 218, 1868.

the two bones. In the Bird incapable of flight the humerus is solid; in the Bird remarkable for the long-continued power of soaring in upper regions of the air the shaft of the bone is a 'thin shell of compact osseous tissue.' The relation of the weight of the volume of air occupying the capacious cavity of the Argala's wing-bone to the total weight of its body need not be taken into account in considering the problem of flight, but the relation of a hollow instead of a solid humerus is a legitimate element in the endeavour to solve that complex kind of animal locomotion. To say that a certain amount of weight in the bird is essential to the momentum of flight is no argument against the reduction to such requisite weight of the body to be upborne. Every structure so tending to lighten the body of a volant animal within the required limit is, and ought to be, recognisable as physiologically related to flight.

By the pneumaticity of the bones of the Pterodactyle, it might be inferred, from a single bone or portion of bone, to have been an animal of flight. For, although certain volant Vertebrates, *e. g.* the Bat and the Swift, may not have air-bones, no Vertebrate save a volant kind has air admitted into the limb-bones. But the effect of such admission, of such substitution of a lighter for a heavier material, is to diminish the weight without impairing the strength of the bone; the legitimate, if not sole, inference, therefore, is that it contributes to perfect the mechanism of flight.

It is a purely adaptive character, and the insignificant, barely appreciable, difference of weight due to difference of temperature in a given bulk of air makes the pneumaticity of the skeleton as available and advantageous to a cold-blooded as to a warm-blooded volant Vertebrate.

In concluding the description of the subjects of the present Monograph I am moved again to express my sense of acknowledgment for the most instructive of the evidences of *Dimorphodon macronyx* due to my friend from the beginning of our palæontological pursuits, the EARL OF ENNISKILLEN, F.R.S.; and, whilst fulfilling this pleasurable duty, I would add a testimony to one whose loss Palæontology has much reason to deplore,—to the unwearied and undaunted explorations of the precipitous cliffs of Lyme-Regis by MARY ANNING, to which, and to her singular tact of discernment of the feeblest evidence of a fossil in that dark matrix, science is indebted for the discovery of the first evidence of a Pterosaur in 'Lias' of the locality, which has since yielded the grounds for the reconstruction of the strangest representative of the order.

Ramphorhynchus Meyeri, Pl. XIX, fig. 5.—In further illustration of the characters of *Dimorphodon macronyx* I have added to Pl. XIX a figure of a long-tailed Pterosaur from the lithographic slate of Pappenheim, which, in the feebleness of its hind-limbs and the general proportions of the tail, resembles *Ramphorhynchus Gemmingi*, V. M.[1]

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[1] See Von Meyer, op. cit., pl. ix, fig. 1.

The present specimen, from Dr. Häberlein's collection, now in the British Museum, shows the fifth or 'wing-toe' of the foot, ib. fig. 5, *v*, which had not been preserved in previously described specimens of the genus.[1] At least thirty-four vertebræ extend beyond the sacrum; thirty-eight caudals are the reckoned by VON MEYER in the specimen of his *R. Gemmingi* with the best preserved tail;[2] but this difference would not have yielded sufficient ground for specific distinction. There are, however, differences in the length of the parts of the hind limb which indicate this to have been longer in proportion to the tail and the 'symphysis mandibulæ' than in *R. Gemmingi*.

	R. Meyeri.		*R. Gemmingi* (pl. ix, V. M., op cit.).	
	in.	l.	in.	l.
Length of femur	1	2½	1	0
,, tibia	2	0	1	8
,, 1st toe	1	6	1	2½
,, 2nd toe	1	9	1	4
,, 3rd toe	1	11½	1	6
,, 4th toe	1	10½	1	3
,, 5th toe	0	9		

In both specimens the number of phalanges of the toes increases from the first or innermost to the fourth, in the usual saurian ratio, 2, 3, 4, 5. In *Ramphorhynchus Meyeri* the fifth toe consists, as in *Dimorphodon*, of two phalanges, the first being six lines in length, the second three lines, and ending in a point. The metatarsal of this 'wing-toe' is short, broad, and flattened, with a convex outer border at its basal half.

The bones of the left hind limb are well preserved in the specimen figured.

The caudal vertebræ are surrounded by the bone-tendons. Their proportions, as shown in the figure, accord with those in *Dimorphodon*, Pl. XIX, fig. 4.[3] The posterior dorsal vertebræ of *Ramphorhynchus Meyeri* show the broad diapophyses supporting the ribs, which are more slender than those at the fore part of the chest. The symphysis mandibulæ is one inch six lines in length, including the edentulous pointed end. Four pairs of long slender laniary teeth are preserved at the fore half of the symphysis. The teeth at that part of the lower jaw in *Ramphorhynchus Gemmingi* are fewer in number and less closely arranged.[4]

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[1] "Ein Stummel wur nicht mit Sicherheit zu ermitteln."—Von Meyer, op. cit., p. 72.

[2] Op. cit., p. 69.

[3] This figure has the neural surface downward in the Plate.

[4] Compare with Von Meyer, op. cit., pl. ix, fig. 1, and pl. x, fig. 1.

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PLATE XVII.

