

IX. On DINORNIS (Part XVI.): containing notices of the Internal Organs of some species, with a description of the Brain and some Nerves and Muscles of the Head of the *Apteryx australis*. By Professor OWEN, F.R.S., F.Z.S., &c.

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[PLATES XLV. to XLVII.]

§ 1. Introduction.

I AVAILED myself of the section of the mutilated cranium of *Dinornis giganteus*, described and figured in Part XIV.<sup>1</sup>, to take a cast of the cavity (Pl. XLV. figs. 11, 12, 13), which affords an instructive representation of the brain of that species.

As my papers on the bones of *Dinornis* were preceded by a description of the osteology and myology of *Apteryx*, so I propose now to communicate some notes and figures made in the year 1848 from dissections of the brain and certain nerves of the head of the *Apteryx australis*, which I have kept back until I have been able to get satisfactory evidence of the brain of the *Dinornis*, with a view to bringing out the characteristics of which my investigations of that organ in the small surviving representative of the gigantic *Dinornithidæ* of New Zealand were mainly conducted.

§ 2. Brain of *Apteryx*.

The brain of the *Apteryx australis* (Pl. XLV. figs. 1–10) is of an ovate subdepressed form,  $1\frac{1}{2}$  inch in length, 1 inch 3 lines in breadth; the cerebral hemispheres (*a*) overlap the optic lobes and four-fifths of the cerebellum (*c*); they are defined anteriorly from the olfactory lobes (fig. 2, *r*) by a curved linear depression (*a'*), convex forward.

Thus, as in most Mammals, three of the primary cerebral vesicles, or divisions of the brain, are exposed by removal of the calvarium, whilst no part of the mesencephalon comes into view.

At the base of the brain (ib. fig. 3) the myelon (*m*) expands into a long macro-myelon (*d*). This shows on each side the small pneumogastric swelling (*v*), and the larger trigeminal one (*tr*); it then expands vertically, as well as laterally, at *d*, for the grey centres in connexion with the “*crura cerebri*” (fig. 4, *k*), the smaller fascicules diverging to the cerebellum and the mesencephalon. The length of the macromyelon (“*oblong medulla*” of Anthropotomy) is half an inch, its extreme breadth 4 lines; the under surface is impressed by a median line or furrow for the basilar artery (fig. 3, *e*), which is formed, as in birds generally, by the two “*arteriæ communicantes*” (*f*) sent

<sup>1</sup> Trans. Zool. Soc. vol. vii. p. 138, pl. 13. fig. 9.

backward from the cerebral divisions of the entocarotids (*g*). The basilar artery transmits or receives the branches from the vertebral arteries (*h*). A division of the macromyelon, defining a "pons," is not more definitely marked than in most other birds.

The cerebellum (Pl. XLV. figs. 1 & 2, *c*) is of a subcompressed, subconical shape; it gives  $6\frac{1}{2}$  lines in vertical, 5 lines in transverse diameter, and 6 lines in antero-posterior extent at the base. A rudimentary appendage or prominence represents the side lobes: the superficies is multiplied by about fifteen transverse folds, averaging  $1\frac{1}{2}$  line in depth; their grey and white matters are shown in the section (ib. fig. 6, *c*). About seven of these folds are visible on the exposed surface of the cerebellum (figs. 1, 2, *c*). A short fissural trace of the primitive cavity (ib. fig. 6, *c'*) communicates with the macromyelonal one, called "fourth ventricle."

The distinctive peculiarity in the base view of the brain in *Apteryx* is the small relative size of the optic lobes (figs. 3 & 4, *b*). M. Dareste was struck with the peculiarity in the specimen of the brain of an *Apteryx* in the Museum of Comparative Anatomy in the Garden of Plants. He speaks of the optic lobes as "à peine visible à l'extérieur"<sup>1</sup>, and justly notices this confirmation by comparative anatomy of the relation of the optic lobes to vision, which relation MM. Flourens and Mayer had inferred from physiological experiment.

The optic lobes, reduced as they are in *Apteryx*, adhere, however, to the ornithic type by the degree in which they have diverged laterally from each other in the course of the brain's acquisition of its mature characters<sup>2</sup>; they are ovate and subdepressed. The optic thalami (ib. fig. 4, *i*) form a larger and more definite tract than in other birds, and contribute in a greater degree to the "radix optica," or chiasma.

The cavity or ventricle of the small optic lobe is shown in the section (fig. 6, *b'*), and in the base view (fig. 4, *b'*), in which the macromyelon, removed by a transverse section through the back parts of the optic lobes (*b b'*) and the "crura cerebri" (*k*), exposes the rudimental hippocampal enlargements (*l*) and the fissures (*m*) by which the artery of the "choroid plexus" penetrates the lateral ventricle.

The cerebral hemispheres (*a, a'*, figs. 1 & 2) are smooth: a feeble indent at the side of the base indicates the "Sylvian fissure," which receives a branch of the cerebral entocarotid (fig. 3, *g*); there is a more feeble indication of a mid longitudinal tract at the upper and hinder part of the hemisphere (fig. 2, *a*), and still more feeble indication of a transverse frontal depression marking off, as it were, an anterior lobe (ib. *a'*). The structure of the hemisphere adheres closely to the avian type. Each "crus" expands and commingles its white fibres with grey matter to form a large ganglion or "corpus striatum" (fig. 5, *n*), from the outer side of which the neurine, chiefly of the white

<sup>1</sup> Annales des Sciences Naturelles, Zoologie, 1856. His notice of this specimen is as follows:—"Le cerveau de l'*Apteryx*, tel que je l'ai entrevu au travers de ses membranes, m'a paru présenter des particularités intéressantes. Malheureusement je n'ai pu obtenir l'autorisation de le disséquer, ou même seulement de le dépouiller de ses membranes."—*Tom. cit.* p. 50.

<sup>2</sup> Anat. of Vertebrates, vol. ii. p. 119.

fibrous kind, expands, ascends, and arches inward over the great ganglion, becoming thinner as it approaches the median line, where it descends in contact with the corresponding part of the opposite hemisphere as a thin film forming the inner or median and the posterior wall of the "lateral ventricle" (Pl. XLV. figs. 7 & 8, *a''*). This is exposed by a longitudinal section of the thicker part of the roof (*a'* in fig. 5, and in Pl. XLVI. fig. 2), the smooth ventricular surface of the ganglion being shown at *n*. In Pl. XLV. fig. 7, the thin inner wall of the ventricle (*a''*) is exposed by removal of the "corpus striatum" and the thicker part of the ventricular wall (fig. 5, *a'*). The "corpus striatum" is impressed by equidistant transverse vascular linear grooves.

Figure 10 shows a vertical transverse section of the hemispheres, where they are united by the "anterior commissure" (*o*): the depth of the interhemispherical fissure (*p*) is seen below the commissure; and the shape of the section of the ventricular cavity is shown at *q*. A similar section, 3 lines in advance (fig. 9), shows the ventricle (*q*) shrunk to the under and inner surfaces of the hemisphere. The section across the base of the rhinencephalon (fig. 8) exposes the continuation of the ventricle (*q*) into that foremost primary division of the brain.

The rhinencephalon (figs. 1 & 2, *r*) is as remarkable in the present singular bird for its large size as is the mesencephalon (fig. 5, *b*) for the smallness of its principal elements. The mammalian proportions of the rhinencephalon (figs. 3, 4, *r*) involves the development of the fore part of the prosencephalon, including those continuations of fasciculi of white with grey matter forming the "crura rhinencephali," the homologues of what are described in Anthropotomy as the "roots of the olfactory nerves." It is that which gives rise to the semblance of "anterior lobes" of the hemispheres on the upper surface of the brain of the *Apteryx* (fig. 2, *a'*), and to the tumid tracts below continuing the hemispheres in advance of the chiasma and its minute optic nerves (figs. 3 & 4, *aa*). The prosencephala (fig. 1, *a*) overhang about two-thirds of the rhinencephala (ib. *r*). One may distinguish at the under part of the hemispheres an outer and an inner division of the "crura rhinencephali" (ib. *r'*) by feeble degrees of prominence; but they are not divided, as in Mammals, by a "perforate tract," or by the definite superficial fascicle of white fibres.

