III. *On the* Archeopteryx *of* von Meyer, *with a description of the Fossil Remains of a Long-tailed species, from the Lithographic Stone of Solenhofen. By Professor* Owen, *F.R.S. &c.*

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The first evidence of a Bird in strata of the Oxfordian or Corallian stage of the Oolitic series was afforded by the impression of a single feather, in a slab of the lithographic calcareous laminated stone, or slate, of Solenhofen; it is described and figured with characteristic minuteness and care by M. Hermann von Meyer, in the fifth part of the 'Jahrbuch für Mineralogie*.' He applies to this fossil impression the term *Archeopteryx lithographica*; and although the probability is great that the class of Birds was represented by more than one genus at the period of the deposit of the lithographic slate, and generic identity cannot be predicated from a solitary feather, I shall assume it in the present instance, and retain for the genus, which can now be established on adequate characters, the name originally proposed by the distinguished German palæontologist †.

At the Meeting of the Mathematico-Physical Class of the Royal Academy of Sciences of Munich, on the 9th of November, 1861, Professor Andreas Wagner communicated the discovery, in the lithographic slate of Solenhofen, of a considerable portion of the skeleton of an animal with impressions of feathers radiating fanwise

* 1861, p. 561.

† A specific diagnosis deduced from the characters of a single feather presupposes that such characters are common to every feather of the bird so defined, and the impression of a second feather differing greatly in its shape and proportions, as in Plate IV. fig. 8, would represent a distinct species in Palæontology; otherwise the characters afforded by a feather cannot be held to be distinctive of a species.

From the number of species of *Pterodactylus*, some having short, some having long tails, in the lithographic slate of Bavaria, it is probable that there may have been different species of *Archeopteryx* so characterized: the future possible discovery of a short-tailed *Archeopteryx* with impressions of feathers corresponding with that of the *Archeopteryx lithographica*, v. Meyer, would impose upon its describer the duty of applying a new specific name to the long-tailed *Archeopteryx* with the differently-shaped feathers, to which the name *lithographica* would thus prove to have been wrongly applied. Moreover, as winged reptiles are not peculiar to the lithographic modification of oolitic deposits, the term *lithographica* may prove as little distinctive of an *Archeopteryx* as of a *Pterodactylus*.

On these grounds the author distinguished in his original communication, as in the Catalogue of the Fossils in the British Museum, the species of *Archeopteryx*, indicated by the specimen which, for the first time, has yielded any knowledge of the specific characters of one of the genus, by the term expressive of the best-marked of those characters, and by which *Archeopteryx macrura*, Ow., differs most conspicuously rom every other known species of bird.

from each anterior limb, and diverging obliquely in a single series from each side of a long tail.

These and other particulars of the fossil Professor WAGNER gave on the authority of M. WITTE, Law-Councillor (Oberjustiz-Rath) in Hanover, who had seen the fossil in the possession of M. HÄBERLEIN, District Medical Officer (Landarzt) of Pappenheim.

Upon the report thus furnished to him, Professor WAGNER proposed for the remarkable fossil the generic name *Griphosaurus*, conceiving it to be a long-tailed Pterodactyle with feathers. His state of health prevented his visiting Pappenheim for a personal inspection of the fossil; and, unfortunately for palæontological science, which is indebted to him for many valuable contributions, Professor WAGNER shortly after expired.

I thereupon communicated with Dr. HÄBERLEIN, and reported on the nature and desirability of the fossils in his possession to the Trustees of the British Museum: they were accordingly inspected by my colleague Mr. WATERHOUSE, F.Z.S.; and an interesting and instructive selection, including the subject of the present paper, has been purchased for the Museum.

The specimen is divided between the counterpart halves of a split slab of lithographic stone: the moiety (Plate I.) containing the greater number of the petrified bones exhibits such proportion of the skeleton from the inferior or ventral aspect.

The lower half of an arched furculum (merry-thought, 58) marks, by its relative position to the wings, the fore part of the trunk. From this portion of the furculum to the root of the tail measures $4\frac{1}{2}$ inches; the length of the caudal series of vertebræ (*Cd*, *Cd'*) is 8 inches; but the terminal tail-feathers extend 3 inches further, making the length of the tail 11 inches. From the end of the tail to the anterior border of the wing-feather impressions is 1 foot $8\frac{1}{2}$ inches. From the outer border of the impression of the left wing (*d*) to that of the right wing measures 1 foot 4 inches. The front margin of the slab of stone has been broken away short of the anterior border of the impression of the outspread left wing, and the head or skull of the specimen may have been included in that part of the quarry or stone from which the present slab has been detached. The preserved parts of the feathered creature indicate its size to have been about that of a Rook or Peregrine Falcon. The exposed bones on one moiety of the split slab (Plate I.) are—

The lower portion of the furculum (58) above mentioned.

Portion of the left os innominatum, showing part of the ilium (62) and ischium (63), with the acetabulum (*a*).

Twenty caudal vertebræ (*Cd*) in a consecutive and naturally articulated series.

Several slender curved ribs (*pl*), most of them sternal (*h*), irregularly scattered about the region of the trunk.

Left scapula (51').

Proximal half of left humerus (53'), entire, and part of the distal half.

Left radius (54') and ulna (55').

Left carpus (56′) and portion of a metacarpal bone (57′).
Right scapula (51).
Right humerus (53), wanting part of the bony wall and the proximal end.
Right radius (54) and ulna (55).
Two metacarpal bones (57).
Two unguiculate phalanges (I and II).
Right femur (65), tibia (66), and bones of the foot (68, *i*, *ii*, *iii*, *iv*).
Left femur (65′) and tibia (66′).
Impressions of the quill-feathers of the wings and tail. Impressions of parts of finer feathers and down at the side of the body.

The opposite moiety of the split slab contains only one claw-bone (Plate I. fig. I′), belonging to the impression of the unguiculate digit (I) of the right wing, and a few slender curved rib-like bones, in addition to those shown on the lower moiety; of which bones the counterpart displays the impressions, and in some instances, as in the femora, the thin outer crust of the shaft.

The furculum, pelvis, and bones of the tail are in their natural undisturbed position, as in the skeleton of the animal. The left scapula has been displaced backward, and lies outside of, and nearly parallel with, the left os innominatum. The left humerus extends outward and a little forward from its scapular articulation, from which it has not been dislocated. The antibrachium is bent directly inward towards the trunk; and the wing-feathers, of which twelve primaries may be counted, diverge about an inch or less in advance of the carpus.

The right scapula retains almost its natural relative position to the trunk, and is imbedded in the matrix, exposing its lower sharp margin. The right humerus extends backward; the right antibrachium is bent forward, outside of and close upon the humerus; the two metacarpal or proximo-phalangeal bones (57) extend forward in the same direction, but have been dislocated inward. Impressions of about fourteen long quill-feathers, from 6 to 7 inches in length, like those of the left wing, diverge from an extent of about 3 inches, parallel with and outside of the metacarpo-phalangeal bones.

The right femur extends from its acetabular articulation backward and a little outward, reaching as far as the eighth caudal vertebra. The tibia extends directly outward and backward from the knee-joint; the metatarse is bent upon the tibia obliquely forward and inward; and the toes extend in nearly the same direction, the foot being contracted. The left femur is dislocated from the pelvis; its head is opposite the eighth caudal vertebra; the shaft extends forward and a little outward; the tibia extends from the knee-joint more directly outward and a little forward.

The best-preserved impressions of the quill-feathers of the wing measure 6 inches in length, with a breadth of vane of nearly 1 inch; the anterior series of barbs being the shorter, or the anterior part of the vane being less broad than the posterior part; and the end of the vane is obtusely rounded, as at *d*, Plate I., and in fig. 7, Plate IV. The area covered by the diverging quill-feathers of the left wing measures 6 inches across its widest part, near the ends of the feathers; that of the right wing occupies a space of 11 inches from before backward; but this difference is due to the three posterior primaries being dislocated from the rest and directed backward. The under part of the wing being exposed, a few shorter feathers, 'under-coverts,' are seen crossing rather obliquely the 'primaries': one of these (Plate IV. fig. 7 *a*) is exquisitely preserved.

The impressions of the tail-feathers may be discerned from the third to the last caudal vertebræ (Plate I. *Cd*), the right series being complete; the anterior fifth of the left series being wanting. Twenty feathers succeed each other, from before backward, on the right side; and the last thirteen feathers of the left side are preserved. The principal tail-feathers correspond in number with the tail-vertebræ, and diverge, outward and backward (a pair from each vertebra), at an angle of 45° with the line of the tail, becoming more acute towards the end (Plate I. *Cd'*), where the two feathers forming the pair from the sides of the last caudal vertebra extend nearly parallel with each other, and in the axis of the tail, about $3\frac{1}{2}$ inches beyond the end of that vertebra. The length of the anterior tail-feathers is about an inch, and they gradually increase to a length of about 5 inches in the 15th, 16th, and 17th pairs (Plate IV. fig. 8); and gradually decrease, with a more backward direction, to the last pair, which have a length of 3 inches 8 lines. Thus the tail, which is about 11 inches in length, gradually expands to a breadth of $3\frac{1}{2}$ inches opposite the last two vertebræ, and terminates by an obtusely rounded or almost squared or truncate end.

In general shape and proportions it resembles rather the tail of a Petaurus or Squirrel than of a modern bird; while the wings, in their present state of preservation, agree in form and proportion with those of the Gallinaceous or 'round-winged' birds.

