Range of Variation
Exemplified in Species of Dinornis.

Having given in the preceding Section details of the characters of the vertebrae of Dinornis compared with those in Struthio, I have taken for the subject of the present Section the skeletons of those Moas which exemplify the extent of variation of the family or genus as it is shown in the gradation from slenderness to robustness of form.

The species so selected are:—Dinornis gracilis (Plate CXII. fig. 1, and Plate CXIII. fig. 1), D. casuarinus (Plate CXII. fig. 2), D. didiformis (Plate CXL), D. rheides (Plate CIX.), and D. crassus (Plate CVIII. and Plate CXIII. fig. 2). The two extremes in this series are exemplified in the latter Plate.

Under all these modifications, the essential characteristics of the osseous framework of the genus are retained, and the differences are due to proportion of parts, affecting also, in a certain degree, the shape of the bone, as in the skull and sternum. The chief seat of the proportional modifications, with less change of form, is the hind limb.

The length of the trunk, as represented by the dorsal and sacral vertebrae, retains a nearly constant proportion to the general size of the bird; it consists in all the species of the same number of vertebrae, viz. twenty-four, of which seven are dorsal and seventeen sacral. The number of vertebrae in the neck appears to be fifteen. I give these numbers as the rule or sum of my personal observations; exceptions, characteristic of species, may be ultimately determined; but I suspect the difference of one or two in the cervical series of certain mounted skeletons at Christchurch may be due to accident. The length of the hind limb varies in its proportion to the trunk, and chiefly through modifications of the tibia and metatarsus.

Thus in Dinornis gracilis the length of these two bones exceeds that of the trunk by 10 inches; in D. casuarinus the excess is 3 inches; in D. didiformis and D. rheides the two admeasurements are equal; in D. crassus the length of the trunk exceeds that of the tibia and metatarsus.
The presence of a back toe, inferred from the structure of the metatarsus, in *Dinornis ingens* and *D. dromioides* (p. 135), was subsequently confirmed by the acquisition of the proximal phalanx of that toe in *D. robustus* (Plate XLIX, figs. 1, i, 4 & 5), in *D. crassus* (Plate CXIII, fig. 2), and in *D. rheïdes* (Plate CIX).

The indication, it is true, on which the inference was hazarded is of the faintest character; and the diminutive size and functionless condition of the high-placed 'hallux' accord therewith. The attachment of this rudimental toe was merely ligamentous. The probability, however, I think, is, that, in the species of *Dinornis* in which the little bones have not been picked up with the larger parts of the skeleton, the absence of the hallux is due to that accident, rather than to non-development of the toe in such species. Its presence in the foot of species with the integument of that part preserved, as in *Dinornis ingens*¹, the metatarsus of which shows no conspicuous trace of such attachment, exposes the weakness of any conclusion from that character.

I therefore abandoned the generic character founded on the inference and subsequent discovery of the hallux shortly after the suggestion of such taxonomic value. One could not place *Dinornis giganteus* and its probably local variety, *Dinornis robustus*, in distinct genera, because no complete series of bones, including those of the hallux, had been found in the North Island, where *D. giganteus* seems to represent the *D. robustus* of the South Island; neither could the species *didiformis* be retained as a *Dinornis*, and the species *dromioides* be distinguished as a Palapteryx, on like grounds; nor *D. elephantoïdes* be similarly separated from *D. crassus*².

The scapular arch, like the hallux, was originally inferred (p. 124) from an articular fossa of the sternum (Plate XXXV, fig. 2, c, e); and the inference as to the small proportional size of such arch, in comparison with that of the Ostrich and other existing wingless birds, was confirmed by the determination of the confluent coracoid and scapula in the *Dinornis robustus* (p. 170, Plate LXIV, figs. 2, 3 & 4).

Small and shallow as were the depressions in the sternum of that species to which the coracoid had been ligamentously attached, these indications are less definite in the sternum of some other species; and with regard to the scapular arch, as to the hallux, it has been surmised that such arch was naturally absent in some kinds of *Dinornis*, as, for example, in the skeleton of *D. crassus* (Plate CVIII.), *D. rheïdes* (Plate CIX.), *D. gravis* (Plate CX.), *D. didiformis* (Plate CXI.), *D. gracilis* and *D. casuarinus* (Plate CXII.). I incline to the belief, however, that the skeletons in the Museum of Natural History, Christchurch, Canterbury Province, from which the photographs of those species were taken, are deficient in respect of the scapular arch, through the accident of the non-discovery of that small and slender rib-like bone, rather than that it was not originally present.