### § 3. Cerebral nerves of *Apteryx*.

The rhinencephala occupy special compartments or fossæ at the fore end of the cranial cavity. The olfactory nerves (Pl. XLV. fig. 2, *s*) perforate the anterior and inferior wall of the rhinencephalic chamber by several foramina, but are closely invested and united by the neurilemma, especially along their upper surface, so as to appear, for an extent of 8 or 9 lines, each as one large olfactory nerve. From the underpart of these fasciculi, filaments pass down to the broad ethmoturbinals (fig. 1, *ae*); the rest of the nerves are dispersed upon the septum narium and the middle turbinals (ib. *ai*), which seem to prolong forward and to make one huge mass with

the ethmoturbinals of convolute bony laminæ covered with highly vascular pituitary membrane. The smaller and more remote anterior turbinal (ib. *ao*), rarely ossified, receives its nerves from the nasal branch (*x*) of the trigeminal.

The optic nerve is but one-fifth of a line in diameter, and about half an inch in length (Pl. XLV. fig. 4, *t*): its course to the eyeball is shown by dividing and reflecting the "obliquus superior" (Pl. XLVI. fig. 2, *o*), the "rectus superior" (ib. *r*), and the nasomaxillary division of the trigeminal nerve (ib. *w*).

The fifth or trigeminal nerve (Pl. XLV. fig. 1, *tr*) arises from the ganglionic enlargement of the macromyelon in connexion with or covered by the fibres of the transverse crus of the cerebellum. After a course of a line and a half, in which it leaves the cranium, it divides into two. The upper division (Pl. XLV. fig. 1, *w*) passes forward, ascending obliquely, traverses the orbit, diving beneath the "rectus superior" (Pl. XLVI. fig. 1, *r*), and the "obliquus superior" (ib. *o*), sending a filament here to the ciliary ganglion: it then, emerging at the upper and fore part of the orbit, subdivides. Prior to its subdivision it rests internally on the dura mater, closing an unossified part of the cranial wall external to the large rhinencephalic fossa. The branch (Pl. XLV. figs. 1 & 2, *x*, and Pl. XLVI. figs. 1 & 2, *x*) here reenters, as it were, the cranium, and emerges external to the cribriform plate by a canal larger than any of the olfactory foramina. The canal perforates the lacrymal bone, then grooves the outside of the turbinal mass (*ae*), and next perforates the base of the maxillary branch of the nasal: afterwards, inclining mesiad and sinking into the naso-premaxillary cavity, it gives branches to the anterior turbinal (ib. *ao*), attaching itself to the septum narium, near the lower margin, and becoming lost upon the septal membrane.

The branch (Pl. XLV. figs. 1 & 2, *y*) passes more directly forward, impresses the outer side of the upper (*ae*) and middle (*ai*) turbinals, and is continued more superficially beneath the horny sheath of the beak as far as the terminal disk perforated by the nostrils; it is diminished by filaments given off to the formative membrane and softer layer of the sheath to its termination at the tactile disk. The division corresponding to that called "third division," or "inferior maxillary nerve" (fig. 1, *6*), sends off two nerves to the muscles of the mandible; these are derived from the non-ganglionic origin of the trigeminal: the main part, from the ganglion, is continued forward, sending off a branch to the outer tegument at the base of the mandible; it then enters the mandibular canal (fig. 1, *z*), and is continued forward to the end of the mandible.

The "eighth" nerve arises by two sets of roots from the same macromyelonal tract—the anterior set of three (Pl. XLV. fig. 1, *1*), and the posterior one of two filaments (ib. *2*): these combine in passing out of the skull, and emerge at the "vagal" foramen, whence the nerve (ib. *3*) is continued further than usual before swelling into the ganglion and dividing into the glossopharyngeal (ib. *4*) and the pneumogastric (ib. *5*; see also figs. 1 & 2 in Pl. XLVI.). I need not go into the further distribution of these nerves, as they cease to mark any part of the skeleton.

Between the origins of the trigeminal and vagal nerves in Pl. XLVI. figs. 1 & 2, are shown that of the "portio dura" of the seventh pair, and the origin of the acoustic nerve.

#### § 4. *Cranial Cavity of Apteryx.*

I may here supplement a former Monograph on the Osteology of the *Apteryx* by a notice of the characters and foramina seen in the interior of the cranium. The largest of the foramina is the foramen magnum, which looks downward and backward. The cerebellar protuberance of the occiput projects a little beyond the foramen; it is bounded on each side by a venous canal, which, emerging from the cranium behind the petrosal, grooves vertically the occiput, and again pierces the bone at the upper margin of the foramen magnum. In most skulls of the *Apteryx* the right of these canals with its upper and lower holes is larger than the left. Near the lower border of the great foramen, on each side the condyle, is a minute "precondylar foramen;" in advance and external thereto is the larger "vagal" fossa and foramen. Above this are the minute foramina conducting the acoustic filaments to the labyrinth. These are overarched by a remarkable development of bone within the "tentorium," forming in the dry skull a nearly horizontal plate, 3 lines by 1 line, terminating mesiad in a rounded and slightly thickened border. Beneath the back part of this plate is a large venous foramen. The superior semicircular canal raises a well-defined prominence on the petrosal platform continued into the above-described plate. The macromyelonal fossa is wide and moderately deep. It is bounded anteriorly by the posterior ridge of the trigeminal fossa and by the intervening hind wall of the sella. The foramen ovale leads from the back part, and the foramen rotundum from the fore part, of the fossa. The sella is deep and hemispheroid; it is tapped behind by the entocarotids. The chiasmal tract rises vertically from its fore part with an irregular aperture on each side larger than is needed for the optic nerves. The chief peculiarity of the cranial cavity is the enormous rhinencephalic fossa, divided by the "lamina perpendicularis." The dura mater closing these fossæ is not ossified, so that in the dry skull the turbinals, upon which the olfactory nerves perforate the membrane to ramify, are here exposed. The cranial walls show a thin pneumatic diploë above the paroccipitals, but in the rest of the section they are thin and compact.

#### § 5. *Brain of Dinornis.*

Returning to the brain of the *Apteryx*, the side view (fig. 1) is contrasted (in Pl. XLV.) with that of the *Dinornis* (fig. 11), the upper view (fig. 2) with fig. 12, and the under view (fig. 3) with fig. 13.

The *Dinornis* differs in the minor relative size of the cerebrum to the cerebellum, which latter (figs. 11 & 12, *c*) rises wholly behind and uncovered by the hemispheres (*a*). The cerebrum appears to be broader, because it is so much shorter, relatively, than that of the *Apteryx*; its upper surface is much more accentuated. A broad and high

longitudinal tract (*a*), next the mid line, is divided from the outer part of the hemispheres; and this is partially subdivided into a posterior (*a''*) and anterior (*a'*) portion by a shallow depression answering to the "Sylvian fissure."

The optic lobes (figs. 11, 12, 13, *b, b*) are, relatively as well as absolutely, larger than in *Apteryx*, corresponding with the indications, given by the orbits or bony beds, of the larger and better-developed organs of vision in *Dinornis*, the species of which we may conclude to have been diurnal; they are visible in the upper view (fig. 12, *b, b*) as well as in the side view (fig. 11).

