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T. Jeffrey Parker

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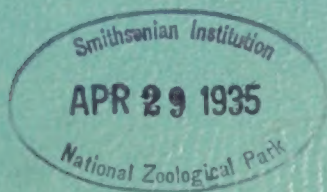
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## TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON.

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*Continued on page 3 of Wrapper.*



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XV. *On the Cranial Osteology, Classification, and Phylogeny of the Dinornithidæ.* By T. <sup>homo</sup>JEFFERY PARKER, D.Sc., F.R.S., Professor of Biology in the University of Otago, Dunedin, New Zealand.

Received December 5th, 1892, read February 14th, 1893.

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I. INTRODUCTORY.

A FIRST glance at the magnificently illustrated series of memoirs by Sir Richard Owen on the osteology of the Dinornithidæ gives the impression that the whole subject has been exhausted; but a more careful perusal, aided by a comparison with the recent works of Lydekker (12) and Hutton (9), is enough to show that the material at Sir R. Owen's disposal was far from complete, that skulls were assigned to the skeletons of certain species on purely conjectural grounds, and that some of the figures were even made up of portions belonging to different species. The reason of this confusion is that it is extremely seldom that the bones of a single individual skeleton, or even the parts of a single individual skull, are found associated together and apart from those of other individuals.

It is to this circumstance that the chief difficulty of the present investigation was due—the difficulty of assigning correct names to the various skulls examined. To mention only the two most recent authorities: Lydekker describes four genera and nineteen species; Hutton seven genera and twenty-six species: species associated in a single genus by the one are widely separated by the other: and, most confusing of all, skulls assigned by Lydekker to certain species are considered by Hutton to have been wrongly associated with the leg-bones upon which the species were founded. Moreover, while my enquiries fully confirm the view that the Dinornithidæ are divisible

into several genera, the generic groups, as deduced from a study of the skulls, do not agree with those of either of the authors referred to. It seems reasonable, however, to claim that, if constant and definable differences can be shown to occur in the skulls, these should outweigh mere differences in the size and proportions of the limb-bones.

I have derived the greatest assistance throughout the investigation from frequent correspondence with Captain Hutton, who has, with rare generosity, placed at my disposal the wide knowledge of the whole Moa question gained during the course of his extended, and still partly unpublished, researches. Sir James Hector has most kindly lent me the entire collection of Moa skulls in the Colonial Museum, Wellington, including the unique skull of *Mesopteryx*, species  $\beta$ , figured on Plate LX. figs. 20 & 21. Dr. H. O. Forbes has been good enough to lend me the large series of skulls in the Canterbury Museum, recently collected by himself at Enfield, near Oamaru, as well as the skulls from four skeletons in the Canterbury Museum, articulated under the superintendence of the late Sir Julius von Haast. Mr. A. Hamilton, Registrar of the University of Otago, has placed at my disposal the large collections made by himself at the Te Aute swamp, near Napier, and at Castle Rocks, Oreti River, Southland—the latter collection including several immature skulls which have been quite invaluable for my purpose. I am also indebted to Mr. Hamilton for the drawings from which figs. 59–64 are taken. Mr. R. J. Kingsley has lent me the skull of a fine individual skeleton in his possession, the type of *Dinornis torosus*, Hutton. Mr. J. Thomson, Lecturer on Applied Mechanics in this University, has devoted a great deal of time and trouble to taking the photographs from which Plates LVI., LVIII., & LX. are copied. And, lastly, during my visit to England I have received the kindest help from Prof. Newton, Dr. Henry Woodward, Mr. A. Smith Woodward, and Mr. H. M. Platnauer. To all these gentlemen I beg to return my most sincere thanks.

## 2. LIST OF SPECIMENS EXAMINED.

As the nomenclature of many species is still doubtful, and as it is desirable to refer to certain individual specimens in the various collections to which I have had access, the following list is given in order to facilitate identification:—

### Genus DINORNIS, Owen.

#### 1. DINORNIS MAXIMUS, Owen.

- a. The skull belonging to the large skeleton in the British Museum (Natural History) and numbered 46050 (Lydekker, Cat. Foss. Birds, p. 232).
- b. Portions of a skull in the same Collection, numbered 46631–3 (figured by Owen, Extinct Birds of N. Z. pl. lxii.).