² In a letter from Capt. Hutton, dated "Otago Museum, May 6, 1876," he writes: "We have in the Museum legs, with the hind toe belonging to them, of *D. ingens*, *D. casuarinus*, and *D. gravis."
Its rudimental condition in respect of size is exemplified in the figure of the skeleton of *Dinornis robustus* (Plate XCVI, fig. 1), where it is shown in its natural connexion with the outer angle of the fore border of the sternum.

The reduction of the side elements of the arch to their primitive type form, as 'pleur-apophysis' (*scapula*) and 'hæmapophysis' (*coracoid*), is replete with interest to the student of the vertebrate archetype; and it still remains a question whether to the ridge indicative of the articular cavity in more modified and developed conditions of the arch there might be attached an appendage serially homologous with those (epipleural plates) of succeeding costal arches, and specially homologous with the humerus.  

Supposing it to be ultimately determined that the scapular arch, as well as its appendage, the wing, be developed in certain kinds of Moa and not in others, the question might be mooted whether a generic distinction could be sustained on such grounds, and whether a non-development of the rudimental scapular arch was coincident with a non-development of the rudimental hallux. Should such coincidence be ultimately demonstrated, the taxonomist would have stronger grounds for a genus *Palapteryx*, as well as a genus *Dinornis*, than have hitherto been afforded.

But if the determination of acceptable genera of the *Dinornithidae* has been opposed by the numerous specimens of bones discovered since the species were propounded, on characters yielded by a few bones, or by a single one, the addition of such specimens, by hundreds, to the Museums now established by the enlightened Colonists in the capitals of the several provinces of New Zealand have confirmed, in the main, such species. Such is the conclusion arrived at by Dr. v. Haast, of the province of Canterbury, to whom I am indebted for the photographs of the series of skeletons he has articulated for the Museum of Christchurch; and I may refer to the able article "On the Dimensions of *Dinornis* Bones" ², by Captain F. W. Hutton, C.M.Z.S., for a similar encouraging result of the examination of the collection "of the remains of more than 200 birds" of the *Dinornithidae*, now in the Museum of Otago, under his care.

Of *D. robustus* and *D. ingens* he remarks that the remains in this collection "were too few to warrant certain conclusions, but they appear to be distinct species." Dr. v. Haast's materials have enabled him to express a more decided opinion. I should, however, have felt less surprise if the suggestion that they may be but local varieties of the same species had been sustained.

*Dinornis struthioïdes*, of which evidences in the Otago Museum were "much more common than of the other two" (*viz. robustus* and *ingens*), is, in Capt. Hutton's opinion, a species "very distinct and easily recognized from any other."

"I refer five metatarsi to *D. rheïdes*, but I was unable to find in the whole collection

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¹ See the observations on this point at p. 170.
² Trans. of the New-Zealand Institute, vol. vii. 1875, p. 274.
a single femur small enough to answer to Professor Owen's dimensions." The femur in the skeleton of this species (Plate CIX, fig. 1) repeats, however, the length of 9 inches.

In the collection from the Glenmark Swamp, South Island, are bones that scarcely differ, save in size, from the dimensions of the type bones of Dinornis didiformis from the North Island. They are noted as of a large variety of that species. Capt. Hutton remarks:—"The bones that I have arranged under the name D. didiformis belong probably to a new species. The tibia is well marked and quite distinct; but the femur and metatarsus that I have associated with it pass almost into D. casuarinus, but are rather smaller. D. casuarinus is undoubtedly a good species, easily distinguished by its tibia."

Possibly the Dinornis of the South Island, with the tibia characteristic of the D. didiformis of the North Island, may need to be noted, for the convenience of naming the bones, as Dinornis Huttonii. The acute observer to whom it would give me pleasure to dedicate such species, proceeds to state:—"D. gravis also appears to me to be a good species, although the tibia very closely approaches to that of D. casuarinus, but is more robust, the length being only about three and a half times the circumference of the middle of the shaft, while in D. casuarinus it is more than four times the circumference."