No demarcation of a "pons" can be satisfactorily traced on the cast; but the trigeminal swelling is plain. The length of the macromyelon is 11 lines, its breadth is 9 lines.

The cerebellum shows a pair of low lateral lobes (fig. 11, *c'*) at its fore part, and behind this the depression answering to the upper semicircular canal. The length of the cerebellum is 1 inch 2 lines, its breadth at the lateral lobes is 1 inch. The vertical diameter of the epencephalon (ib. *c, d*) is 1 inch 4 lines; the breadth of the mesencephalon (fig. 13, *i, b*), taken outside of the optic lobes, is 1 inch; the length to the fore part of the chiasma is 8 lines; each optic nerve (*t*) has a thickness of 2 lines. The breadth of the cerebrum (fig. 12, *a, a''*) is 2 inches 2 lines; its length is 1 inch 7 lines; its depth, or vertical diameter, is 1 inch 1 line. The breadth of the rhinencephalon (*r*) is 8 lines; the length of each lobe in advance of the cerebral hemisphere is  $2\frac{1}{2}$  lines. They are relatively less than in *Apteryx*.

The hypophysis, as represented by the cast of the "sella" (figs. 11, 13, *y*) is of considerable size; there is an indication of a better-developed pineal gland (fig. 12, *p*) than in the *Apteryx*.

#### § 6. *Trachea of Apteryx, Struthio, and Casuarius.*

In the *Apteryx australis* the trachea has a nearly uniform diameter throughout its extent; the rings, from 120 to 130 in number, are entire and cartilaginous. When the windpipe is relaxed the rings alternately overlap, and are overlapped by, each other at their sides, appearing to be alternately narrower on one side than on the other; but when the tube is stretched this appearance is lost, though not wholly, the rings then showing a slight difference of breadth in the axis of the tube at their sides. They become gradually smaller in circumference and diameter in the last twenty, which are less closely attached together than in the Ostrich and Emu.

In the trachea of the Cassowary, for the opportunity of examining which I am indebted to Dr. Murie, the rings, mostly entire as in other birds, vary in depth, *i.e.* in the diameter of the hoop parallel with the length of the tube, and they correspondingly vary in thickness (Pl. XLVI. fig. 5). Their excess in these diameters is shown at about one-fourth down the trachea; they become narrowest and thinnest at the terminal tenth part of the tube, where a solution of continuity of the ring begins to show itself along

the mid line of the back part of the tube. The incomplete rings of the bronchi resume the dimensions of those at the beginning and middle of the trachea.

In the Ostrich the bronchial rings are more slender than any of those of the trachea, and rapidly diminish in size as they approach the lungs.

In both Ostrich and Cassowary the tracheal rings examined by me were gristly, or were hardened with a very small proportion of bone-earth.

#### § 7. *Trachea of Dinornis crassus.*

The more completely ossified state of the tracheal rings of *Dinornis* has led to their preservation in more than one species; and I have received from time to time specimens of such rings more or less closely associated with parts of the skeleton, in largest numbers with that collection of *Dinornis* remains obtained by Mr. Walter Mantell from the fine dark soil, or morass, at Ruamoā, Middle Island of New Zealand, and purchased for the British Museum.

In working out this matrix from the base of the skulls of *Dinornis crassus*, described in a former Memoir<sup>1</sup>, I detached from beneath the position of the palato-nares a group of four bony hoops or rings of an oval form, averaging 9 lines in long diameter, 7 lines in short diameter; the depth of the rim of the bony hoop varied from one line to half a line; its thickness was about a quarter of a line. The outside of the ring is convex and finely rugose; the inside is less convex and smooth.

It is probable, though I cannot hold it as certain, that, because these slender rings were found at or near the position of the upper larynx, therefore they were from the beginning of the windpipe; for the dislocation of the parts of the skeleton in all the individuals so represented in the marshes of Ruamoā, as far as can be gathered from the account given by Mr. Mantell, might well admit of displacement of parts of the bony trachea.

Admitting this doubt as to their precise position in the windpipe, still the probability is so great that tracheal rings preserved in contact with parts of the skeleton were parts of the same bird, that the rings here described may be reasonably referred to the *Dinornis crassus*.

There is, moreover, a significant degree of correspondence between the number of tracheal rings of the type of those attached to the skull, but collected without note of precise relations, probably scattered in the matrix, and the number of individuals of *Dinornis crassus* indicated by bones of the skeleton; that is to say, both tracheal rings and skeletons or bony evidences of *D. crassus* are amongst the most plentiful of the species there found.

The rings or hoops, upwards of 150 in number, provisionally referred to *Dinornis crassus*, are associated together by the character of shape and size. In general they are less slender than those cemented to the skull-base; but they present a certain range in

<sup>1</sup> Part XIII., Trans. Zool. Soc. vol. vii. p. 129.

the thickness, especially the depth, of the wall of the ring. The extreme of the latter, or breadth in the axis of the windpipe, is 3 lines, as at fig. 2, *b*, Pl. XLVII.; but this is partial, the hoop decreasing to 2 lines and  $1\frac{1}{2}$  line at part of the circumference, in a few at the small ends of the ellipse, or the lateral parts of the hoop; the more common breadth is from 2 lines to  $1\frac{1}{2}$  line (Pl. XLVII. fig. 1, *d*); those found at the base of the skull, and inferred to be from the upper part of the windpipe, were 1 line, decreasing partially to  $\frac{1}{2}$  a line, in depth. There is less range of thickness in the elliptical rings of *Dinornis crassus*, as, *e. g.* from  $\frac{1}{10}$  to  $\frac{1}{8}$  of a line, seldom getting to  $\frac{1}{6}$  (ib. figs. 1 & 3). There is a certain range of size and of shape of the ellipse: thus, in fig. 1, *a, b*, exceptional instances of subcircular rings are figured; in fig. 3, *a, b*, the long axis is 10 lines, the short one 9 lines; in fig. 3, *c*, the long axis is  $11\frac{1}{2}$  lines, the short one 8 lines. Most of the rings have intermediate proportions; in a few the ellipse is less regular, one side inclining to flatness. There is a variety also in the configuration of the surfaces of the hoop; instead of the outer surface being convex from the upper to the lower margins, as in the slender rings detached from beneath the skull, it is flat, especially in the broader varieties, in which the inner surface preserves a slight convexity in the same course; in some rings the outer surface is slightly concave from edge to edge (as in fig. 2, *b*).

Of the tracheal rings referred to *Dinornis crassus* some are preserved in groups, cemented in their consecutive arrangement upon and by the matrix. These groups include one of seven rings (fig. 4), two of six rings, one of five rings (fig. 5), two of four rings with part of a fifth (fig. 6), as many of three rings, and more of two rings so kept in natural sequence. In three instances of the "two rings" these show broader and narrower parts of the outer surface, alternating, the extremes being at the small ends of the ellipse, or at the sides of the tube. This character has been noted in recent birds, especially in the Waders<sup>1</sup>, the appearance being that presented by the tracheal rings of the present extinct Moa (fig. 7, *a, b, c*); but the analogy of *Apteryx* (*antèa*, p. 386) led me to test the relation of the appearance to reality.

Succeeding in working out the cementing matrix in one instance, and exposing the inner surfaces of the two interlocked rings, I found, as I had anticipated, that the outward appearance was due in some degree to intussusception, the inner surface being broader where the outer surface was narrower, and *vice versâ*. Nevertheless a slight inequality of breadth is shown in some detached rings at the ends of the ellipse; and it may indicate that they come from a part of the windpipe situated where it was subject to most flexure in the bendings of the bird's neck.