The measurements of this last-named skull do not differ from those of *D. robustus*<sup>1</sup>.

<sup>1</sup> Through the kindness of Captain Hutton, I have just examined a very fine skull of *D. maximus* belonging to Mr. McEwen, of Christchurch. There is nothing to distinguish it from *D. robustus*.—June 1895.

2. *DINORNIS ROBUSTUS*, Owen.

- a.* The skull belonging to the very fine individual skeleton found at Tiger Hill, Otago, and now in the Museum of the Philosophical Society, York.

This specimen is referred by Hutton to his *D. potens*, but I am more than doubtful whether the distinction from *robustus* can be maintained, and prefer to place it in the present species.

- b.* The skull belonging to an individual skeleton found at Highley Hill, Otago, the property of Dr. T. M. Hocken. (Otago University Museum.)
- c.* An imperfect and partly restored skull from Hamilton Swamp, Otago. (Otago Univ. Mus.)
- d.* Mandible belonging to an individual skeleton found at Shag Valley, Otago. (Otago Univ. Mus.)
- e.* Associated premaxillæ, maxillo-jugal arch, quadrate, and mandible from Maungatua, Otago. (Otago Univ. Mus.)
- f.* A cranium from Enfield, Otago. (Dr. H. O. Forbes's collection.)

This species is figured by Owen, *Trans. Zool. Soc.* vol. v. pls. liii. & liv. (*Ext. Birds of N. Z.* pls. lxii. & lxiii.).

3. *DINORNIS TOROSUS*, Hutton.

- a.* Skull belonging to a nearly perfect skeleton, the type of the species, found in the Takaka district, Nelson. (Mr. R. J. Kingsley's collection.)
- b.* A nearly complete skull from Hamilton Swamp. (Otago Univ. Mus.)

Captain Hutton considers that this skull is probably referable to *D. struthioides*, but I can see no differences of any importance between it and the previous specimen.

This species is figured by Owen as *D. ingens*, *Trans. Zool. Soc.* vol. vii. pl. xv. (*Ext. Birds of N. Z.* pl. lxxxii.); also by Jaeger, as *Palapteryx ingens*, *Reise der Novara, Paläontologie*, pls. xxv. & xxvi.

4. *DINORNIS*, species *a.*

- A damaged cranium of the same size as that of *D. torosus*, but differing from it in having the temporal and lambdoidal ridges in contact. (Coll. H. O. Forbes.)

Genus *PACHYORNIS*, Lydekker.1. *PACHYORNIS ELEPHANTOPUS*, Owen.

- a.* Six crania with separate premaxillæ, maxillo-jugal arches, quadrates, and mandibles, from Enfield; in one instance (Plate LX. fig. 22) premaxillæ and maxillo-jugal arches were found which exactly fitted a cranium, and I have no doubt that they belonged to the same individual. (Coll. H. O. Forbes & Cant. Mus.)
- b.* Two crania, one with (?associated) premaxillæ and mandible; locality unknown. (Coll. Mus. Wellington.)
- c.* An imperfect cranium with associated premaxillæ and mandible from Hamilton Swamp. (Otago Univ. Mus.)

Hutton (9, p. 133) has brought forward evidence for considering that this skull should be associated with the leg-bones upon which the species *crassus* was founded; if this were the fact it would, according to the nomenclature I have adopted, be placed in the genus *Emeus*, which genus would then change places with *Pachyornis* in my table of classification (p. 427). I learn, however, by recent communication with Prof. Hutton that he is still somewhat uncertain upon this point, and I think it will give rise to less confusion if I follow Owen and Lydekker and assign the present skull to the leg-bones upon which the species *elephantopus* was founded.