Dimorphodon macronyx.

Skull and parts of the skeleton : nat. size.

From the Lower Lias of Lyme Regis. In the British Museum.

TE XVII.

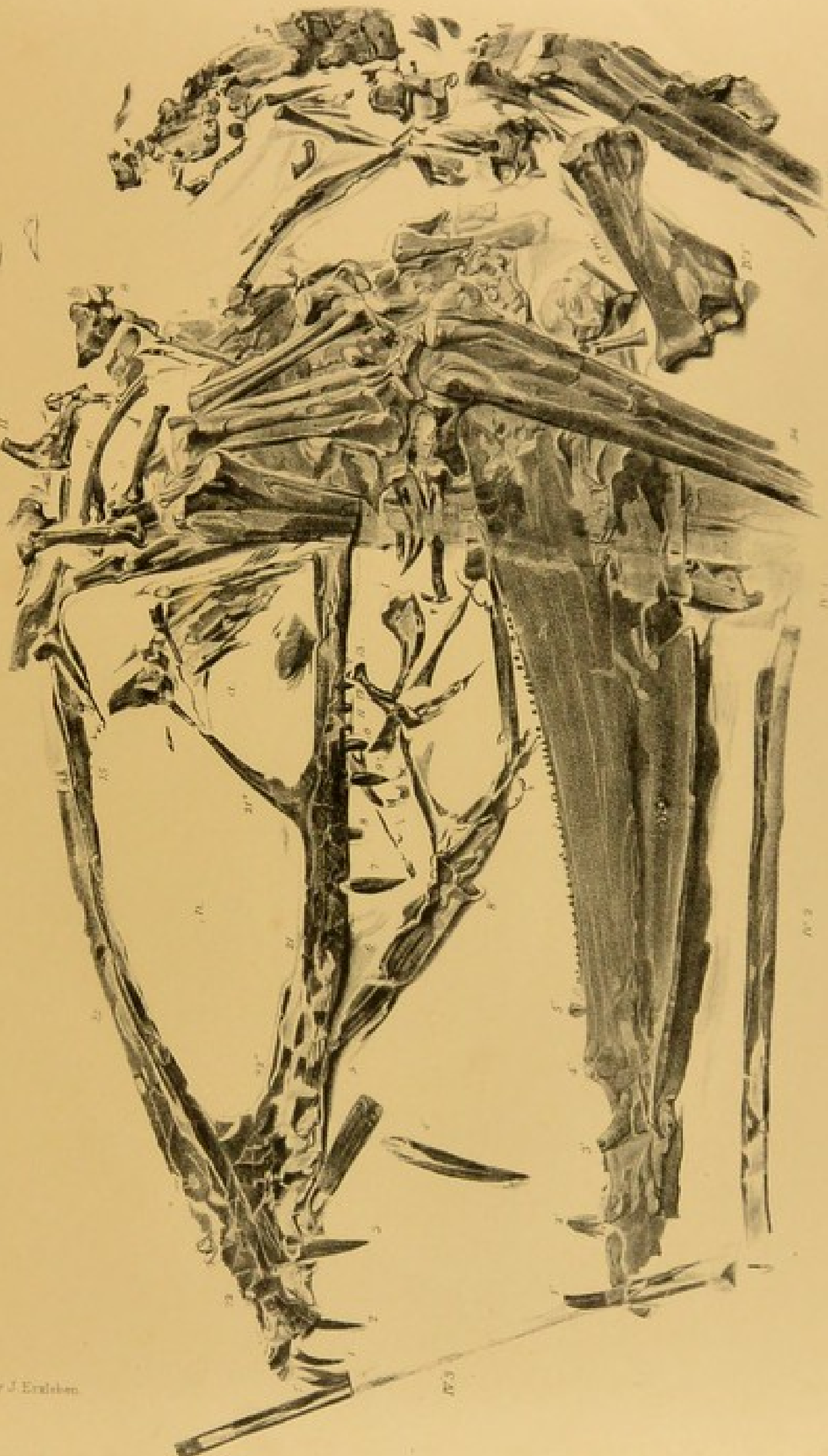
odon macronyx.

the skeleton: nat. size.

ne Regis. In the British Museum.

T. XVII.

DIMORPHODON MACRONYX



From nat. on Stone by J. Erxleben

W. West imp.

PLATE XVIII.

Dimorphodon macronyx.

Skull and parts of the skeleton: nat. size.

From the Lower Lias of Lyme Regis. In the British Museum.

XVIII

on macronyx.

the skeleton: nat. size.

e Regis. In the British Museum.

T XVIII

W. West imp.

PLATE XIX.

Dimorphodon macronyx.

Fig.

1. Bones of fore foot and part of wing-finger.
2. Pelvis.
3. Anterior caudal vertebræ.
4. Vertebræ of entire tail, with surrounding bone-tendons.

From the Lower Lias of Lyme Regis, Dorsetshire.

Rhamphorhynchus Meyeri.

5. Dorso-lumbar, sacral, and caudal vertebræ, part of pelvis, with bones of the pelvic limbs.
6. Fore part of mandible and teeth.

From the Lithographic Slate, Pappenheim, Bavaria.