<sup>1</sup> "They are alternately narrower at certain parts of their circumference and broader at others; and in these cases the rings are closely approximated, as it were interlocked. This structure is most common in the Grallatores, where the rings are broadest alternately on the right and left sides."—*Anat. of Vertebrates*, ii. p. 219.



§ 8. *Larynx of Dinornis crassus?*

The portion of a thin, hollowed, shield-shaped piece of bone (Pl. XLVII. fig. 8, *a, b*) I take to belong to the upper larynx, and to be part of the thyroid element. To its lower border has coalesced, as is sometimes found in existing birds, the first tracheal bone or hoop (*c*), which, as usual, is incomplete; the coalescence is limited to the two ends of this half ring; the slit of separation between it and the thyroid is 9 lines in extent, giving the breadth of this slender bone as half a line; it projects anteriorly like a folded lower border in advance of the actual lower border of the thyroid, which is the more prominent part on the inner or concave side of the thyroid. One might expect the rings near to or following this to have similar slender proportions, like those worked out of the matrix beneath the skull of *Dinornis crassus*; lower down the wind-pipe they gained in depth.

From another mass of matrix, exhibiting a portion of a broad tracheal ring, I worked out the part of the expanded terminal one, to which, in the entire or recent state of the parts, the bronchi are attached; it answers to that supporting the cross bar shown at *t*, fig. 103, 'Anatomy of Vertebrates,' vol. ii. p. 222, in the Raven, and ranks among the parts of the lower larynx. The specimen shows the contiguous portions of two cavities, meeting at a sharp straight ridge (fig. 9, *a*), 8 lines in extent, which was produced into the cavity of the trachea, dividing the tube from before backward; the concavities on each side are the beginnings of the divisions or the continuations of the trachea into the bronchi. The margins of the expanded bone, continued from one (probably fore) end of the dividing ridge, are rather thickened. Cemented by the matrix to this part of the lower larynx was one, probably the first, of the bronchial bones (fig. 9, *b c*); it is incomplete, varying in breadth from 2 lines to nearly 3 lines, and may have surrounded two-thirds or three-fourths of the bronchus. At the broader part the outer surface is rather convex from the upper to the under margin; at the narrower part this surface is concave. It seems to answer to that part of the lower larynx figured at *a*, fig. 103, *tom. cit.* p. 222.

§ 9. *Trachea of Dinornis rheides?*

To a smaller species of *Dinornis*, probably *D. rheides*, I refer a series of rings, about 80 in number, similar in shape and general character to those of *Dinornis crassus*, but of a smaller size (Pl. XLVII. figs. 10–12).

The range of variety of size is here rather less. The largest ring yields, in long diameter, 9 lines, in short diameter 7 lines (fig. 11); the smallest gives 7 lines and 6 lines in the same diameters (fig. 10). The average, or common size, is 8 lines in long and  $6\frac{2}{3}$  in short diameter (fig. 12); the ellipse is more perfect and constant in the rings of this species, and the concavity from edge to edge of the outer surface of the hoop is more constant and more marked than in *Din. crassus*. The depth of the hoop is greater,

relatively, and is maintained through a greater extent of the windpipe, as it seems; this dimension is 2 lines, with slight change at parts of the circumference.

Of this species there is one specimen of a sequence of four rings in the same portion of matrix (fig 12), another piece with three rings, and three or four with two rings. The extreme of depth of hoop is reached at part of the circumference of the ring (fig. 11, *a, b*).

#### § 10. *Trachea of Dinornis elephantopus?*

The tracheal rings of the third series are remarkable for their great breadth and thickness. There are about 80 of these, of a full elliptical, subcircular, or circular shape, with an average diameter or long diameter of 9 lines. The specimen figured (Pl. XLVII. fig. 13, *a, b*) shows the average size or common character of these strong, broad, well-ossified tracheal rings. The exterior surface is rugose, the inner one smoother, both surfaces straight or even from one margin to the other; the margins are flat, as if made by a clean cut, and show irregular perforations, probably vascular, of the osseous tissue. The thickness of the hoop is rarely uniform, the difference being, in several rings, as great as in that figured in 15, *a*; there is also, occasionally, a variety in the breadth at different parts of the circumference of the hoop, though rarely to the extent shown in fig. 16, which, from its small size, may possibly be a bronchial hoop.

#### § 11. *Trachea of Dinornis ingens?*

About 70 tracheal rings show an average of size and shape as in that of fig. 17, *a, b, c*; the extremes in regard to depth of hoop, in this series, are given in figs. 19 & 20. The bone, in all, is of unequal thickness, longitudinally rugose, but unequally so, on the outer surface, smooth within (fig. 18, longitudinal section). On the rougher part of the ring the bony substance stands out in the form of granules or ridges, the latter running in the direction from one margin to the other (figs. 19 & 20, *b, b*). These margins (figs. 17 & 19, *a*) are flat or "truncate," as in the smaller rings (figs. 13-15, *a*) of the present robust type; but here the margin is more uneven, with risings and depressions, somewhat irregular, but on the whole at right angles to the outer and inner surfaces.

In this series were specimens of two partially confluent rings, or of a broad hoop twisted upon itself spirally, so as to simulate two hoops. Of these specimens one is represented at fig. 21, *a, b*, a second at fig. 22; fig. 23 shows more plainly a partial confluence of the two bony rings. Seven rings of the average size of those provisionally attributed to *Dinornis ingens* (Pl. XLVI. fig. 6) occupy an extent of the trachea equalling that which includes thirty-nine in *Casuarius galeatus* (ib. fig. 5).

#### § 12. *Trachea of Dinornis robustus?*

I have finally to notice the largest specimens in the present collection, which exemplify the most extraordinary degrees of thickness and strength of bone which have been hitherto observed in the windpipes of Birds.

I think it not improbable that an osseous hoop like that represented in fig. 24, *a*, *b*, might, if received as a solitary fossil, have passed rather for a section of the shaft of a pneumatic limb-bone, being as large, for example, as such section of the femur of a Cassowary, but thicker in the walls. He must have been a bold, as well as acute, palæontologist who would have pronounced it one of the rings of a bird's windpipe. I have now, however, received upwards of thirty specimens, averaging the dimensions of that of fig. 24. They are, most of them, rather more elliptical, less circular, than the smaller hoops of a like type (figs. 17-23). The long diameter averages, as in fig. 24, 1 inch 2 lines, the short diameter 1 inch, outside measure; the area, which is a more regular ellipse, gives  $10\frac{1}{2}$  lines and 9 lines in the two diameters. The breadth, or we may now say the length, of the hoop's wall, *i. e.* from the upper to the lower margin, averages 9 lines and  $7\frac{1}{2}$  lines, not being uniform all round; the difference of thickness is greater, viz. from  $2\frac{1}{2}$  lines to  $\frac{1}{2}$  a line (fig. 24, *a*, and fig. 32).

The contrast between the outer and the inner surfaces of the tracheal hoops in *Dinornis* becomes greater as these increase in size. In the present series, which may belong to *Dinornis robustus*, the irregular longitudinal striation prevails over the external surface of the bone; but there are other characters.

At one or two parts of the circumference a part of that surface (figs. 24, 26, 28,  $\times$ ) projects beyond the rest, usually from the middle third part between the upper and lower borders; these elevations, or the elevation, if it be single or continuous, are limited to one side of the hoop, and to that which is most convex or least flattened. The degree of elevation is slight, from a fourth to a sixth of a line; the surface is smoother than the parts above and below. These elevations I take to indicate the interval between the surfaces of insertion or attachment of fibrous substance connecting one ring to the next in a more special manner than the general external investment of the hoops, the fibrous character of which may be indicated by the general longitudinal striation of the external surface. The smoother part of that surface is usually opposite the side showing the broad and low elevation. Besides the foregoing accentuations of the outer surface, many of the hoops show coarser granulate outgrowths at the rougher part of the bone.