2. PACHYORNIS IMMANIS, Lyd.

Cast of a cranium in the Nat. Hist. Museum, numbered A. 201, and described by Lydekker, Foss. Birds, p. 344. I doubt whether this specimen can be specifically distinguished from *elephantopus*<sup>1</sup>.

This species is figured by Owen, as *Dinornis elephantopus*, Trans. Zool. Soc. vol. vii. pl. x. (Ext. Birds of N. Z. pls. lix. & lxxvi.). The best skull from Enfield is figured from beneath on Plate LX. fig. 22.

3. PACHYORNIS, species  $\alpha$ .

a. A cranium from Shag Point, differing from *P. elephantopus* in its greater breadth, especially across the postorbital processes, and in having the temporal and lambdoidal ridges in contact. (Coll. A. Hamilton.)

Figured in outline, Plate LXI. figs. 26 & 39, and Plate LXII. fig. 50.

b. A skull with greatly damaged cranium, from a skeleton named *Dinornis struthioides* by Sir J. von Haast, is probably to be referred here. (Canterbury Museum.)

Both these skulls may belong to very muscular individuals of *P. elephantopus*; but I hardly think so, as in all the specimens undoubtedly referable to that species the temporal and lambdoidal ridges are distinct. They may ultimately be found to belong to *D. rheides*, the skull of which is not known.

4. PACHYORNIS, species  $\beta$ .

A single cranium from Glenmark, differing from *P. elephantopus* in being decidedly narrower in proportion to its length.

5. PACHYORNIS, species  $\gamma$ .

A single cranium, from Enfield, differing from *P. elephantopus* in its much smaller size, but agreeing with it in other respects. It is very possibly a mere variety, but I have found no intermediate sizes.

<sup>1</sup> In the 'Transactions of the New Zealand Institute,' vol. xxvi. (1893), I have described a skull of *Pachyornis* which is about 10 per cent. larger in nearly all dimensions than *P. elephantopus*, and have referred it provisionally to *P. immanis*.—June 1895.

6. PACHYORNIS, species *a*, Lydekker.

The cranium in the British Museum (Nat. Hist.), No. 32197, so named by Lydekker (Foss. Birds, p. 320).

7. PACHYORNIS, species *b*, Lydekker.

A cranium in the Nat. Hist. Museum, numbered 32205, and described by Lydekker, *l. c.* p. 345. It agrees in all measurements, except a narrower temporal fossa, with *P. elephantopus*.

Genus MESOPTERYX<sup>1</sup>, Hutton.

## 1. MESOPTERYX CASUARINA, Owen.

- a.* Twenty-nine crania, with several mandibles, premaxillæ, quadrates, and maxillo-jugal arches, from Enfield<sup>2</sup>. (Cant. Mus. and coll. H. O. Forbes.)
- b.* A cranium from Hamilton Swamp. (Otago Univ. Mus.)
- c.* A cranium from Glenmark Swamp, Canterbury. (Cant. Mus.)
- d.* A cranium from Castle Rocks. (Coll. A. Hamilton.)

The examination of this large series of skulls has convinced me that *didina*, Owen, and *huttonii*, Owen, are synonyms of *casuarina*; there is a perfect gradation between the larger skulls (*casuarina*) and the smaller (*didina*). The same gradation is found by Prof. Hutton in the case of the leg-bones from Enfield, but as there are considerable differences between the two ends of the series he prefers to keep the species distinct.

- e.* A skull in the Natural History Museum, numbered 32210. A typical but unusually large specimen.
- f.* A skull in the same collection, numbered 32214, 32199.

This species is figured by Owen as *Dinornis rheides* (with mandible of *Pachyornis*), Trans. Zool. Soc. vol. vii. pl. xii. (Ext. Birds of N. Z. pl. lxxv.). The best of the Enfield skulls is figured in Plate LX. fig. 19.