7. Second phalanx of wing-finger of *Pterodactylus validus.*
8. Distal end, and section of shaft, of tibia of *Pterodactylus curtus.*
9. Ib. ib., side view, of do. do.
10. Section of second phalanx of wing-finger of *Pterodactylus nobilis.*

From the Wealden of Sussex.

All the specimens of the natural size. In the British Museum.

E XIX.

n macronyx.

er.

bone-tendons.

Lyme Regis, Dorsetshire.

nchus Meyeri.

tebræ, part of pelvis, with bones of the

late, Pappenheim, Bavaria.

dactylus validus.
of *Pterodactylus curtus.*

of *Pterodactylus nobilis.*

lden of Sussex.

size. In the British Museum.

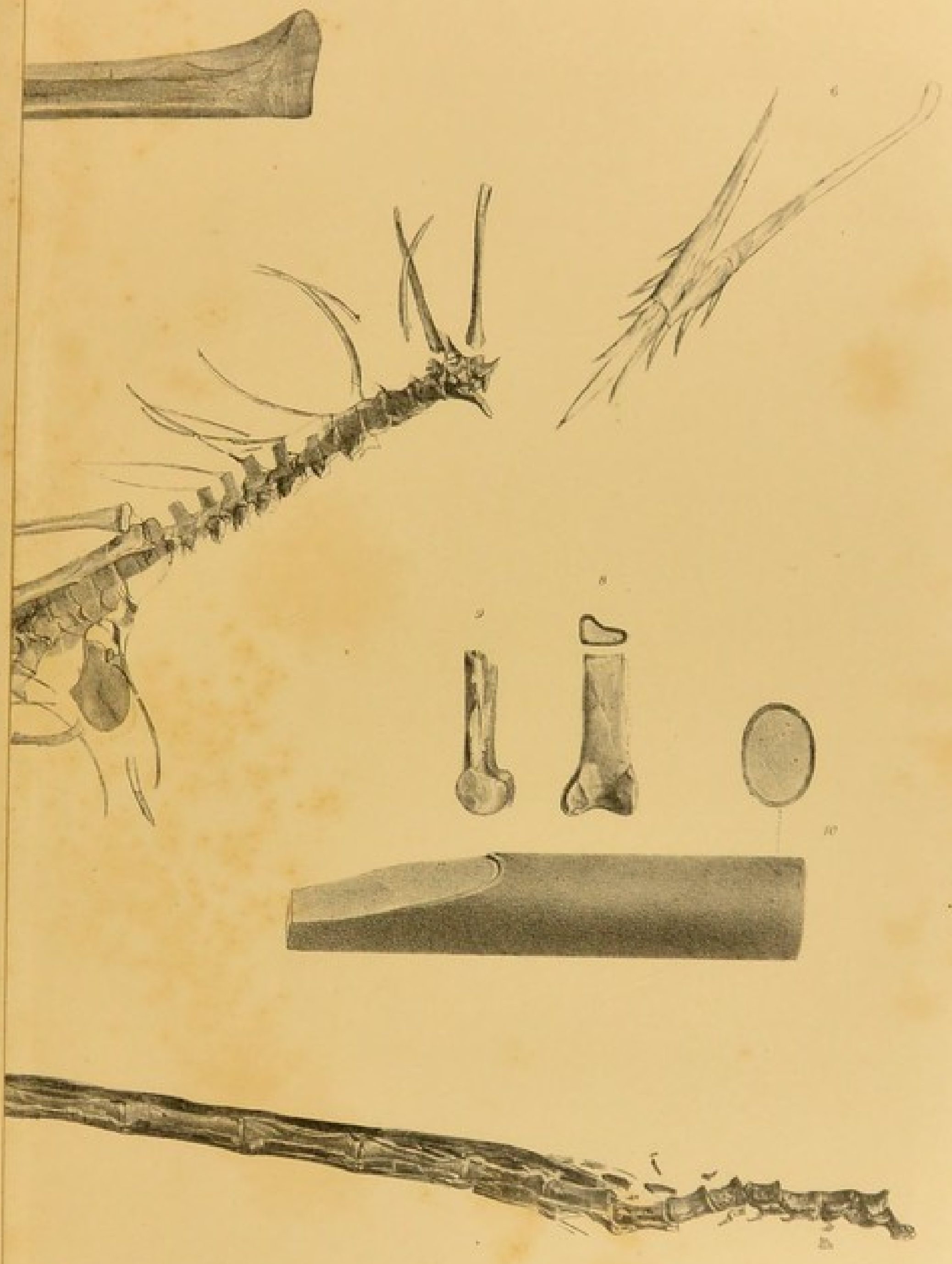


PLATE XX.

Dimorphodon macronyx.

Fig.

1. Restoration of the skeleton: nat. size.

2. Restoration of entire animal: reduced (see 'Scales' at foot of plate).

3. Side view of the skull of a recent Saurian (*Lyriocephalus*).

PLATE XX.

Dimorphodon macronyx.

eton : nat. size.

imal : reduced (see 'Scales' at foot of plate).

of a recent Saurian (*Lyriocephalus*).