In almost all of the present series of rings the longitudinal lay of the outer surface, from one margin to the other, if it is not straight, tends rather to convexity. The longitudinal lay of the smooth inner surface is more uniformly straight; but there is a feeble transverse rise, or linear impression, indicative of a tract on the inside corresponding to the elevation on the outside of the hoop.

In the present, as in the preceding series, there are differences of length, breadth, and thickness of the wall of the hoops; the two extremes of the first dimension are shown in the subjects of figures 25 & 26. There are also six instances of confluence of two hoops; in no received example is co-ossification of the tracheal rings carried further. Fig. 27 shows two of the shorter variety of hoops coalesced at the flatter and rougher half of their circumference (*b*), the activity there of the ossifying process being further

exemplified by an unusual degree of granulate outgrowths simulating an exostosis: the more convex part of each hoop (*a*), where the line of separation remains open, is comparatively smooth. The two rings (fig. 28, *a b*) have completely coalesced—the original separation, showing them to have been of the long variety, being feebly, though sufficiently, indicated. These also show a markedly flatter side of the ring where the bone is thickest and most irregular. It is to this increase of osseous substance that the flattening is due, the smooth inner surface of the same part following the course of the elliptical section of the air-passage. Lengthwise these anchylosed hoops show a greater longitudinal convexity of the smoother side, and a more feebly longitudinal concavity of the opposite side; but this indication of a bend of the windpipe is better marked in the next anchylosed pair of hoops (fig. 29), although they are shorter, showing the common size. In these, at the convex part of the bend, the coalescence is incomplete.

Figure 30 shows two coalesced rings, where the hoops thin off behind and the bony texture is exposed by abrasion. This texture is coarse, and, with the character of the truncate margins and of the rough parts of the outer surface, gives the hoops or cylinders a cork-like appearance.

Sections of these tracheal rings (fig. 31, *D. ingens?*, and fig. 32, *D. robustus?*) show the varying thickness of the bone at opposite parts of the cylinder, the smoothness of the inner surface, and the denser character of the osseous texture at the thicker part of the wall of some of the rings.

#### § 13. *Trachea of Aptornis defossor.*

With a sternum, pelvis, and some other parts of the skeleton of *Aptornis defossor*, more entire than those described in my Memoir No. XV., and subsequently received, were a few rings of the trachea, of elliptical shape, averaging 7 lines and 5 lines in the two diameters (Pl. XLVI. fig. 7), with a depth of the hoop of  $1\frac{1}{2}$  line. These rings show a pair of narrow notches, one at the upper, the other at the lower margin, at opposite sides of the hoop, at its shorter diameter (ib. *a, c*). In the instance of two of these rings in connexion, the partial and reciprocal overlapping or intussusception was defined by or took place at these notches (ib. *b*).

#### § 14. *Muscles of the Mandible and Hyoid of the Apteryx.*

The illustrations of the myology of the *Apteryx* in my second paper on this bird<sup>1</sup> were mainly devoted to the muscles of the trunk and limbs; I now, therefore, supply figures (Pl. XLVI. figs. 1–4) in which are shown some muscles of the eye, the jaw, and the tongue, either undescribed or briefly referred to in that Monograph.

The origin of the “constrictor colli” (Zool. Trans. *tom. cit.* pl. 31. *a*), by a “broad

<sup>1</sup> Part II. (Myology) Trans. Zool. Soc. vol. iii. p. 277, pls. 31–35.

fasciculus from the outer part of the superoccipital ridge" (ib. p. 228), is shown at *a*, fig. 3. It is reflected back, to expose the homologue of the "biventer mandibulæ" ( $\gamma$ ), a powerful muscle which arises tendinous from the outer and anterior marginal ridge of the paroccipital, swells into a fleshy belly, which again contracts to its insertion into the slightly deflected angle of the mandible.

The external or posterior "temporalis" ( $\alpha$ ) and the internal or anterior "temporalis" ( $\beta$ ) have their origins exposed in fig. 3, Pl. XLVI., and their entire course shown in fig. 4, ib. The external muscle derives its origin from the lower and lateral part of the parietal as far back as the mastoid (8)<sup>1</sup>. The origin of the internal portion continues the curved line forward from the parietal to the postfrontal. The fibres of the external portion pass obliquely forward, external to those of the anterior portion, to be inserted into the fore part of the outer surface of the marginal coronoid elevation of the mandible. The fibres of the anterior portion ( $\beta$ , fig. 4) descend less obliquely, and more directly embrace, by their insertion, the long and low, sharp, straight coronoid ridge in *Apteryx*; the hinder fibres descend vertically, and are continued backward to the hind end of the ridge. Both portions, like the more collective mass of carneous fibres of the temporal in Man and Mammals, pass behind the horizontally extended arch of bone formed by the zygomatic portions of the squamosal (27) and the malar (26). This relation I deem worthy the attention of the unbiased student of the homologies of the bones marked respectively 8, 27, 26, in fig. 4, and in the illustrations of the skulls of *Dinornis* &c. in preceding Memoirs. If the hind end of 27, where it joins the tympanic (28) as in Man and Mammals, were to expand into overlying junction with the mastoid (8) and parietal (7), it would also contribute to the surface of origin of the temporalis muscle. By adopting the homology propounded by Cuvier and Hallmann of the bone (8) as with the "temporal" or "squamosal" of Mammals, the anatomist falls into the necessity of introducing a new bone into the cranium of the bird, and of completing its zygomatic arch by a "quadrato-jugal."

From the posterior third of the lower border and inner surface of the zygomatic arch rises the masseter muscle ( $\eta$ , fig. 3, Pl. XLVI.), answering, in regard to its origin and the forward inclination of the fibres as they descend, to the deep portion of the mammalian and human masseter: the insertion is into the lower half of the outer side of a short tract of the mandible behind the insertion of the "temporal" muscles.

The "orbicularis palpebrarum" (fig. 3, *c*) sends some of its hinder superficial fibres over the part of the zygoma giving origin to the masseter, which are lost in the superficial fascia of that muscle. I noted the great strength of the "orbicularis palpebrarum" in my first Memoir on the Anatomy of the *Apteryx* (Trans. Zool. Soc. vol. ii. p. 294).

<sup>1</sup> As in Man, the temporal muscle is described as extending its origin "from the curved line on the frontal and parietal bone above to the mastoid portion of the temporal behind."—GRAY'S 'Anatomy, Descriptive,' &c., 8vo, 1858, p. 200. The "temporalis externus" in birds answers to the posterior portion of the mammalian "temporal muscle."

In fig. 3 a bristle is represented passing through the "punctum lacrymale" and along the lacrymal duct into the nasal chamber, where it terminates between the second and third turbinals. In fig. 4 are shown three of the ligaments of the lower jaw. The "occipito-mandibular ligament" (*m*) is attached above to the paroccipital ridge (*4*), crosses the back part of the "membrana tympani," but behind the "meatus auditorius," to be fixed into the external and posterior articular ridge of the mandible. The "tympano-mandibular" ligament (*n*) is attached above to the back part of the articular cup for the "squamosal," and below to the anterior and external articular ridge. The "zygomatic-mandibular ligament" (*o*) is attached to the slightly expanded hind end of the zygomatic element or representative of the squamosal, and below to the outer side of the mandible between the temporal and masseteric insertions; some fibres of the masseter are derived from both these ligaments, respecting which I may quote the remark from my first Memoir on *Apteryx*, "that they are an essential part of the mechanism of a beak which is destined to be forcibly thrust into the ground, and used in a variety of ways to overcome considerable resistance" (*tom. cit.* p. 264).