<sup>1</sup> Reichenbach's name *Synornis* has priority for this genus, having been applied to the type species *casuarina*; but, as Lydekker has pointed out (11, p. 254), this name clashes with *Synornis*, Hodgson, and I have therefore adopted Hutton's name *Mesopteryx*, the type species of which (*M. didina*) is probably only a small form of *casuarina*. [Captain Hutton (Trans. N. Z. Inst. vol. xxvii. 1894) now considers that *Meionornis*, Haast, is the correct name of this genus.—June 1895.]

<sup>2</sup> According to Mr. Forbes (2) the Moa-remains from Enfield belong chiefly to the species *elephantopus*, *ingens*, and *rheides*. This is hardly correct; the vast majority of the skulls belong to the species now under discussion, a few to *Pachyornis elephantopus*, and one or two to *Dinornis*, sp., and *Emeus*, sp. My determinations are confirmed by Prof. Hutton's measurements of 351 metatarsi from this abundant deposit sent to the Canterbury Museum. He finds that 181, or more than half, are referable to three doubtful species—*casuarina*, *didina*, and *huttonii*, all of which I include under *casuarina*; of the rest he assigns 40 to *rheides*, 38 to *crassus*, 40 to various species of *Dinornis*, and 52 to species of *Pachyornis*.

2. MESOPTERYX, species *a*.

A cranium and mandible from Te Aute, near Napier. (Coll. A. Hamilton.)

This skull was referred by Prof. Hutton to *Cela geranooides*, but the evidence for the determination appears to me to be insufficient, and I think it best to leave the name in abeyance<sup>1</sup>.

Figured in outline, Plate LXI. figs. 28 & 41, Plate LXII. fig. 52.

3. MESOPTERYX, species *β*.

An entire skull found by Mr. A. M'Kay in a limestone fissure on Salisbury Tableland, Nelson. (Col. Mus., Wellington.)

This skull, which was found associated with the cervical vertebræ, is one of the most perfect ever discovered. It does not correspond with any of the figures or descriptions I have met with and appears to belong to a species the skull of which has not hitherto been described.

Figured on Plate LX. figs. 20 & 21.

4. MESOPTERYX, species *γ*.

The skull on a mounted skeleton of *M. didina*, from Hamilton Swamp. (Otago Univ. Mus.)

This skull differs from the Enfield specimens of *M. casuarina* in the form of the orbit, which is right-angled as in *Dinornis*.

Figured in outline, Plate LXI. figs. 30 & 44, and Plate LXII. fig. 54.

## Genus ANOMALOPTERYX, Reichenbach.

## 1. ANOMALOPTERYX DIDIFORMIS, Owen.

- a*. Three perfect crania with premaxillæ, maxillo-jugal arches, quadrates, and mandibles; all found in the same cave (with the skeletons) at Castle Rocks, Southland. (Mr. A. Hamilton's collection.)
- b*. One perfect and several imperfect immature crania, from the same locality. (Coll. A. Hamilton.)
- c*. A cranium with (?associated) premaxillæ; locality unknown. (Colonial Museum, Wellington.)

These skulls are assigned to this species in accordance with Prof. Hutton's researches (9, p. 123), confirmed by Mr. Hamilton's discoveries at Castle Rocks. The skull referred by Lydekker (12, p. 275) to this species is apparently that of *Mesopteryx didina*.

The most perfect of the immature crania referred to above is figured on Plate LVIII. figs. 12 & 13.

<sup>1</sup> Since writing the above, Captain Hutton has lent me for examination a cranium which he considers to be that of *Megalapteryx tenuipes*, since it was found in a cave associated with bones of that species. The skull was a good deal damaged, but appears to agree very closely with that of *Mesopteryx*, species *a*.—*June 1895*.

## 2. ANOMALOPTERYX PARVA, Owen.

Skull of the very fine individual skeleton in the Natural History Museum, numbered A. 3, and figured and described by Owen, Trans. Zool. Soc. vol. xi. pl. lii.

It is an open question whether this species is distinct from *didiformis*; I am inclined to think it is merely a small variety, and only keep it separate in order to give measurements of the type specimen.