The scapula (Plate I. 51', and Plate II. fig. 1, 51) is 1 inch 10 lines in length, 4 lines across the articular end, $2\frac{1}{2}$ lines across the neck, and very gradually expanding, towards the base, to a breadth of 3 lines. In its slightly bent, lamelliform or sabre-shaped figure, and in the concavity between the glenoid articulation and the short acromial projection on the outer side, it closely resembles the scapula of a bird.

In the *Pterodactylus suevicus* (Plate II. fig. 3, 51), a species which accords in general size with the *Archeopteryx*, the scapula is broader in proportion to its length, and exhibits a slight double or sigmoid flexure lengthwise.

The extent of the furcular arch (Plate I. 58, and Plate IV. fig. 1), or connate clavicles, which is preserved, measures from end to end, following the curve, about 2 inches; the breadth at the apex of the curve is 2 lines; but this is obtuse, and the piers diverge at a right angle, but curving from each other; so that the arch is an open or rounded one, not contracted and pointed as in the true Gallinaceous birds; the furcular bone, moreover, is as thick as the slender part of the shaft of the humerus.

No skeleton of the Pterodactyle has shown a furculum. The best-preserved specimens, such as the *Pterodactylus suevicus*, figured by QUENSTEDT *, exhibit the scapula and coracoid entire, without a trace of clavicle, separate or confluent.

The prominence beyond the left scapula (Plate I. 51′) suggested at first view the humeral end of the coracoid, but I believe it to be part of the humerus corresponding with the tuberosity on the ulnar side of the sessile semioval head, overarching the pneumatic foramen in the bird. The humerus of *Archeopteryx* (Plate I. 53, 53′, and Plate II. fig. 1, 53) is nearly 3 inches in length, with the same slight sigmoid flexure as in the bird. The pectoral ridge (ib. *b*) has a basal extent of 1 inch: the breadth of the humerus at this part is 6 lines, one-half of which breadth appears to be due to the pectoral ridge. In contour it most resembles that in the *Corvidæ* (Plate II. fig. 4), the border being continued almost straight down from the low upper angle; but there is a better-marked lower angle in *Archeopteryx*, where the border of the process curves with a slight concavity to subside in the shaft.

The Pterodactyle (Plate II. fig. 3, 53) presents a well-marked difference from the bird in the greater extent to which the pectoral ridge projects from the shaft of the humerus, and in the minor relative extent of its base. The humerus, moreover, is straight, shorter in proportion to the antibrachium, and thicker in proportion to its length, with a different character of the distal articulation. In *Archeopteryx* the humerus closely resembles that of the bird, and presents about the same proportion, in length, to the trunk as in the Peregrine Falcon (Plate II. fig. 2, 53), the Touraco, and most *Gallinæ*.

The radius (Plate I. 54, and Plate II. fig. 1, 54) is slender and straight. The ulna (*ib.* 55) is thicker, rather longer, and slightly bent, leaving a well-marked interosseous space between the two bones: it expands at both ends to contribute the chief share in both the elbow- and wrist-joints. The right ulna (Plate I. 55) shows the convexity at the part of the proximal end next the radius, as in modern birds. Both ulna and radius closely resemble the antibrachial bones of the bird. The length of the ulna is 2 inches 8 lines—bearing nearly the same proportion to the humerus as in some *Scansores* and *Gallinaceæ*.

In Pterodactyles (Plate II. fig. 3) the radius (54) and ulna (55) are of equal thickness, are straight, leave no interosseous space, take equal shares in the formation of the elbow- and wrist-joints, and the antibrachium is always much longer than the humerus.

A single carpal, of large size, wedged between the end of the radius and the base of a metacarpal, is shown on the left side of *Archeopteryx* (Plate I. 56), indicating a structure of the wrist like that in the bird.

On the right side an irregular mass of spar occupies the position of a thick carpus or metacarpus, twisted inward at right angles to the antibrachium; but this is a doubtful indication. An inch from the antibrachium, nearer the medial line, but, like the antibrachium, directed forward, are two longish bones, with expanded proximal articulations and straight shafts, growing slender to their distal ends, which come in contact (Plate I. 57,

* Ueber *Pterodactylus suevicus*, 4to, Tübingen, 1855.

and Plate II. fig. 1, 57). The proximal articular surfaces are convex, indented by grooves; that of the shorter bone is 4 lines in advance of that of the longer. The latter is 1 inch 5 lines in length, or about half the length of the ulna; its small distal end is obtuse, and may have been articular. The contiguous shorter bone extends beyond the end of the other, and seems to terminate by a small convex condyle. These appear to be metacarpals; they bear the same relation of length to the antibrachium as do the two terminally coalesced metacarpals in the bird (Plate II. fig. 2, 57). If they be the homologues of these, they retain their original individuality or distinctness, and they are more equal in thickness. If they be proximal phalanges of the two digits answering to those which constitute the penultimate joint of the pinion of the bird (Plate II. fig. 2, IV), they differ in being relatively longer and more equal in length and thickness.

Half an inch from the outer of the two bones of the pinion, and external to, but on the same transverse parallel as, its distal articulation, is the impression of a slender bone, about 11 lines long, extending forward in the same line or direction as the above pinion-bones. At the distal end of the slender bone is the impression of part of a compressed curved bone, grooved along the side, 4 lines in length, 1 line in breadth; this dimension slightly decreasing as the bone recedes, curving from the longer slender supporting bone: it is most like the basal half of an ungual phalanx, supported by a long and slender penultimate phalanx (Plate I. II).

In advance and external to the foregoing is the bone itself, of a corresponding penultimate phalanx, 11 lines in length, half a line in thickness of shaft; expanded at both ends, but most so at the distal one, which supports a beautifully perfect claw-phalanx, preserved in the opposite slab (Plate I. I′), and indicated by its impression (*ib.* I) in the moiety which retains most of the bones of *Archeopteryx*. The claw-phalanx is 8 lines in a straight line, $2\frac{1}{2}$ lines broad at the base, with a degree of curvature equal to that of the claw-phalanx of a Raptorial bird; grooved along the side; with the base produced, at the under or concave side, for the insertion of the flexor tendon, and with a sharp apex.

This claw resembles that of the mid-claw of the hind foot (Plate I. *iii*); but the bone, which plainly appears to be in penultimate phalangeal relation with it, is twice as long and only half as thick as the penultimate phalanx in the foot, and the repetition of the same character of penultimate phalanx in the less definite or less perfect indication of the other claw (Plate I. II) indicates that the hand of *Archeopteryx*, besides being concerned in supporting the remiges or quill-feathers of a wing, also supported two moderately long and slender free digits, each terminated by a strong, curved, sharp-pointed claw (as in the restoration, Plate II. fig. 1, 57, I, II, III, IV).

It is true that the parts of the present skeleton show a certain amount of dislocation, and one of the claw-bearing digits might have belonged to the left wing; but this is less probable than that they are on their right side. So much of the skeleton of the hand as is exposed to view in the present specimen unquestionably accords in its proportions with that of the bird (compare fig. 1, 57, with fig. 2, 57, Plate II.).

The anterior of the three digits which are developed in the bird's pinion (*ib.* fig. 2, II) remains free, and in some species supports a claw or spur *. The digit answering to the middle one in the pinion of birds of flight, supports, in *Apteryx*, a terminal curved claw. But if my interpretation of the appearances above described in the present fossil be correct, *Archeopteryx* differs markedly from all known birds in having two free unguiculate digits in the hand; and these digits, in the slenderness of the penultimate phalanx, do resemble the unguiculate digits in the hand of the Pterodactyle (Plate II. fig. 3, II). But the claw has not the characteristic depth or breadth of that of the Pterodactyle; and there is no trace of the much-lengthened metacarpal and phalangeal bones of the fifth digit, or peculiar wing-finger, of the flying Reptile (*ib.* V).

Had the manus of *Archeopteryx* been constructed for the support of a membranous wing, the extent to which the skeleton is preserved, and the ordinary condition of the fossil *Pterosauria* in lithographic slate, render it almost certain that some of these most characteristic elongated slender bones of the wing-finger (Plate II. fig. 3, V, 1, 2, 3, 4) would have been preserved if they had existed in the present specimen. But, besides the negative evidence, the positive proof of the ornithic proportions of the hand or pinion, of the existence of quill-feathers, and the manifest attachment of the principal ones, or 'primaries,' to the carpal and metacarpal parts of a short terminal segment of the limb, sufficiently evince the true class-affinity of the *Archeopteryx*.

The pelvis is chiefly represented by a bone on the left side (Plate I. 62), bearing the nearest resemblance to the iliac bone of a bird. A circular acetabulum, 3 lines in diameter (ib. *a*), is defined by a sharp border backed by matrix, not by bone. An oblong plate of bone extends in advance of the acetabulum 11 lines, with a breadth at the acetabulum of 7 lines, diminishing to a breadth of 4 lines, and then expanding to one of 5 lines. The margin of the bone next to the sacrum is nearly straight; the opposite or outer border is sinuous, being concave as it leaves the acetabulum, and then convex with an obtusely rounded anterior end. The exposed surface is smooth and polished. Transversely this surface is concave at the medial, convex at the lateral half. The bone is continued backward along the medial side of the acetabulum, of a breadth equal to that of the cavity; and behind it for the same extent, with a breadth of 7 lines, where it is interrupted by the well-defined curve of the anterior border of a large oval vacuity, one boundary of which is broken away at 6 lines' distance from the acetabulum.