The short struthious tongue of the *Apteryx*, described at p. 264 of the first Memoir, is shown at *l* in fig. 1, Pl. XLV. The "mylo-hyoideus" muscle is reflected from its origin (at *h*, fig. 3, Pl. XLVI.) to expose the "genio-hyoid" muscle, which arises from the inner and under part of the mandibular ramus, nearer the angle than the symphysis, and sends backward its fibres to embrace the "thyrohyal" element (*k*) of the tongue-skeleton to near the free hind extremity; the pair tend to protrude or draw forward the tongue. In fig. 3 are also shown the circular fibres of the pharynx and beginning of the œsophagus (*f*), also the commencement of the trachea (*g*).

The portion of the cutaneous system of muscles for which I retained the old term "platysma myoides" (*Zool. Trans. tom. cit.* p. 279, pl. 31. *e*), has its rather strong, but flattened, tendinous origin from the external ridge of the hinder surface of the mandible, shown in fig. 3, and the expansion of its thin sheet of carneous fibres (at *e*) inserted into the skin covering the throat. This pair of muscles must tend, acting together, to support and compress the upper larynx and pharynx.

In both figures (3 & 4) are shown the inserted portions of the "longus colli posticus" (*o\*\**), of the "complexus" (*y*), of the "trachelo-mastoideus" (*z*), and of the "rectus capitis lateralis" (*d*). Full descriptions and figures of these muscles are given in Memoir II., on the *Apteryx*, *tom. cit.* pp. 283-286, pls. 32, 33, 34, & 35.

## DESCRIPTION OF THE PLATES.

(All the figures are of the natural size.)

## PLATE XLV.

*Apteryx australis.*

- Fig. 1. Side view of the brain, *in situ*, with dissection of nerves and of organ of smell.  
 Fig. 2. Upper view of the brain, *in situ*, with olfactory and trigeminal nerves.  
 Fig. 3. Base of brain, with cerebral arteries and origin of nerves.  
 Fig. 4. Base of brain, the cerebellum exposed by removal of the macromyelom.  
 Fig. 5. Side view of the brain, dissected to show the corpus striatum.  
 Fig. 6. Section of cerebellum and of part of cerebrum.  
 Fig. 7. Cavity of the lateral ventricle of the brain.  
 Fig. 8. Section of rhinencephala, showing their ventricle.  
 Fig. 9. Section of the fore part of prosencephala.  
 Fig. 10. Section, showing the anterior commissure.

*Dinornis giganteus.*

- Fig. 11. Side view of brain.  
 Fig. 12. Upper view of brain.  
 Fig. 13. Base view of brain (represented by a cast of the cranial cavity).

## PLATE XLVI.

- Fig. 1. Dissection of the brain, of the fifth, seventh, and eighth nerves, and of the muscles of the eyeball of *Apteryx australis*.  
 Fig. 2. Further dissection of the same parts, with the course of the optic nerve.  
 Fig. 3. Dissection of the muscles of the mandible and tongue of *Apteryx australis*.  
 Fig. 4. Ligaments and muscles of the mandible of the same.  
 Fig. 5. Portion of the trachea of the Cassowary (*Casuaris galeatus*).  
 Fig. 6. Portion of the trachea, including seven tracheal rings of *Dinornis (ingens?)*.  
 Fig. 7. Tracheal rings of *Aptornis defossor*.  
 Fig. 8. Stones from the gizzard of *Dinornis elephantopus*<sup>1</sup>.

<sup>1</sup> These pebbles constitute about one-third of the heap of such found within the space encompassed by the ribs and sternum of the skeleton of *Dinornis elephantopus* exhumed from the bog at Glenmark, Canterbury Settlement, Middle Island, New Zealand, of which the sternum is described in Part XIII., Zool. Trans. vol. vii. p. 115. No such pebbles occur, naturally, within a distance of thirty miles of that locality.

I submitted them to the examination of the experienced officers in the Department of Mineralogy, British Museum, and append the following note from THOMAS DAVIES, Esq., Assistant in that Department:—

“The pebbles supposed to have been contained in the gizzard of the *Dinornis* consist exclusively of varieties of quartz more or less crystalline or compact—sometimes amethystine, and also approaching in texture and colour the black cherty variety called Lydian stone or Basanite; the two latter, however, are apparently of more exceptional occurrence. All are much worn, preserving little trace of their original fragmentary outline.”

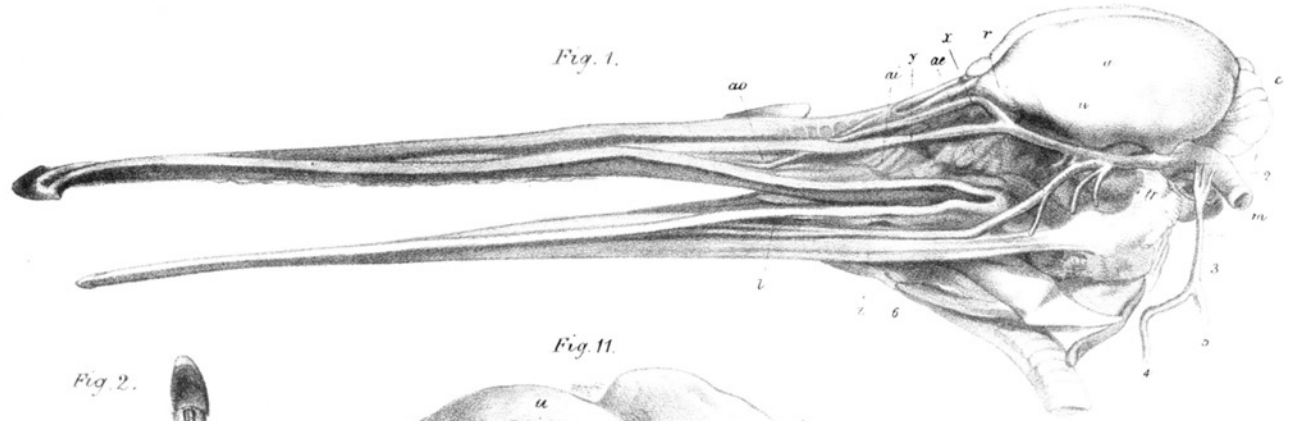
I have received pebbles smoothly rounded by the triturating work of the gizzard of the *Dinornis*, from other localities, under similar relations to the skeleton; their significance in association with bones of the trunk has probably been overlooked.