Capt. Hutton reports that "in a limestone cave at 'Doctor's Creek, Waritaki' (South Island), a nearly complete skeleton of a Moa was found, the bones lying in their proper position, wanting only the head, a few cervical and caudal vertebrae, and two small phalanges of the outer right toe;" and he concludes them to have belonged to the same individual.

He gives the following admeasurements of the leg-bones:—

<table>
<thead>
<tr>
<th></th>
<th>Femur. inches</th>
<th>Tibia. inches</th>
<th>Metatars. inches</th>
</tr>
</thead>
<tbody>
<tr>
<td>&quot;Length&quot;</td>
<td>11·80</td>
<td>21·1</td>
<td>9·1</td>
</tr>
<tr>
<td>Circumference at middle</td>
<td>6·83</td>
<td>5·6</td>
<td>6·0</td>
</tr>
<tr>
<td>Breadth proximal</td>
<td>5·1</td>
<td>6·3</td>
<td>4·15</td>
</tr>
<tr>
<td>Breadth distal</td>
<td>6·1</td>
<td>3·75</td>
<td>5·3</td>
</tr>
</tbody>
</table>

If these dimensions be compared with those of the type femur of Dinornis crassus (ante, p. 133, Plate XL, fig. 4), it will be seen that, with the exception of the breadth of the distal end of the bone, the Waritaki specimen closely agrees with the dimensions of the specimen from Waikawaite, recorded in the general 'Table of Admeasurements,' p. 356. I have elsewhere remarked that limb-bones seem subject to variety as they recede in position from the trunk. The excess of breadth of the distal end, 6·1 as against 5·25, relates to a larger tibia, which agrees in size with that referred by Capt. Hutton to a "var. major of D. crassus" in his Table B, p. 278 (tom. cit.).

1 See ante, p. 357, addition to Note 8.
The metatarsal, though shorter than the shortest variety of the compound bone which I have referred to *D. elephantopus* in my "Table" (p. 356), nearly equals in some dimensions, and exceeds in proximal breadth, the metatarsal of *D. elephantopus*.

The rich collection of limb-bones of Moas in the Otago Museum appears to exemplify a course of variation from my type of *Dinornis crassus* through the *D. crassus*, var. major, of Hutton to *D. elephantopus*.

It remains to be seen whether the femur follows pari passu the variations of the tibia, and especially of the metatarsus; above all, whether the dimensions of the trunk-bones, as exemplified in Plates IX. and CVIII., vary in the ratio of those of the metatarsi referred to *D. crassus*, *D. crassus*, var. major, and *D. elephantopus*.

The opinion of an observer who has "made 2000 measurements" in the rich series under his care ought to carry weight; and his conclusion on the species in question is thus given:—"Still, notwithstanding all that I have said, I am convinced that it will be necessary to retain the names both of *crassus* and *elephantopus* to mark both ends of the series as characterized by the proportions of the metatarsus, the length of which in *D. crassus* is more than four times the breadth of the middle shaft, while the length is less than four times the breadth in *D. elephantopus* and *D. gravis".1

We have been accustomed to associate with the idea of a bird lightness, grace, swiftness of movement, exceptional command of aerial space; the converse of all these associations is shown in the framework of the thick-limbed, broad-bodied Moa represented in Plate CXIII., fig. 2. The bird stands as a colossus on a basis hard to be shaken, suggestive of herculean strength; it is 'of the earth earthy.' The exaggerated proportions of the limbs are heightened by contrast with the slender neck and diminutive head. Truly and emphatically has the deduction from the bone-fragment (Plate facing p. 72) been fulfilled—viz. that it bespoke the former existence in New Zealand of a bird "heavier and more sluggish than the Ostrich, and with shorter and thicker legs."

The figured skeleton of *Dinornis crassus* includes 15 cervical and 7 dorsal vertebrae; the two anterior sacrals support movable ribs, the number of these being 9 pairs. In the subject of Plate CVIII., the fore part of the iliac bone is mutilated, exposing the spine of the first sacral (8th dorsal by the character of the movable ribs). The second, third, and fourth ribs articulate by sternal portions with the sternum.