I conclude that here is shown the left os innominatum, including the anterior two-thirds of the ilium, and the anterior half, or more, of the coalesced ischium. The anterior iliac border of the acetabulum ends abruptly and obtusely, precisely at the part where the acetabular end of the os pubis articulates with the ilium in the young

* *E. g.* Syrian Blackbird (*Merula dactyloptera*), Spur-winged Goose (*Anser gambensis*), Jacana (*Parra jacana*). The Screamer (*Palamedea cornuta*) has two spurs; the Megapode (*Megapodius*) has a tubercular rudiment of a pinion-claw.

bird; the ischium, however, appearing to meet that part of the ilium at a lower level (in the exposed surface of the fossil), and sending a very short process towards the acetabulum. The ischium (Plate I. 63), behind the acetabulum and external (as it lies) to the oval interspace between it and the ilium, shows the anterior curved boundary of a smaller or narrower vacuity, which I take to have intervened between the ischium and pubis.

We have here, therefore, plain indications of a large ischio-iliac interspace, answering to that called 'great ischiatic foramen or notch' (ib. *i'*), and the smaller ischio-pubic vacuity called 'obturator foramen' (ib. *o*), under conditions of size, formation, and relative position to the acetabulum, known only in the class of birds. The acetabulum itself, moreover, instead of being a bony cup, is a direct circular perforation of the os innominatum, as in birds.

Sufficient is known of the pelvis of the Pterodactyle to show that the ilium is relatively shorter and narrower than in the present fossil; that the pubic and ischial bones are distinct, short, broad, subtriangular plates, and that they contribute to form, with the ilium, a bony cup for the head of the femur.

Whether the pubis has retained its individuality in *Archeopteryx*, or has been broken away from the part of the ilium indicative of the place of its original attachment and relations to the acetabulum, I cannot determine. So far as the appearance of the pelvis can be discerned and, by me, interpreted, they give no evidence of a reptilian structure.

A confused mass of coalesced vertebræ, much shorter and broader than those of the tail, covers the proximal end of the right femur, and extends forward between it and the left innominatum. The sparry material which has crystallized in the vacuities of all the widely and apparently pneumatically excavated bones of the *Archeopteryx* chiefly represents the sacral portion of the spine, in which a series of six or seven short and broad transverse processes, in close contact on the right side, can alone be distinguished. From this indication, the sacrum would seem to have been at least 2 inches in length, and nearly 1 inch in breadth. The inferior or central surface, as in the case of the slightly dislocated left innominatum, is towards the observer, but is much mutilated.

The broad, subquadrate, short, compressed spines of one or two lumbar vertebræ are dimly discernible in front of the sacrum. No trace of the vertebral column in advance of these is visible, nor any part of the sternum; trunk, neck, and head are all wanting. The remains of *Archeopteryx*, as preserved in the present split slab of lithographic stone, recalled to mind the condition in which I have seen the carcase of a Gull or other seabird left on estuary sand after having been a prey to some carnivorous assailant. The viscera and chief masses of flesh, with the cavity containing and giving attachment to them, are gone, with the muscular neck and perhaps the head, while the indigestible quill-feathers of the wings and tail, with more or less of the limbs, held together by parts of the skin, and with such an amount of dislocation as the bones of the present specimen exhibit, remain to indicate what once had been a bird.

Perhaps the most decisive mark of the class-relationship of the *Archeopteryx* is afforded by the bones of the pelvic appendage or extremity, especially of the foot.

The mark of reptilian nature on which CUVIER mainly relied in his masterly analysis of the Pterodactyle's skeleton, was the separate state of the tarsals, and of the metatarsals supporting the digits, with the different number of joints in each digit. In the present specimen, a single coalesced tarso-metatarsal bone (Plates I. & III. fig. 1, $_{68}$) articulates at one end with the tibia; at the other, by a trifid trochlear end, with three toes (*ii*, *iii*, *iv*) directed forward: a shorter opposing toe (*i*) is connected with the metatarse a little above and behind the inner trochlea.

The femur (Plates I. & III. fig. 1, $_{65}$) is 2 inches $4\frac{1}{2}$ lines long, and 2 lines in diameter at the middle of the shaft, which is slightly bent, with the concavity backward. In the Pterodactyle (Plate III. fig. 4, $_{65}$) the femur is straight. In some birds (*Corythaix*, Plate III. fig. 2, $_{65}$) it shows the same bend as in *Archeopteryx*.

The tibia of *Archeopteryx* (*ib.* fig. 1, $_{66}$) is 3 inches 2 lines long, with a shaft of $1\frac{1}{2}$ line in diameter; it is straight. On the left side (Plate I. $_{66'}$), where its back surface appears, it shows the division of the hinder border of the upper articular surface into two lobes; but these are thicker, more rounded or convex, and with a deeper mid-cleft than in those birds that best show this division. In the fossil, however, the sharper contour of this part of the bone is indicated by the thin layer imbedded in the depression on the counterpart slab.

The right tibia (*ib.* $_{66}$) exposes its inner or tibial side, and neither the bone nor the impression exhibits a procnemial ridge. The head of the tibia is produced obtusely below the fore part of the knee-joint. The procnemial production varies much in different birds; in some *Raptores* (*Falco trivirgatus*, Plate III. fig. 3, $_{66}$), and in most *Volitores*, it would not leave a more marked indication than in *Archeopteryx*. The distal end of the tibia expands anteriorly, and the contour shown by the inner surface of the right tibia, and the hinder and inner part of the left one, agrees with the peculiar structure of that part in birds.

In the proportion of the tibia to the femur, exceeding as it does the latter bone by rather more than one-fourth of its own length, *Archeopteryx* (Plate III. fig. 1) resembles some birds (Grouse, Touracos (*ib.* fig. 2), many *Insessores*); but the thigh is proportionally longer in *Archeopteryx* than in the majority of birds, especially those (e. g. *Cursores*, *Grallatores*) which are remarkable for the length of leg. In the Pterodactyle (*ib.* fig. 4) the tibia ($_{66}$) is more nearly of equal length with the femur ($_{65}$). Whatever trace or proportion of the fibula may have existed in *Archeopteryx*, if preserved, is buried in the matrix beneath the exposed parts of the tibia.

There is no indication, in either the fossil bones or their impressions, of a separate or distinct tarsus. The upper end of the coalesced metatarsals (Plates I. & III. fig. 1, $_{68}$) shows the calcaneal process and the tendinal groove on its inner side. The thin bony crust of the inner side of this single composite bone adheres to the impression on the counterpart slab; the cast of the medullary cavity in the usual clear, light-coloured spar represents the major part of the shaft; but the innermost and the middle of the three distal condyles, or trochlear joints, are well preserved. The length of the tarso-metatarsal to the end of the mid-trochlea is 1 inch 10½ lines, to the end of the inner trochlea 1 inch 8½ lines: this characteristic bird-bone in *Archeopteryx* thus resembles the same in *Gallinaceæ* and some other groups in which the inner trochlea is least produced, and differs from the *Raptores* (Plate III. fig. 3) and others in which the trochleæ terminate on the same or nearly the same level.

The short metatarsal of the innermost or back toe (Plate III. fig. 1, *i*) begins at the lower third of the metatarsus (68); has an extent of attachment, shown to be ligamentous by a linear tract of matrix, of 2½ lines; and its convex articular end is about the same distance above the inner trochlea as that is above the middle trochlea of the connate metatarsals. Thus the proportion of the metatarsus to the tibia resembles the average or common proportion in birds (*ib.* fig. 2), having neither the extreme length of the Grallatorial, the extreme shortness of the Volitorial, nor the robustness of the Raptorial modifications (*ib.* fig. 3) of this characteristic bone.

The difference from the Reptilian structure, and especially from the Pterosaurian modification thereof (Plate III. fig. 4, 68), is here most striking. The tarsus (ib. *a l*) is a distinct segment in the volant reptiles, and the metatarsals (*ib.* 68) equally retain their distinctness, and correspond in number with the toes. The entire tarso-metatarsal segment of the limb in the Pterodactyle is much shorter in proportion to the tibia than in *Archeopteryx* and most birds.

The innermost or back toe of *Archeopteryx* (Plate III. fig. 1, *i*) consists of two phalanges, each 4 lines in length: the second phalanx is curved, slender, pointed, with an obtuse process on the under or plantar side of the articulation, closely resembling the claw-phalanx of the bird: the toe is shorter and more slender than in the *Raptores* (*ib.* fig. 3, *i*, 1, 2), longer and more slender than in the *Rasores*, more curved than in the *Grallatores*, corresponding in its proportions, as in the relative length of the proximal phalanx, with the same toe in perching birds. The second toe (*ib.* fig. 1, *ii*), the innermost of the three directed forward, consists of three phalanges (1, 2, 3) of nearly equal length, that of the entire toe being 1 inch 3 lines. The third (ib. *iii*), or mid-toe of the three front ones, is 1 inch 9 lines in length, and consists of four phalanges, the second (2) and penultimate (3) being rather the shortest. These toes, with their claw-phalanges, equally accord in structure and proportions with the Insessorial type of foot. The termination of the claw-phalanx of the outermost (fourth) toe (ib. *iv*) projects beyond and from beneath that of the second toe, indicating a length intermediate between that of the second and third toes, but more nearly that of the second toe: traces of the other joints of the fourth toe are sufficiently plain to determine that it was not bent back, but that it accorded in position and direction with the Insessorial, not the Scansorial, type of foot. All the claw-bones correspond in the proportions of breadth to length with the bird-type of those bones, and not with the compressed deep form which they present in Pterodactyles.