## PLATE XLVII.

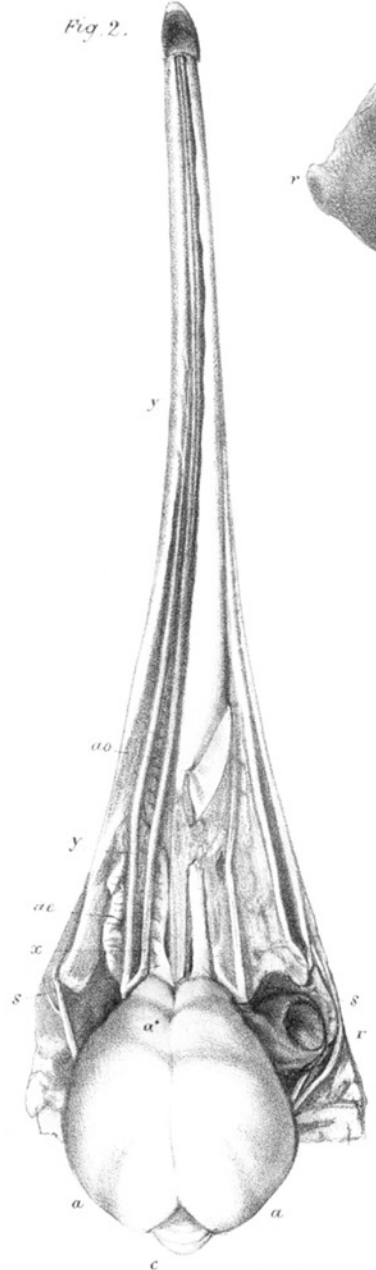
- Fig. 1. Tracheal rings of *D. crassus*: *a*, *b*, *c*, varieties, full view; *d*, oblique view, from near the head.
- Fig. 2. Side views of (*a*) large ring and (*b*) small ring, showing inequality of depth of hoop.
- Fig. 3. Full view of subcircular rings, *D. crassus*.
- Fig. 4. Group of seven tracheal rings, *D. crassus*.
- Fig. 5. Group of five tracheal rings, *D. crassus*.
- Fig. 6. Group of four tracheal rings, *D. crassus*: *a*, front view; *b*, side view.
- Fig. 7. Groups of two rings, showing appearance of alternate breadth and narrowness of parts of hoop: *a*, front view; *b*, back view; *c*, side view.
- Fig. 8. Part of ossified "thyroid cartilage" of upper larynx of *Dinornis crassus*: *a*, outer surface; *b*, inner surface.
- Fig. 9. *D. crassus*: *a*, part of the chief bone of the lower larynx; *b*, *c*, upper bronchial ring.
- Fig. 10. Tracheal rings of *Dinornis rheides*: *a*, *b*, *c*, varieties, in full view; *d*, oblique view.
- Fig. 11. Broad variety of tracheal rings, edge views: *a*, broader side; *b*, narrower side.
- Fig. 12. Group of four tracheal rings, *D. rheides*.
- Fig. 13. Tracheal ring of *Dinornis elephantopus* (?): *a*, full view; *b*, side view.
- Fig. 14. Broader variety of tracheal ring of the same species.
- Fig. 15. Narrow variety of tracheal rings of the same species: *a*, full view; *b*, side view.
- Fig. 16. Side view of bronchial ring? of the same species.
- Fig. 17. Tracheal rings of *Dinornis ingens* (?): *a*, full view; *b*, front view; *c*, back view.
- Fig. 18. Inside view of a tracheal ring of *Dinornis elephantopus* (?).
- Fig. 19. Broad variety of tracheal rings of *Dinornis ingens* (?).
- Fig. 20. Narrow variety of tracheal rings of *Dinornis ingens* (?).
- Fig. 21. Two partially united tracheal rings of *Dinornis ingens* (?).
- Fig. 22. Two partially united tracheal rings of *Dinornis ingens* (?), simulating a spiral.
- Fig. 23. Two partially united tracheal rings of *Dinornis ingens* (?), simulating a spiral.
- Fig. 24. Tracheal rings of *Dinornis robustus* (?): *a*, full view; *b*, back view; *c*, front view.
- Fig. 25. Narrow variety of tracheal rings of *Dinornis robustus* (?).
- Fig. 26. Broad variety of tracheal rings of *Dinornis robustus* (?).
- Fig. 27. Two partially confluent rings of *Dinornis robustus* (?): *a*, smooth united part;  $\times$ , rough anchylosed part.
- Fig. 28. Two confluent rings of the broad variety of *Dinornis robustus* (?).
- Fig. 29. Two partially confluent rings of *Dinornis robustus* (?).
- Fig. 30. Inside view of two confluent rings of *Dinornis robustus* (?).
- Fig. 31. Longitudinal section, showing inner surface of two confluent rings of *Dinornis ingens* (?).
- Fig. 32. Longitudinal section of a tracheal ring of *Dinornis robustus* (?).



*Fig. 1.*



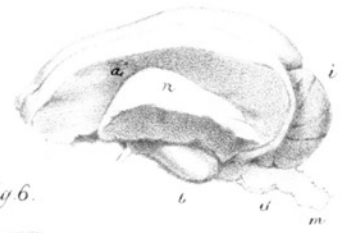
*Fig. 2.*



*Fig. 11.*



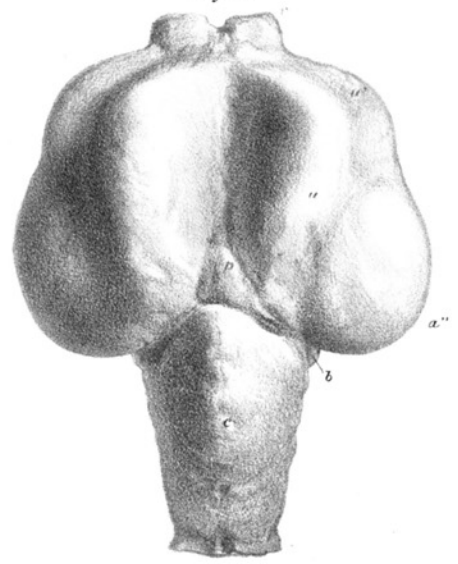
*Fig. 5.*



*Fig. 6.*



*Fig. 12.*



*Fig. 7.*



*Fig. 8.*



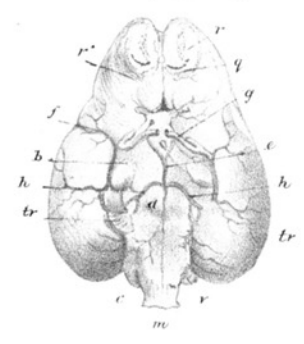
*Fig. 9.*



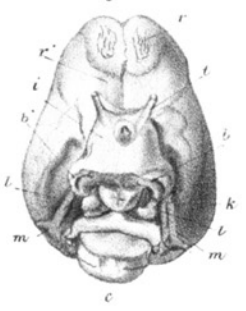
*Fig. 10.*



*Fig. 3.*



*Fig. 4.*



*Fig. 13.*

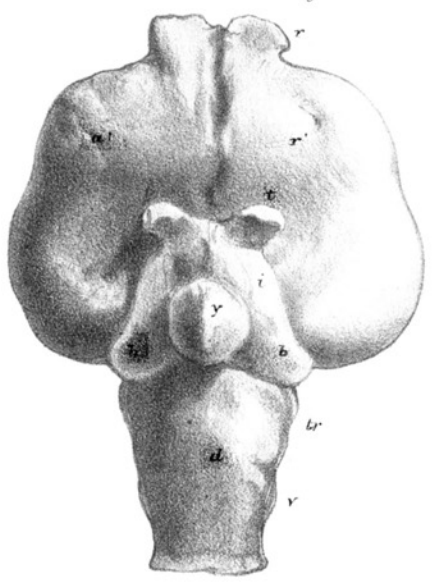


Fig. 1.

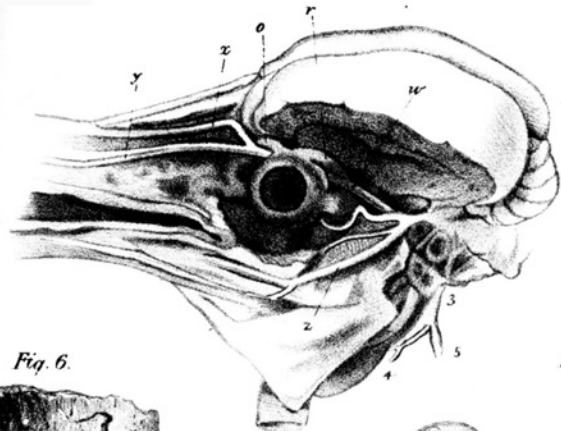


Fig. 2.