As the dinornithic modifications of the palate are more perfectly demonstrated in the skull of a *Dinornis crassus* recently transmitted to me than in those previously described (pp. 262–281), I subjoin a figure of the base of the skull in that species (Plate CXIV., fig. 1), and add the following remarks:

In *Dinornis crassus* the palatal plates of the palatines (ib. 20) are anterior horizontal expansions of those bones which coalesce with the corresponding palatal plates of the maxillaries, not passing freely beneath them. The bony palate behind the premaxillary

1 *Tom. cit.* p. 277. Comp. Dr. Haast’s remarks on *D. elephantopus*, quoted at p. 353 of the present work.
part of the mouth-roof may be truly termed the maxillo-palatine part of that roof, including parts of both bones. In the skull of Dinornis ingens, figured in Plate LXXXII., fig. 3, a portion of the palato-maxillary suture still remains, and a smaller portion is traceable in the present specimen of D. crassus.

Birds have the maxillary, 21, and palatine bones, 20, ossified, as in mammals, from separate centres, but have no maxillo-palatine bone, save by the accident of partial confluence. The specific palatal distinction from D. ingens appears in the course of the suture of the maxillo-palatine plate with the premaxillary. In D. ingens the suture runs across in an irregular wavy line; in D. crassus it presents an angular form, the maxillo-palatine plate being notched to receive the angular palatine process, 22', of the premaxillary.

In D. crassus, as in D. ingens and D. maximus, the slender part of the palatine, continued backward from the palato-maxillary plate, is twisted so as to bring the inner edge of that plate downward, and to turn the horizontal under surface, 20, into a vertical outer surface of the bone, which rapidly gains in depth, and has its upper part bent inward, to complete with the vomer, 13, the hind wall of the palato-narial canal. At the outer and back part of the canal the palatine is thickened at its lower part to articulate with the pterygoid, 24.

The vomer is bifid, as in D. ingens and as in the first-described skull of D. crassus (p. 266, Plate LXXVI.). The parial plates of the vomer overlap the sides of the presphenoids, 9, of which the anterior apex, 9', coalesced with the narial septum, projects beyond the vomer, and partially divides the prepalatine vacuity. The anterior ends of the halves are overlapped by the vomerine processes of the premaxillaries. Each half of the vomer consists of a deep vertical bony plate, almost meeting below the presphenoidal rostrum, expanding at both ends anteriorly to join the premaxillary and the palato-maxillary plates, and there bounding the palato-nares anteriorly; posteriorly expanding in a greater degree, and curving outward and forward to join the palatines, and form the posterior boundaries of the palato-nares. These apertures are each 1 inch 7 lines in length, 5½ lines in breadth; the breadth across both apertures is 1 inch 11½ lines, the additional half line giving the interval between the halves of the vomer.

The suture between the vomer and palatine, as one looks down upon the skull's base, runs along the bottom of the vomero-palatine or postnarial fossa, along a shallow channel there; it seems obliterated near the postero-external rather thickened border of that fossa. From this border the pterygoid process of the palatine is divided by a triangular shallow depression. The pterygoid bone, 24, is short, three-sided, with the sharp angle between the inner and outer facets of the under surface of the bone turned downward, and continuing backward a similar ridge on the under part of the palatine. The pterygoid has an extent of articulation with the tympanic of three lines in D. crassus, but one of more than half an inch in D. maximus. The pterapophyses are marked 3.'
The thickness of the leg-bones in proportion to the trunk, and of the metatarsi in proportion to their length, in *D. crassus*, *D. gravis*, and *D. elephantopus*, are unique in the class of Birds. They are associated with a greater breadth of the trunk, and especially with a greater breadth of the sternum, in proportion to its length.

The fragmentary condition of the sternum in the series of bones of *Dinornis elephantopus* first received led the articulator of the skeleton in the British Museum to restore that bone by a model on the type of the sternum of a less robust species at that time obtained (pp. 124, 196, Plate XLVIII.). Subsequently acquired specimens (p. 254, Plate LXXII.) have shown this bone to present in *D. elephantopus* the form and proportions of the sternum of *D. crassus* (Plate CXIII.), and afford a correction of the error in the first attempt at a restoration of the skeleton of *D. elephantopus*, as regards the sternum (Plate LXI. fig. 1).