Figured by Owen as *Dinornis parvus*, Trans. Zool. Soc. vol. xi. pl. lii.

Genus EMEUS, Reichenbach<sup>1</sup>.

## 1. EMEUS CRASSUS, Owen.

- a. Two nearly perfect skulls from Shag Point, Otago; in both, the premaxillæ and bones of the palate were fixed *in situ* by the collector Mr. R. S. Booth<sup>2</sup>. (Otago Univ. Mus.)
- b. A similar skull, from the Maniototo Plains, Otago. (Coll. H. O. Forbes.)
- c. Four less perfect skulls from Shag Point. (Otago Univ. Mus.)
- d. About fifty crania belonging to this or the next species, from Shag Point. (Otago Univ. Mus. and coll. A. Hamilton.)

This species is figured by Owen as *D. crassus*, Trans. Zool. Soc. vol. x. pl. xxxi. (Ext. Birds of N. Z. pl. cxiv.); the beak and mandible of the skull figured as *D. crassus* in Trans. Zool. Soc. vol. vii. pl. xi. (Ext. Birds, pl. lxxvii.) belongs to this species, and probably the skull called *D. gravis* on pl. xiv. (Ext. Birds, pl. lxxxix.).

2. EMEUS, species *a*.

- a. An entire skull found by Mr. R. S. Booth at Shag Point. (Otago Univ. Mus.)  
With the unimportant exception of a slight injury to the left antorbital, this skull is absolutely perfect and is probably on the whole the best Moa skull ever found. (See Plate LVI.)
- b. Two less perfect skulls, also from Shag Point. (Otago Univ. Mus.)
- c. About fifty crania belonging either to this or to the preceding species. (Otago Univ. Mus. and coll. A. Hamilton.)

This species is easily distinguished from *elephantopus* by the shorter and narrower beak, but I can find no constant difference between the crania.

Figured on Plate LVI. and Plate LVIII. figs. 9 & 10.

3. EMEUS, species *β*.

The skull on the skeleton of *gravis* in the Canterbury Museum, so named by Sir J. von Haast. (Cant. Mus.)

This skull undoubtedly belongs to the present genus, but appears to exhibit well-marked differences from the two preceding species.

<sup>1</sup> Captain Hutton (Trans. N. Z. Inst. vol. xxvii. 1894) considers that this name should give way to *Euryapteryx*, Haast.—June 1895.

<sup>2</sup> A similar skull was found at the same place by Prof. Hutton and was presented by him to the British Museum; it is figured by Owen in Trans. Zool. Soc. vol. x. pl. xxxi., as *D. crassus*. Lydekker describes it an *Emeus*, species *a*.

4. EMEUS, species  $\gamma$ .

The cranium on a skeleton from Hamilton Swamp, named *D. gravis* by Prof. Hutton. (Otago Univ. Mus.)

This skull agrees in general characters with the present genus, but has right-angled orbits—a character I have never observed in any of the preceding species. Figured in outline, Plate LXI. figs. 34 & 40, and Plate LXII. fig. 58.

## 3. A COMPARATIVE ACCOUNT OF THE SKULL IN THE DINORNITHIDÆ.

The skulls of the Moas are usually found in a more or less fragmentary condition, and it will be advisable, for the sake of convenience, to take this circumstance into consideration and to describe the skull under the following heads:—

- a. Cranium.
- b. Premaxilla.
- c. Maxillo-jugal arch.
- d. Vomer, palatine, and pterygoid.
- e. Quadrate.
- f. Mandible.
- g. Hyoid.