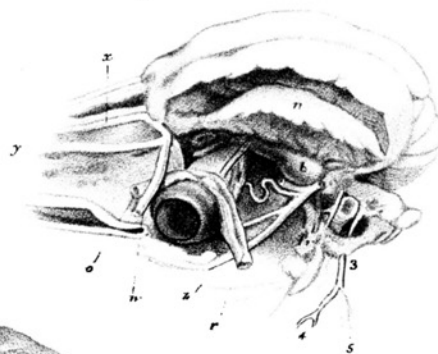


Fig. 6.

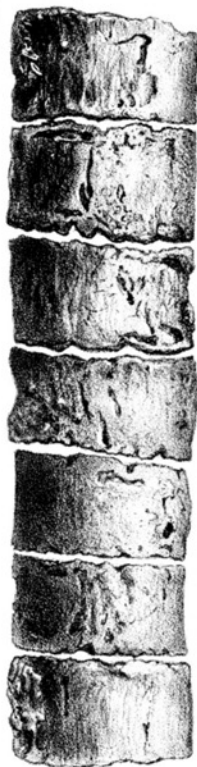


Fig. 8.

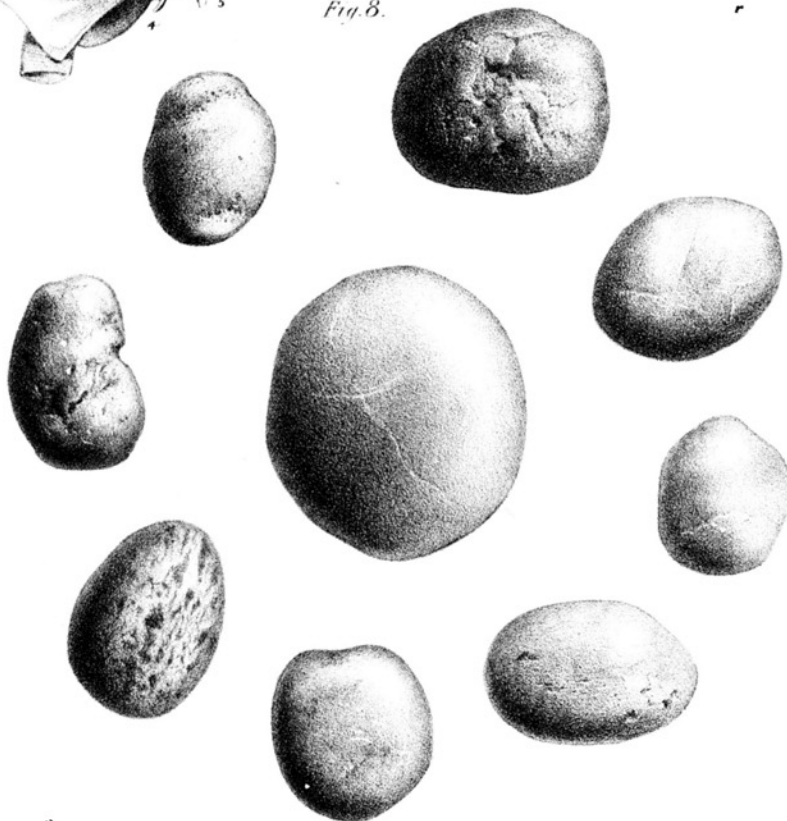


Fig. 5.

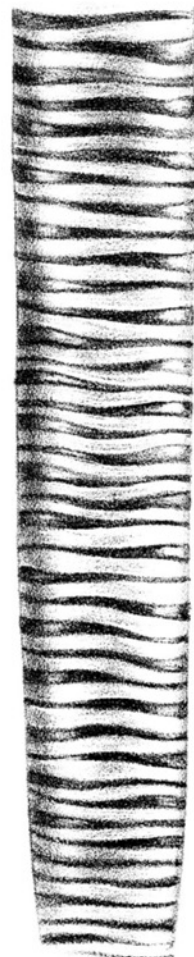


Fig. 3.

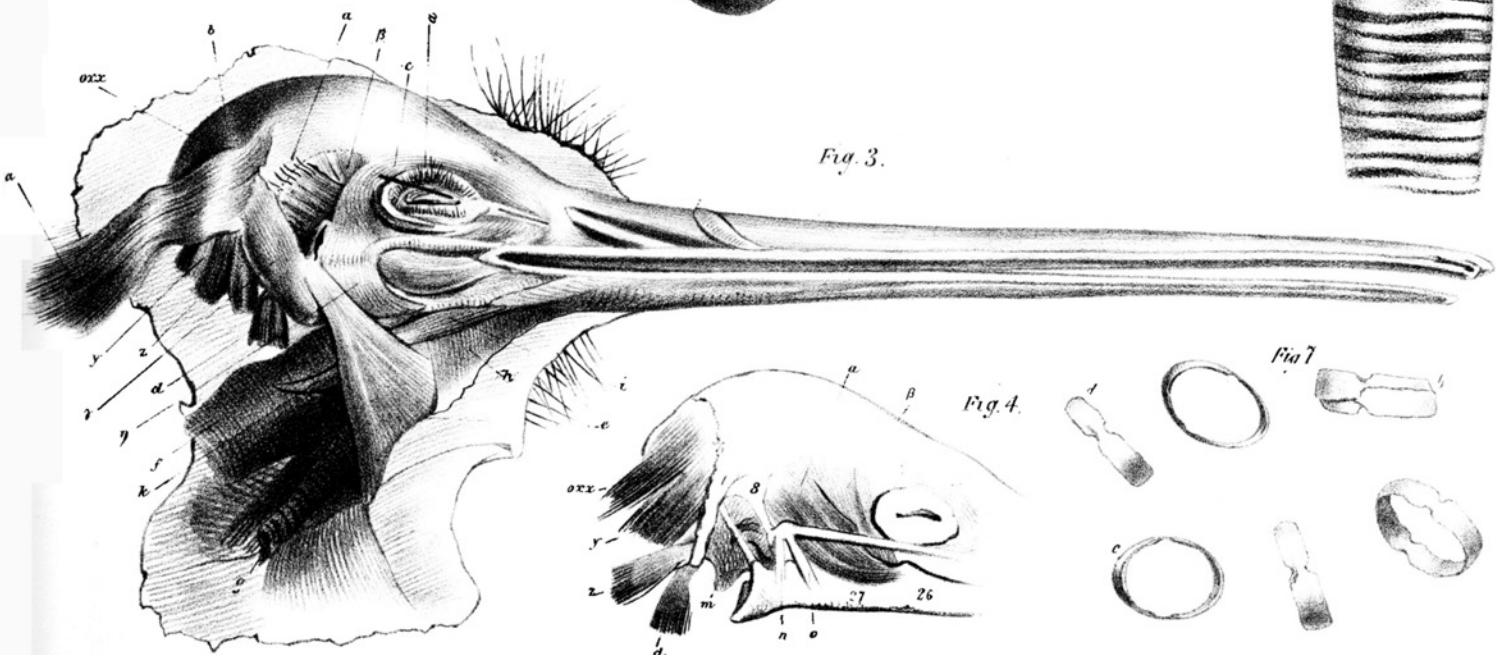
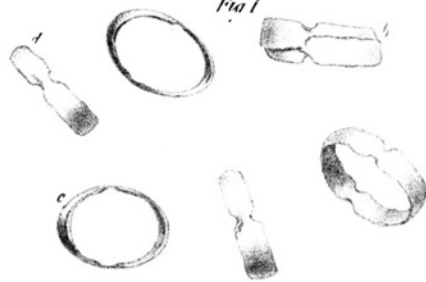


Fig. 4.

Fig. 7.



R. C. del. J. Smith lith.

M & N. Haubert imp.

1. APTERYX AUSTRALIS. 2. CASUARIUS CALEATUS. 3. DINORNIS INCENS. 4. APTORNIS DEFOSSOR. 5. DINORNIS ELEPHANTOPUS.