As in other forms of birds, which for some time may continue rare and scantily represented in collections, the few species there recognized usually offer well-marked differences, as in tints of plumage, proportions of bones, and even in general size; but as knowledge increases, forms or species showing intermediate characters are brought to light, and the previous differences are diminished by gradational modifications, which not only render the diagnosis of the genera difficult, but affect that of the species themselves. Under foresight of this course of knowledge, I have been led to refer to some kinds of *Dinornis* as being 'propagable varieties.'

Under present knowledge certain forms of Moa seem to be limited to the North Island, others to the South Island of New Zealand. The less robust and longer-legged forms appear to have prevailed in the North Island, the more robust and shorter-legged kinds in the South Island.

But already with the advance of knowledge of the extinct *Dinornithidae* exceptions come to light.

If Moas with the character of *D. gravis* and *D. elephantopus* existed only in the South Island to the exclusion of other forms, and if Moas with the characters of *D. gracilis* and *D. casuarinus* held the same exclusive position in the North Island, the genetic relation of such species to food and other conditions of existence respectively peculiar to one or the other insular tract of land might be speculated on as a condition of their origin with some ground of acceptance. But, as in the case of the Geospizas of the Galapagos archipelago, the application of that supposed possible way of operation of nomogony, or secondary law of the origin of species, is unavailable, and the hypothesis in these, as in other cases, falls to the ground.

1 See cut, fig. 35, p. 419; but the more perfect sternum from which this cut was taken was mutilated at the postmedial border, which might originally have been bifid.
Admeasurements of the Skeletons of the subjoined species of *Dinornis*.

<table>
<thead>
<tr>
<th></th>
<th>robustus</th>
<th>elephas-</th>
<th>crassus</th>
<th>rheïdes</th>
<th>gracilis</th>
<th>casearopus</th>
<th>didiformis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of skeleton from point of beak to end of tail, following the curves of the spine, in the easy standing position</td>
<td>8 3 5 8 4 0</td>
<td>3 10</td>
<td>4 9</td>
<td>4 4</td>
<td>4 0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Height of skeleton, in the easy standing position, from sole to vertex, in a straight line</td>
<td>8 0 5 5 3 6</td>
<td>3 4</td>
<td>5 8</td>
<td>4 6</td>
<td>3 8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length of trunk (dorsal and sacral series of vertebrae)</td>
<td>3 0 2 4 2 2</td>
<td>1 10</td>
<td>2 2</td>
<td>2 0</td>
<td>1 9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length of hind limb, in the easy standing position, following the angles of the segments</td>
<td>6 2 4 9 3 10</td>
<td>3 4</td>
<td>4 8</td>
<td>3 3</td>
<td>3 0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

On a review of the several species of *Dinornis* of which the osteological structure is known, the following generic characters may be deduced:—

1. Skull with a rather short, broad, moderately arched bill, not attaining the height of the cranium; occipital condyle not projecting so far back as the upper border of the occipital foramen.

2. Horizontal palatal plates of the palatines and maxillaries more or less confluent, not uniting solidly, but suturally, with the premaxillary and the vomer.

3. An Aptyrygian, not Dromæine, pelvis.

4. A short, broad sternum, with small, ill-defined coracoid pits, and with three posterior notches.

5. Scapula and coracoid small and feeble, forming no angle, or one of 170°, not developing a glenoid cavity at their bony confluence.

6. Four toes; the hallux small and high-placed.

7. Terminal confluent caudals of less vertical extent than the antecedent free caudals.

**DESCRIPTION OF PLATES.**

**PLATE CVIII.**

Side view of the skeleton of *Dinornis crassus*.

**PLATE CIX.**

Side view and front view of the skeleton of *Dinornis rheïdes*.

**PLATE CX.**

Side view and front view of the skeleton of *Dinornis gravis* (see ante, p. 385).

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1 In the articulated skeleton figured the trunk is raised at too open an angle with the leg, and this is also outstretched as in walking.

2 The trunk is raised at rather too open an angle.

3 Ib.

4 Ib.
PLATE CXI.
Side view and front view of the skeleton of *Dinornis didiformis*.

PLATE CXII.
Fig. 1. Side view of the skeleton of *Dinornis gracilis*.
Fig. 2. Side view of the skeleton of *Dinornis casuarinus*.

PLATE CXIII.
Fig. 1. Front view of the skeleton of *Dinornis gracilis*.
Fig. 2. Front view of the skeleton of *Dinornis crassus*.