The structure of the foot, and the proportion which its metatarsal bone bears to the tibia, lead me to restrict the account of the closer comparisons of the bones of *Archeopteryx* with those of other birds to the species of *Insessores* and *Raptores* which best accord with the fossil in general size. The furculum of *Archeopteryx* (Plate IV. fig. 1) presents the proportional strength, thickness, and span of the arch which characterize the diurnal *Raptores* (*ib.* fig. 3): but the piers or crura do not arch into one another below by so open a curve; they have converged in a form more angular, more like that in the Owls (*ib.* fig. 4, *Nyctea nivea*), and still more like that in some *Grallæ*, with a strong furculum, as, *e. g.*, in the Spoonbill (*Platalea leucorodia*) and Argala (*ib.* fig. 5); only, as before remarked, the type of pelvic limb precludes any useful comparison with birds of the Wading order. The furculum in *Columbidæ* and *Cracidæ* (*ib.* fig. 6) is feeble in comparison with that of *Archeopteryx*: in the more typical *Gallinaceæ*, the still more slender piers of the furculum meet at an acute angle, and develope a compressed plate of bone from the apex. The furculum of *Archeopteryx* is that of a bird of a more powerful flight than in the true *Gallinaceæ*. In the *Corvidæ* (*ib.* fig. 2), in which the furculum is narrower in proportion to its length than in *Falconidæ*, the piers unite by a wider curve than in *Archeopteryx*.

The scapula of *Archeopteryx* (Plate II. fig. 1, 51) bears nearly the same proportion in length to the humerus and femur as in some of the more slender-limbed *Falconidæ* (*Falco trivirgatus*, Plate II. fig. 2, 51). But the humerus seems to have been more slender than in the Falcon (*Falco trivirgatus*), which comes nearest to *Archeopteryx* in this respect. The form of the pectoral ridge presents the difference previously pointed out.

In the Kites (*Milvus*) and Perns (*Pernis*) the humerus is proportionally longer than in *Archeopteryx*: in the *Corvidæ* it is proportionally thicker (Plate II. fig. 4, *Corvus corax*). It is by the proportion of the antibrachium (*ib.* fig. 1, 54, 55) to the humerus that *Archeopteryx* departs furthest from the Raptorial and Insessorial types, whilst it closely resembles the true *Gallinaceæ*, the antibrachium being rather shorter than the humerus; and this condition of the wing-bones accords with the indication of the proportions of the primary quill-feathers, as in the short rounded wing of Grouse and Pheasants. The bones of the segment of the hand giving attachment to the primaries are not preserved in the left wing of *Archeopteryx*; two of those on the right side are preserved, and the manus shows, apparently, in the two distinct sets of phalanges, terminated each by a compressed, curved, sharp-pointed claw, the departure, next in importance after the tail, from the structures of modern and known tertiary birds.

Few of the bones, even the best-preserved ones of *Archeopteryx*, permit a close or minute comparison of superficial features and markings with their recent homologues in birds or reptiles.

The osseous remains of *Archeopteryx* being included between the halves of a split slab, it might be supposed that the configuration of the outer surface of the fossilized bone must be demonstrable on one or other of the moieties: it is not so. The long contact of the phosphate with the carbonate of lime has resulted in a certain degree of disintegration or partial decomposition of the former, which has baffled every attempt to detach the matrix from the bone, or the bone from the matrix, where they have come to hand in their original contact. Only in the instances of the bones with the thickest osseous walls, as those of the feet, and especially the claw-bones, is the surface entire; and this has been exposed by the splitting of the slab, and needs no working out by tool.

Were it not for the large proportional size of their cavities, the general configuration of the long bones of the limbs could not have been so well preserved and presented for the requisite comparison. When these bones sank in the soft fine calcareous mud which has hardened into the peculiar stone which the progress of lithographic art has rendered so valuable, the sparry matter in solution, percolating the matrix and entering the cavities of the bones, has slowly crystallized there, and ultimately filled them by a compact body of spar. The degree to which this represents the original bone gives the measure of the pneumatic cavities and cancelli in the skeleton of *Archeopteryx*, and shows that the proportion of the original osseous matter must have been that which we observe in the present day in birds of flight.

The great and striking difference, and that which gives its enigmatical character to this fossil bird's skeleton, is the number, or rather the proportions and distinctness, of the caudal vertebræ; their under surface is exposed, or rather the sparry casts of the cavities of their bodies, the thin crust of the bone adhering to the impressions of the counterpart. The best view of the under surface of the caudal centrum, thus obtainable, shows a slight expansion of the two articular ends, which join those of the contiguous vertebræ by simple flattened surfaces, having the margin obtuse. The mid-line of the under surface is slightly canaliculate, the impression probably of the caudal artery (Plate IV. fig. 8). There is no trace of hæmal arch, or spine, or articular surface for such, in any part of the caudal series; nor is there any appearance of the ossified thread-like ligaments which are so conspicuous in the tail of the Pterodactyle. The first five of these vertebræ show transverse processes progressively diminishing in breadth and length to the fifth caudal: no trace of such processes is visible in the succeeding vertebræ. The length of the first caudal vertebra is $3\frac{1}{2}$ lines; this dimension gradually increases to the eighth caudal, the centrum or body of which is 6 lines in length, and that dimension is retained to the sixteenth caudal, when it gradually diminishes to the last caudal, which is 5 lines in length, and terminates in a point.

The impressions of the quills of the anterior shorter tail-feathers show that they were attached, ligamentously, to the end of the transverse processes in the anterior ones, and in the succeeding caudals to the sides of the vertebræ, each of these vertebræ supporting a pair of plumes. The under surface of the tail-feathers being exposed, the median groove of the shaft of the vane is clearly shown. The barbs of the vane are as distinctly and inimitably preserved in this delicate and fine-grained lithographic matrix

(Plate IV. fig. 8), as in the impression of the single shorter and broader feather from the same formation described by M. HERMANN VON MEYER*. The narrower series at the fore part of one feather overlaps the margin of the broader series of barbs of the preceding feather.

With the exception of the caudal vertebræ, and possibly of the bi-unguiculate and less confluent condition of the manus, the parts of the skeleton preserved in this rare fossil feathered animal accord with the strictly ornithic modifications of the vertebrate skeleton.

The main departure therefrom is in a part of that skeleton most subject to variety. In Bats there are short-tailed and long-tailed species, as in Rodents, Pterodactyles, and many other natural groups of air-breathing vertebrates; and it now is manifest that, at the period of the deposition of the lithographic slate, a like variety obtained in the feathered class. Its unexpected and almost startling character is due to the constancy with which all birds of the neozoic and modern periods present the short bony tail, accompanied in most of them with that further departure from type exemplified by the coalescence and special modification of the terminal vertebræ, to form the peculiar 'ploughshare bone' supporting the coccygeal glands, and giving attachment to the limited number of fanwise radiating *rectrices*, constituting the outward and visible tail in existing birds. All birds, however, in their embryonic state exhibit the caudal vertebræ distinct, and, in part of the series, gradually decreasing in size to the pointed terminal one.

In the embryo Rook (Pl. III. fig. 6), the proper extent of the caudal vertebræ is shown by the divergence of the parts of the ilia (62) to form the acetabula (*a*); and as many as ten free, but short, vertebræ are indicated beyond this part (*Cd*). Five or six of the anterior of these subsequently coalesce with each other and with the hinder halves of the ilia, lengthening out the sacrum to that extent. The tail is further shortened by the welding together of three terminal vertebræ to form the ploughshare bone.

In the young Ostrich from eighteen to twenty such vertebræ may be counted, freely exposed, between the parts of the iliac bones behind the acetabula; of which vertebræ seven or eight are afterwards annexed to the enormously prolonged sacrum, by coalescing with the backwardly produced ilia; while two or three vertebræ are welded together to form the terminal slender styliform bone of the tail, without undergoing the 'ploughshare' modification. In *Archeopteryx* the embryonal separation persists with such a continued growth of the individual vertebræ as is commonly seen in tailed Vertebrates, whether reptilian or mammalian.

The modification and specialization of the terminal bones of the spinal column in modern birds is closely analogous to that which converts the long, slender, symmetrical, many-jointed tail of the modern embryo-fish into that short and deep symmetrical shape, with coalescence of terminal vertebræ into a compressed lamelliform bone, to which

* Jahrbuch für Mineralogie, &c., 1861, p. 561.

the term 'homocercal' applies; such extreme development or transformation passing through the protocercal and usually the heterocercal stages, at which latter stage, in palæozoic and many mesozoic fishes, it was in different degrees arrested.

Thus we discern, in the main differential character of the by-fossil-remains-oldest-known feathered Vertebrate, a retention of a structure embryonal and transitory in the modern representatives of the class, and a closer adhesion to the general vertebrate type. The same evidence is afforded by the minor extent to which the anchylosing process has been carried on in the pinion, and by the apparent retention of two unguiculate digits on the radial side of the metacarpo-phalangeal bones, modified for the attachment of the primary quill-feathers. But when we recall the single unguiculate digit in the wing of *Pteropus*, and the number of such digits, equalling that in *Pterodactylus*, in the fore foot of the Flying Lemur (*Galeopithecus*), the tendency to see only a reptilian character in what may have been the structure of the manus in *Archeopteryx* receives a due check.

The best-determinable parts of its preserved structure declare it unequivocally to be a Bird, with rare peculiarities indicative of a distinct order in that class. By the law of correlation we infer that the mouth was devoid of lips, and was a beak-like instrument fitted for preening the plumage of *Archeopteryx*. A broad and keeled breast-bone was doubtless associated in the living bird with the great pectoral ridge of the humerus, with the furculum, and with the other evidences of feathered instruments of flight.

Explanation of the Plates.

PLATE I.