The cranium is the part most commonly found in large deposits of Moa-bones; crania may occur in hundreds, whilst other portions of the skull are of comparatively rare occurrence. Premaxillæ, quadrates, and lower jaws are not uncommon, while a complete maxillo-jugal arch is rare, and very few skulls have been found with the palatines, pterygoids, and vomer uninjured.

a. *The Cranium.*

In the cranium the following regions may be distinguished:—

- i. The *occipital region*, including the whole posterior portion of the skull; it contains the occipital condyles and foramen and is produced at the sides into the large and prominent paroccipital processes.
- ii. The *cranial roof*, continuous behind with the occipital region.
- iii. The *base of the skull*, also continuous behind with the occipital region; posteriorly it is raised into a prominent squarish elevation, the *basitemporal platform*; anteriorly it is continued into a more or less cylindrical rod of bone, the *rostrum*, which forms the axis of the beak.
- iv. The *lateral surface of the cranium*, presenting three well-marked depressions—the *orbit* in front; the *temporal fossa* immediately behind the orbit and separated from it by a downward projection of the skull-roof, the *postorbital process*; and the *tympanic cavity*, bounded above and separated from the temporal fossa by an outstanding mass of bone, the *squamosal prominence*, and bounded behind by the paroccipital process.



- v. The *ethmoidal region*, lying anterior to the orbits, enclosing the olfactory chambers, and produced forwards into a median vertical partition, the *mesethmoid*, ankylosed below with the rostrum.
- vi. The *cranial cavity*.

i. *The occipital region*. (Plate LVIII. fig. 9; Plate LIX. fig. 14; Plate LXII. figs. 47–58.)

The *occipital condyle* (*oc. con.*) is distinguished by its more or less pedunculate character; its dorsal surface is usually somewhat flattened, and its hemispherical posterior face often presents a well-marked dimple-like depression indicating the position of the notochord. Its median portion is formed by the basioccipital, its lateral portions by the exoccipitals (fig. 14); the latter bones converge from below upwards, so that a very narrow strip of the dorsal surface of the condyle is furnished by the basioccipital (fig. 15).

The *occipital foramen* varies in form from subcircular to squarish; in *Dinornis* the plane of the foramen is nearly at right angles to that of the basitemporal platform, while in the other genera it is distinctly inclined backwards; in the former case the occipital condyle projects beyond the dorsal margin of the foramen, a unique peculiarity pointed out by Owen. In some instances the condyle projects beyond the level of the paroccipital processes, but as a rule the reverse is the case.

Immediately above the occipital foramen is a median vertical ridge (fig. 9), the *occipital crest* (*oc. cr.*; median vertical ridge, Owen), which is connected ventrally with another ridge lying immediately above the foramen, at first close to its dorsal border and afterwards diverging laterad and becoming lost on the paroccipital process. I propose to call this the *supraforaminal ridge* (*sup. for. r.*; lower transverse supraoccipital ridge, Owen); it is well developed in all the species, while the crest, although usually well marked, is often obscure and sometimes absent in *Dinornis*.

The occipital crest passes anteriorly into a transverse ridge which extends laterally on each side to the base of the paroccipital process; the median portion of this *lambdoidal ridge* (*lamb. r.*; transverse occipital ridge, Owen) is frequently double (figs. 1, 9, & 12), a transversely elongated lozenge-shaped area being enclosed between its two divisions; we may thus distinguish an *anterior lambdoidal ridge* (*ant. lamb. r.*), which is dentated and serves as the chief line of insertion of the neck-muscles, from a *posterior lambdoidal ridge* (*post. lamb. r.*). The distinction between the two varies greatly in different species, being best marked in *Anomalopteryx*, and hardly distinguishable in *Dinornis* (Plate LXI. figs. 25–34). On each side of the occipital crest, close to its junction with the posterior lambdoidal ridge, is a more or less well-marked depression, the *supraoccipital fossa* (fig. 9, *s. oc. fos.*).

The precise relation of the lambdoidal suture to the ridges of the same name is difficult to make out, as the ridges are obscure in young specimens, but it appears to be a little in front of the posterior ridge.

The paroccipital processes (*par.oc.pr.*) are large and prominent; in *Dinornis* they are comparatively flat, and their ventral edges are evenly curved and not greatly produced downwards (Plate LXII. fig. 47); in *Mesopteryx casuarina* (fig. 51) they are very convex backwards, and their ventral borders are produced into bluntly pointed processes which extend downwards to the level of the mamillar tuberosities. Other species show intermediate conditions (figs. 47-58). In *Emeus* the supraforaminal ridge stops short at the base of the paroccipital process; in most other species it is continued on to its lower angle.