The moiety of the split slab of Lithographic Slate, containing, with the impressions of the feathers, the major part of the fossilized skeleton of *Archeopteryx*:—nat. size.

n. Concretionary nodules: the larger one consists of matrix, which filled a cavity, *n′*, formed by a thin layer of brownish and crystalline matter; which may be, as suggested by Mr. John Evans, F.G.S., part of the cranium with the cast of the brain of the *Archeopteryx*.

n′. Cavity with a layer of brown matter, in the counterpart slab, which was applied to the nodule, *n*.

Fig. 2. Fore part of the brain of a Magpie (*Corvus pica*, L.).

Fig. 3, *p′*. Premaxillary bone and, fig. 1, *p*, its impression, resembling that of a fossil fish. The other letters and figures are explained in the text.

PLATE II.

Wing-bones—of the *Archeopteryx* (restored, fig. 1), of a Bird (*Falco trivirgatus*, fig. 2), and of a Pterodactyle (*Pterodactylus suevicus*, Quenst., fig. 3), and the humerus of a Raven (*Corvus corax*, fig. 4).

PLATE III.

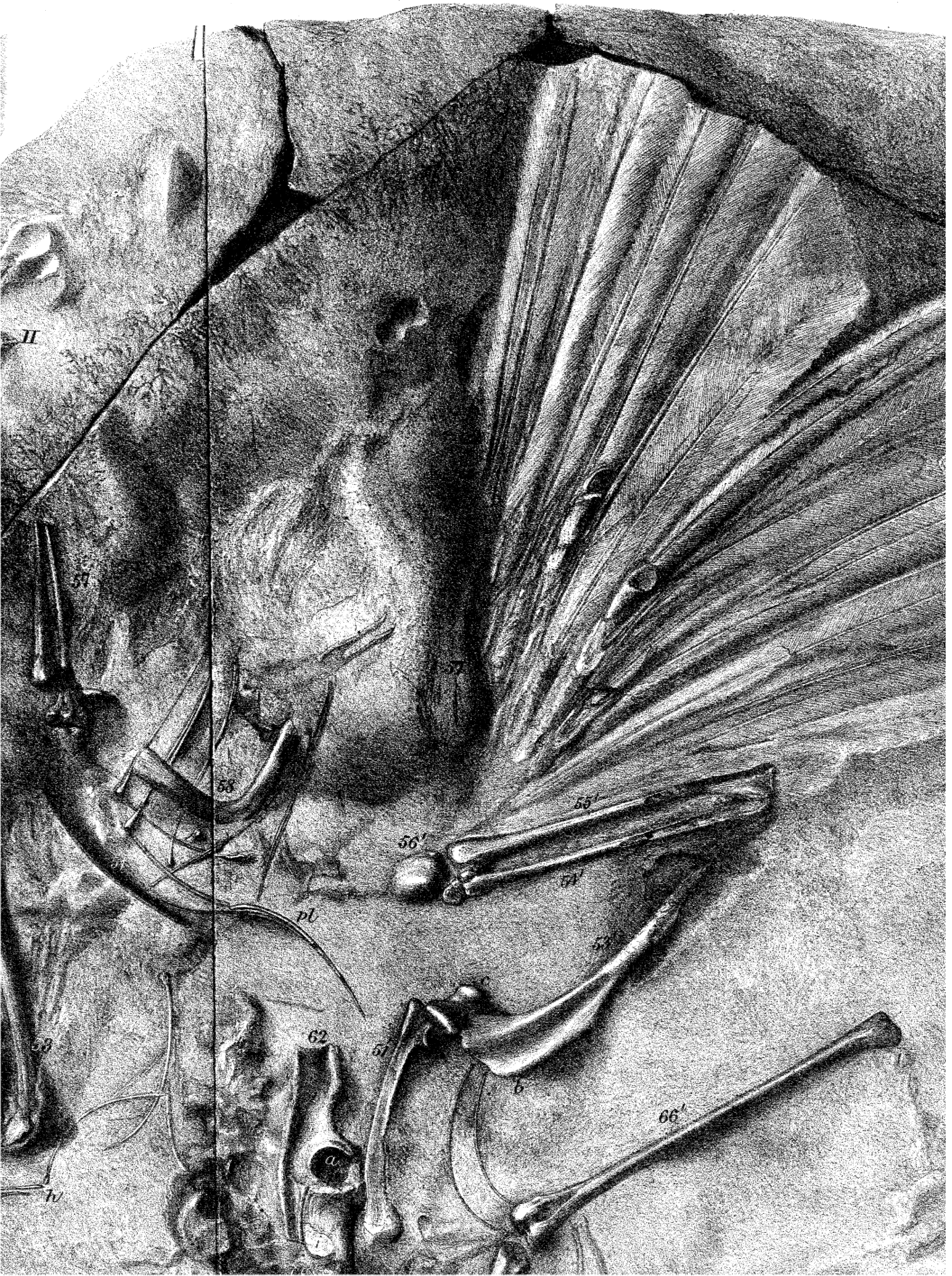
Fig. 1. Bones of the leg of *Archeopteryx*.
Fig. 2. Bones of the leg of a Touraco (*Corythaix*).
Fig. 3. Bones of the leg of a Falcon (*Falco trivirgatus*).
Fig. 4. Bones of the leg of *Pterodactylus suevicus*, Quenst.
Fig. 5. Pelvis and caudal vertebræ of a newly-hatched Ostrich:—nat. size.
Fig. 6. Pelvis and caudal vertebræ of an embryo Rook (magnified 6 diameters).
In both figures, $_{62}$ ilium; $_{63}$ ischium; $_{64}$ pubis; *a*, acetabulum; *Cd*, caudal vertebræ.

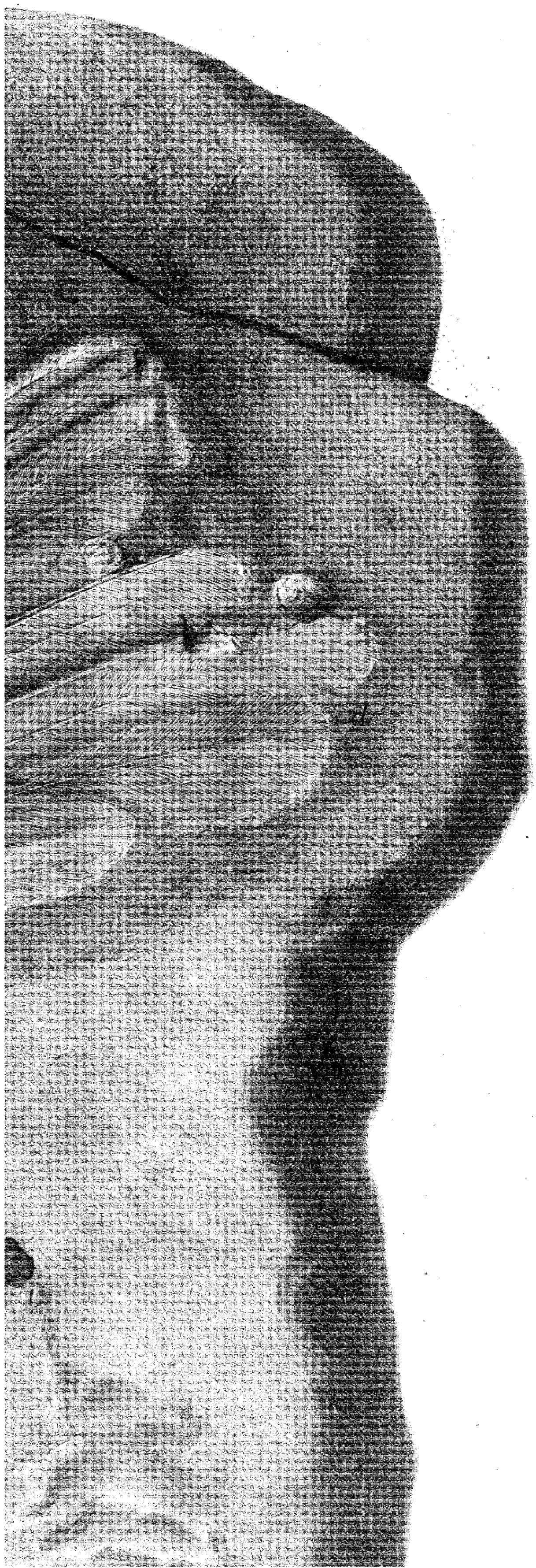
PLATE IV.

Fig. 1. Portion of the furculum of *Archeopteryx*.
Fig. 2. Furculum of a Raven (*Corvus corax*).
Fig. 3. Furculum of a Falcon (*Falco peregrinus*).
Fig. 4. Furculum of an Owl (*Nyctea nivea*).
Fig. 5. Furculum of a Stork (*Ciconia argala*).
Fig. 6. Furculum of a Curassow (*Crax alector*).
Fig. 7. Impressions of the basal part of two 'primaries' and of four entire 'under-coverts' of the left wing of *Archeopteryx*.
Fig. 8. Impressions of the caudal plumes of the 15th and 16th caudal vertebræ of *Archeopteryx*.
Fig. 9. Two bone-cells or lacunæ, femur of *Dinornis*.
Fig. 10. Two bone-cells or lacunæ, wing-bone of *Pterodactylus*. (From Quekett's 'Catalogue of the Histological Series, Museum of the Royal College of Surgeons,' 4to, vol. ii. plate 9. fig. 29, and plate 10. fig. 16, showing identity of character.)


I
II
55
IV

Fig. 1.





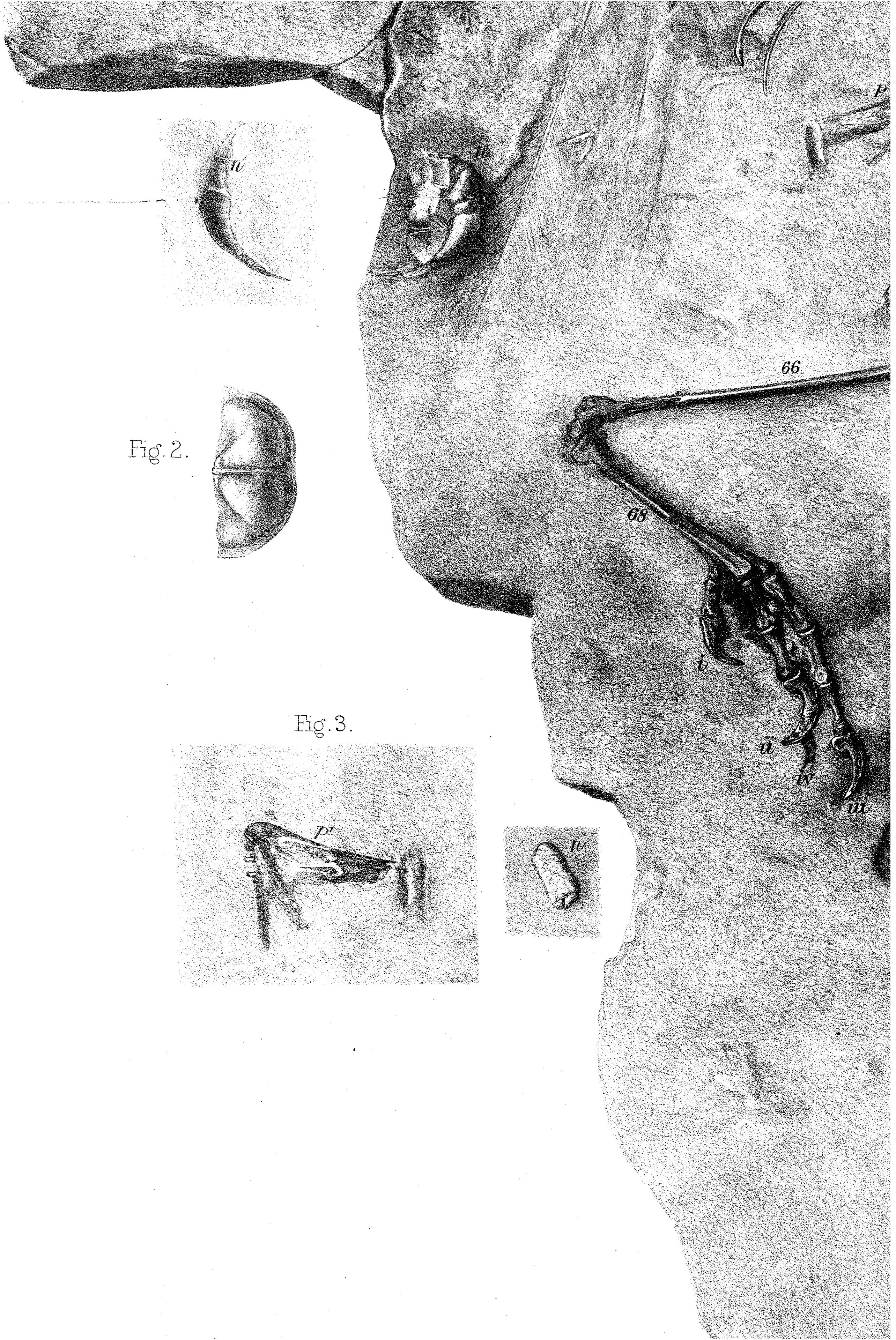


Fig. 2.

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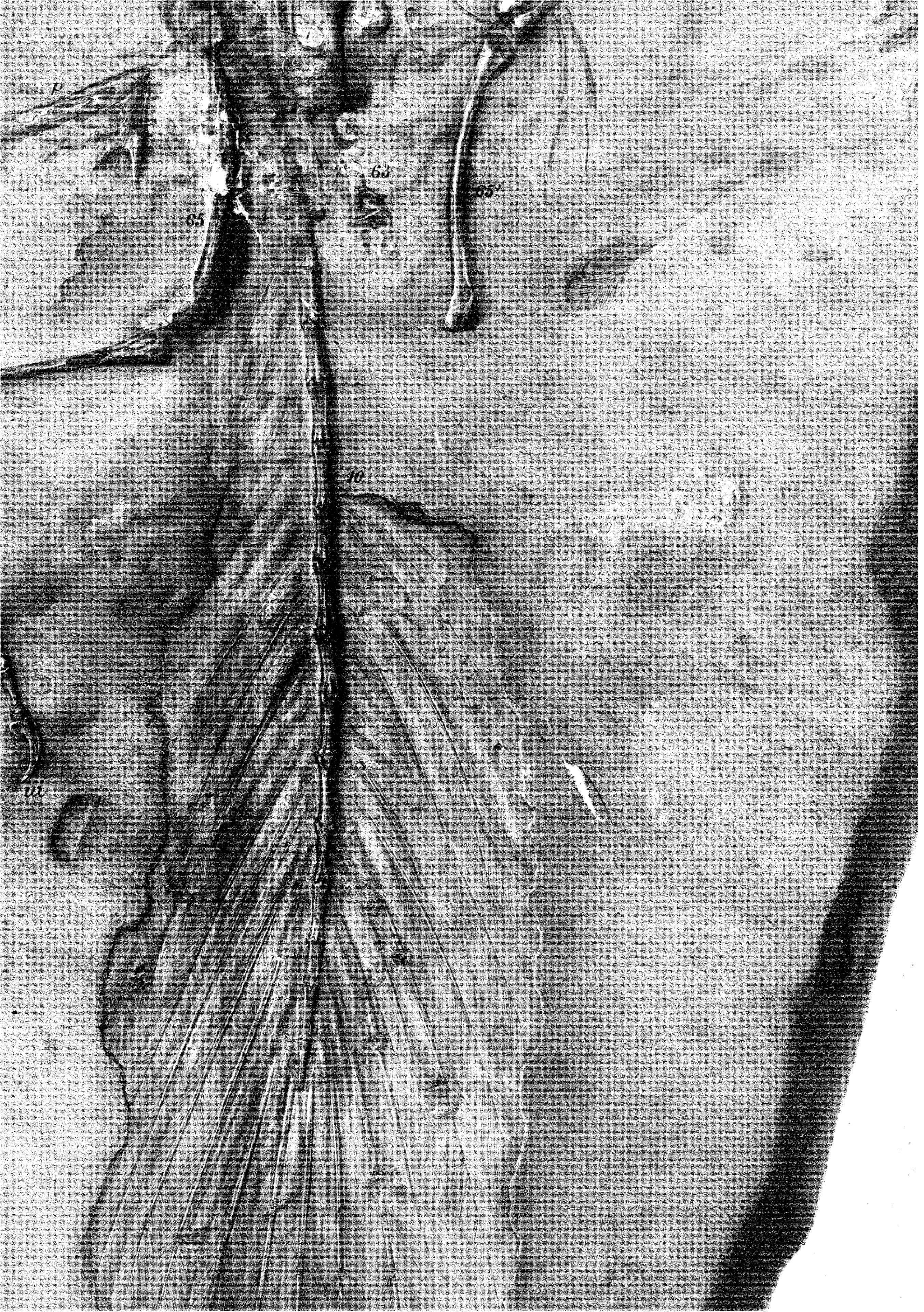
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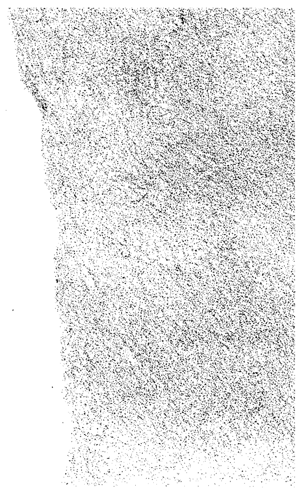
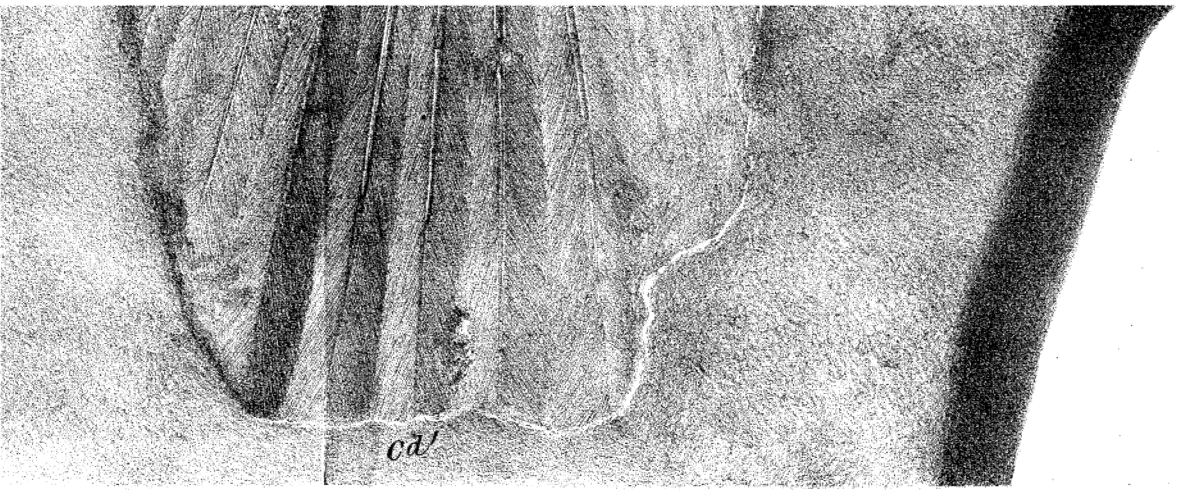
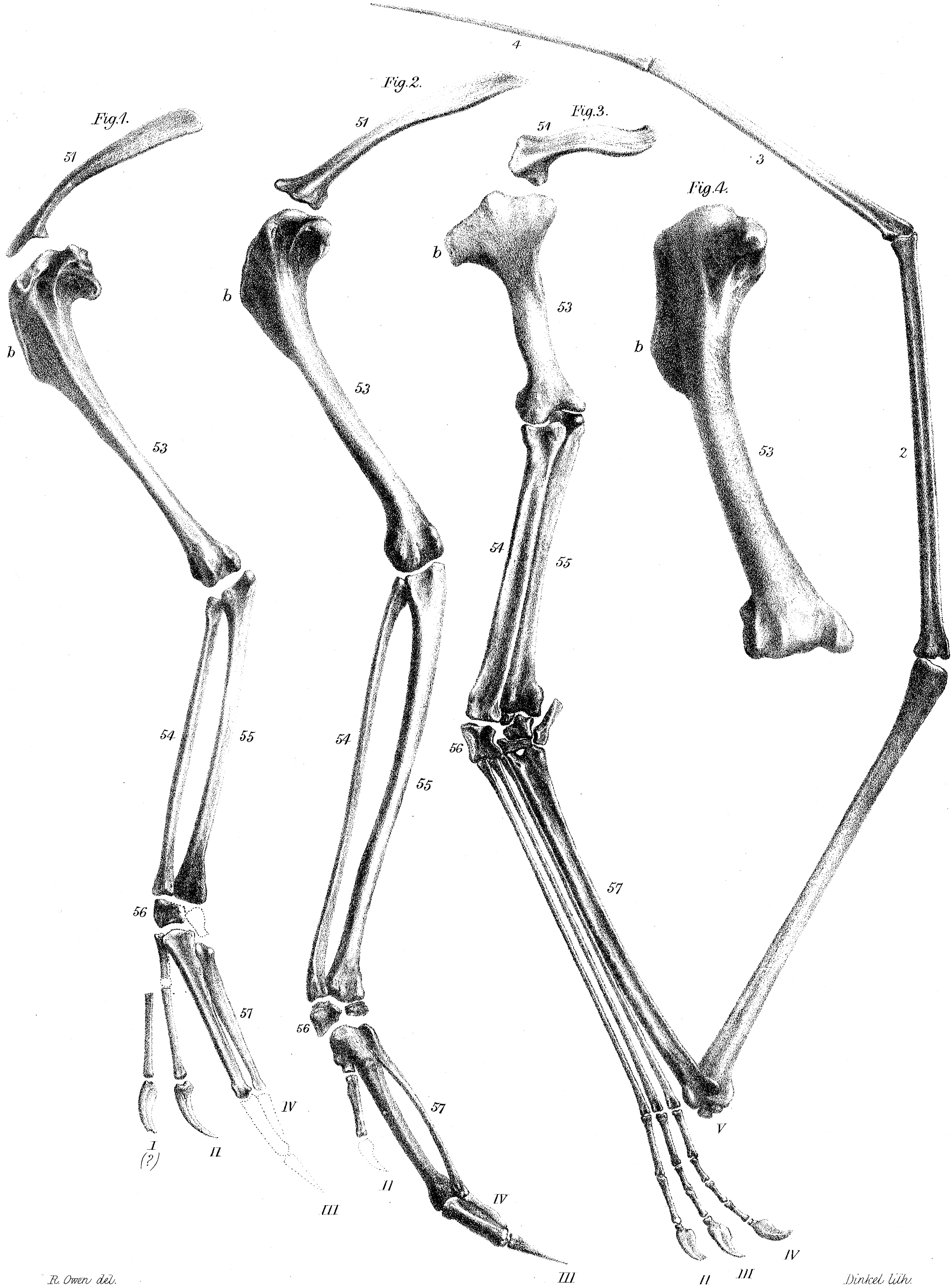


J. Dinkel del. et lith.


cd′

J. Basire, imp.



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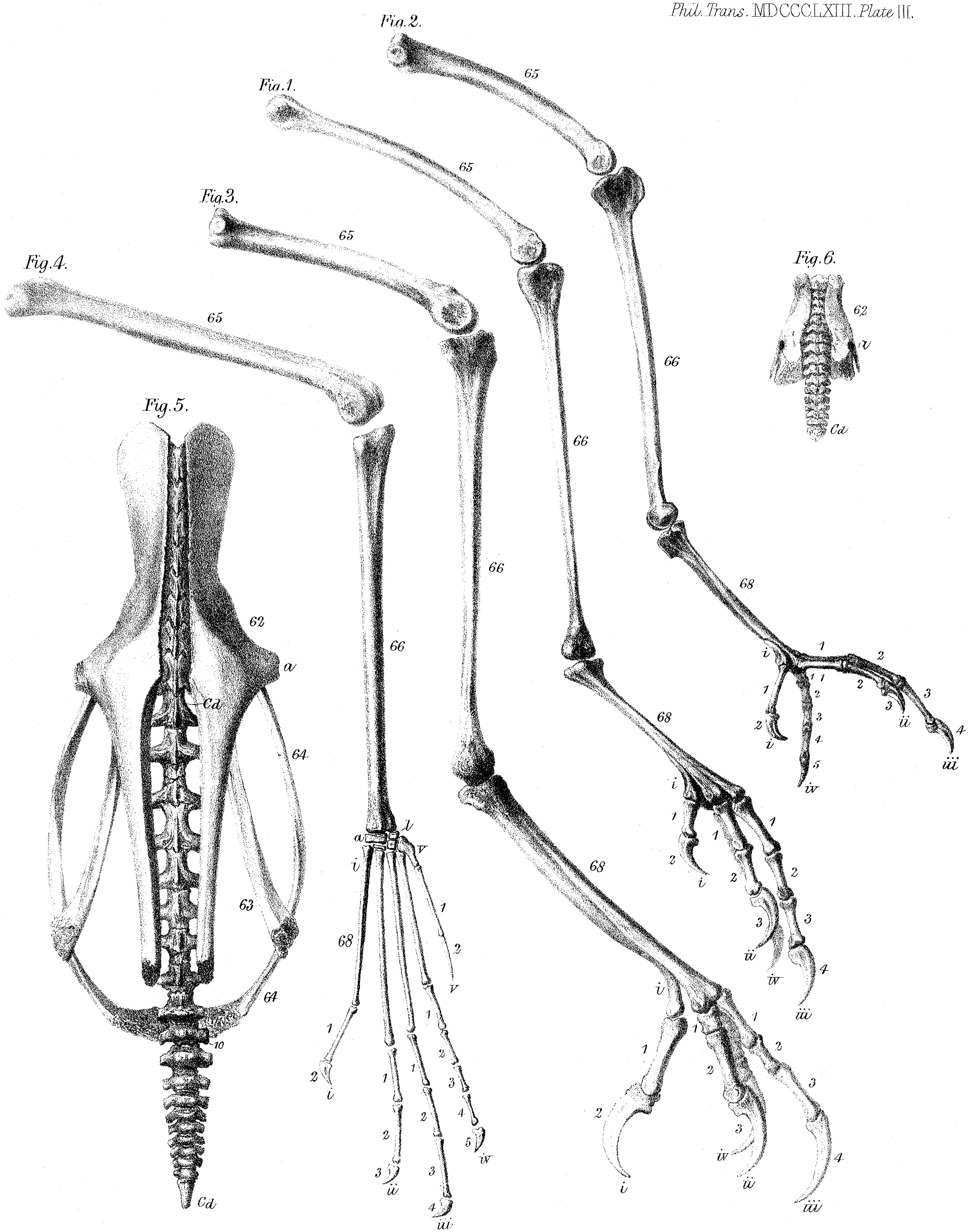

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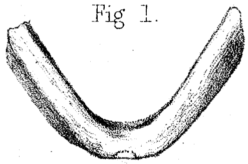
Dinkel lith.

Fig. 1.



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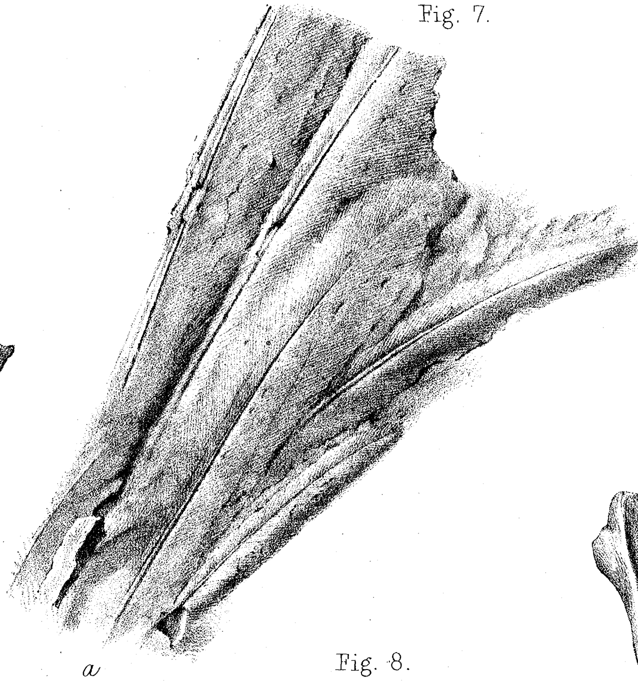

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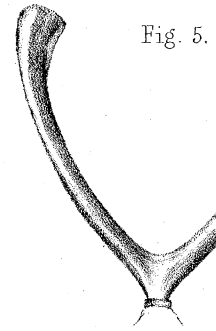

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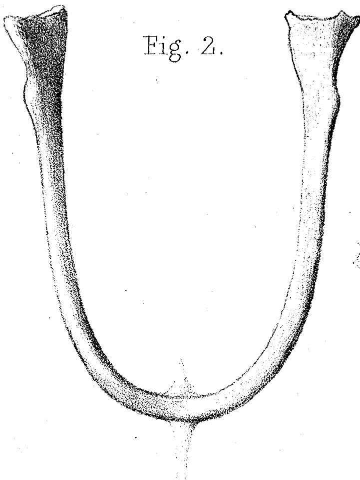

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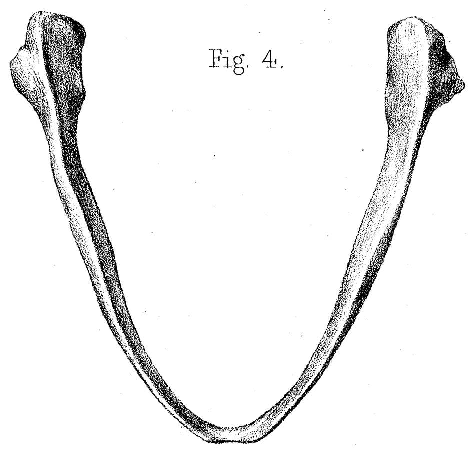
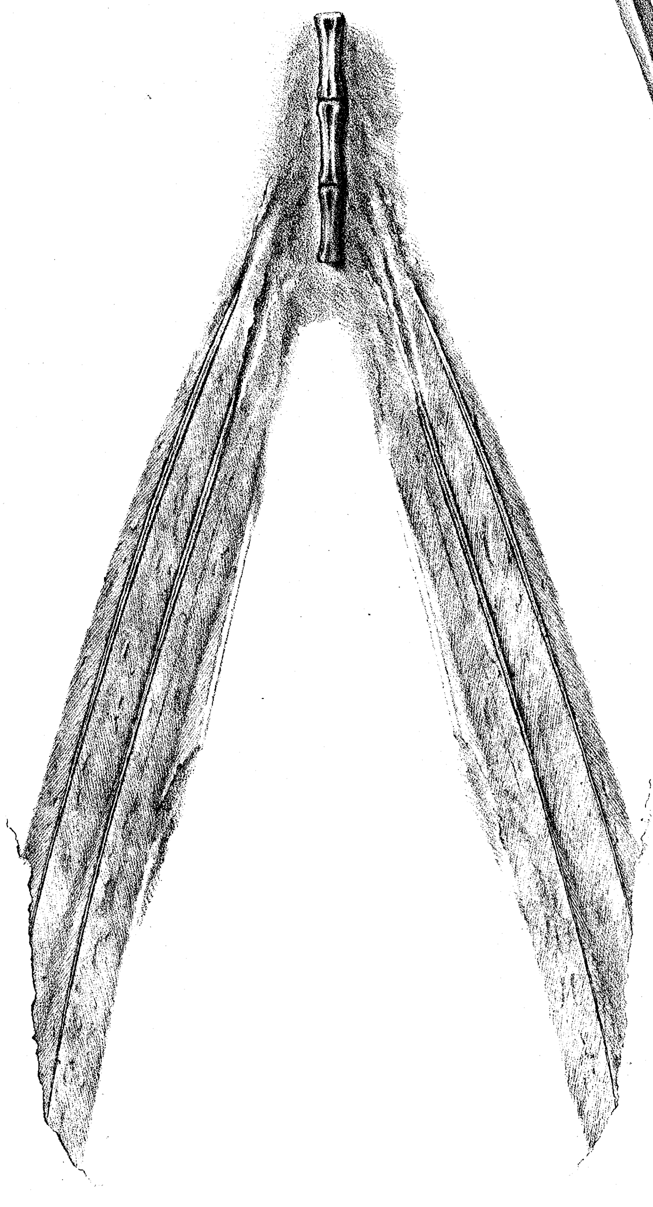


Fig. 8.



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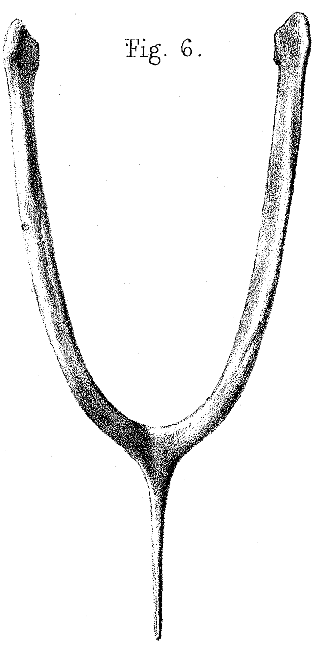

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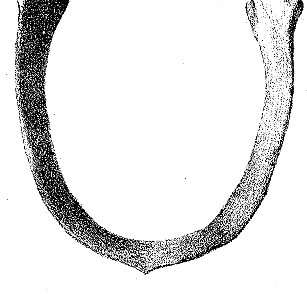

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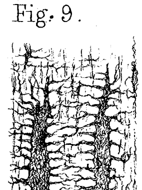

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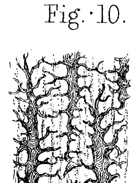

Fig. 1.

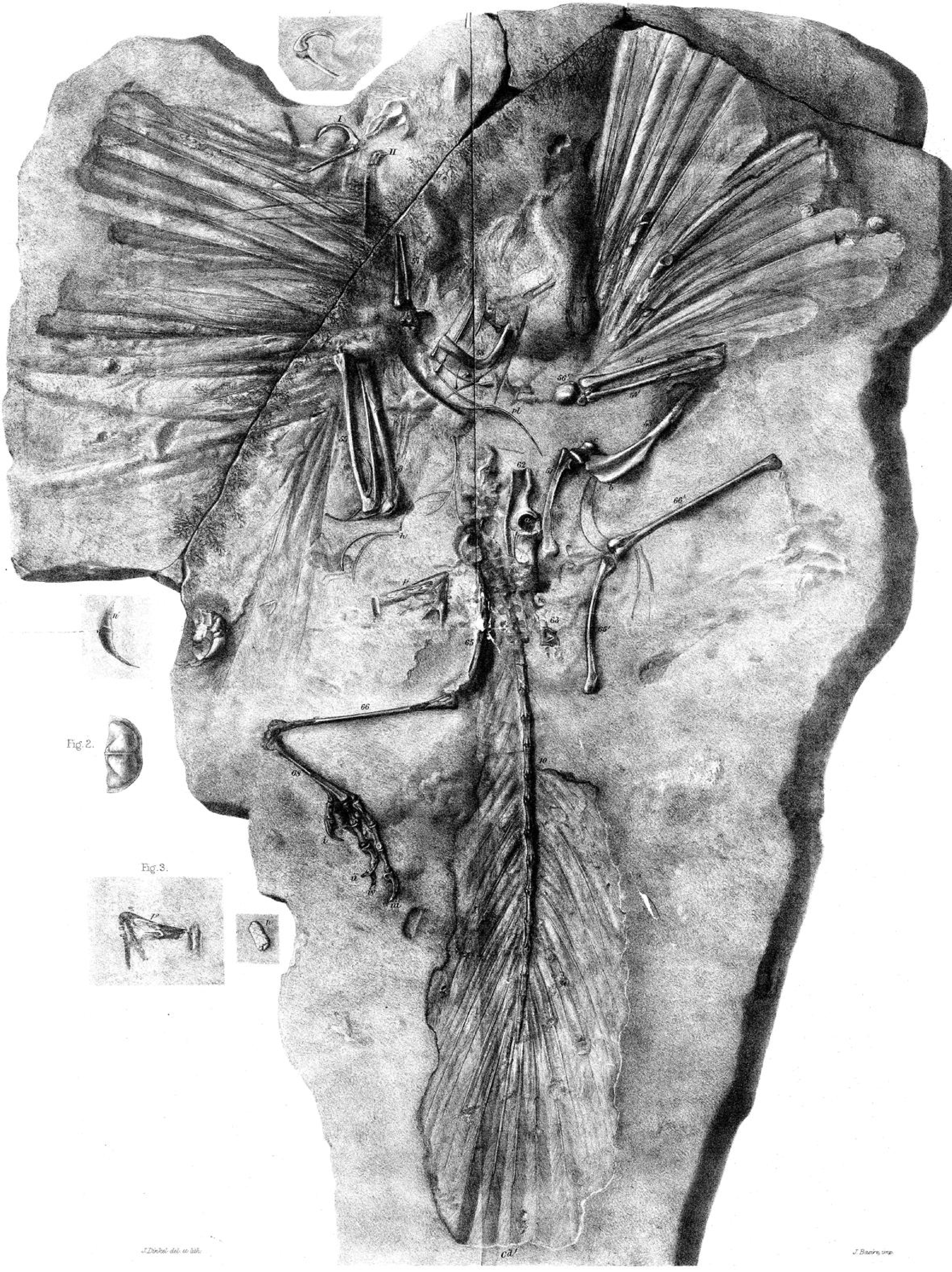

Fig. 2.

Fig. 3.

J. Dinkel del. et lith.

J. Basire, imp.