Externally to the supraoccipital fossa there is frequently a foramen, usually continued into a groove, for one of the cerebral veins. The line of junction between the supra- and exoccipitals is probably situated mesiad of this foramen, but I have not seen a skull in which those two bones are distinct; the paroccipital process is no doubt constituted entirely by the exoccipital.

ii. *The cranial roof.* (Plate LVI. fig. 1; Plate LVII. fig. 5; Plate LVIII. fig. 12; Plate LIX. fig. 17; Plate LX. fig. 20; Plate LXI. figs. 23-34.)

The roof of the cranium is formed mainly by the parietals (*pa.*) and frontals (*fr.*), the coronal suture passing transversely about halfway between the posterior lambdoidal ridge and a line drawn between the posterior margins of the postorbital processes (figs. 5 & 12). It is usually evenly arched both from before backwards and from side to side. The lateral curvature is least in *Dinornis* (fig. 47), in which also, taking the basitemporal platform as horizontal, the anterior or frontal region is considerably deflected (fig. 35). In *Mesopteryx casuarina* (fig. 27), *Mesopteryx*, species *a* (fig. 30), and *Emeus*, species *γ* (fig. 34), the roof is swollen on each side of the middle line, producing a double tumidity; in the other species of *Emeus* (figs. 38, 42, & 46) there are slight unpaired elevations in the anterior and posterior frontal regions, the intervening portion being flat or depressed. The roof is continuous behind with the occipital region and with its squamosal prominences, narrowed between the temporal fossæ, and immediately in front of these produced into the large *postorbital processes* (*post.orb.pr.*), which pass outwards and downwards, forming the posterior boundary of the orbit and almost meeting the maxillo-jugal arch (figs. 3 & 7). In most cases the postorbital process forms an even curve; in *Dinornis* and *Pachyornis* it is divisible into horizontal and descending portions, the former gently inclined downwards, the latter vertical.

Anteriorly the postorbital process passes into the *supraorbital ledge*, which is itself continued into a short *preorbital process* (*pre.orb.pr.*) formed by a part of the ankylosed lacrymal (figs. 5, 7, & 8). The margin of the orbit thus constituted exhibits certain well-marked differences in the various genera and species. In most cases the whole orbital margin is evenly curved or slightly sinuous; in *Dinornis* the supraorbital ledge is at right angles to the postorbital process (figs. 23 & 35); in *Anomalopteryx* the *postorbital angle* thus formed is slightly obtuse (fig. 36). The doubtful crania referred

to *Mesopteryx*, species  $\gamma$  (figs. 30 & 44), and *Emeus*, species  $\gamma$  (figs. 34 & 40), differ from the other species of the genera in which I have provisionally placed them in possessing a distinctly right-angled orbit.

The anterior part of the cranial roof, between the preorbital processes, is formed partly by the frontals, partly by the nasals. The junction between the two bones is well shown in the young skull of *Anomalopteryx didiformis* (figs. 12 & 17), in which, the nasals being lost, each frontal is seen to present a deep triangular notch for the lateral portion of the corresponding nasal, while between the notches the frontals end in a straight transverse border, with which both the mesial portions of the nasals and the nasal process of the premaxilla articulate.

The nasals are in contact by their ventral surfaces with the ethmoid, exposed by their removal in figs. 12 & 17, and unite with one another in the middle line beneath the premaxilla, for the reception of which the mesial portion of the conjoined bones is excavated in the form of a shallow, parallel-sided groove, the *premaxillary fossa* (figs. 23 & 34). Thus the mesial portion of the nasals is hidden in the entire skull, and the roof of the olfactory chamber is formed in this region of a triple layer of bone—premaxilla externally, ethmoid internally, and nasals between. Laterad of the premaxillary fossa the nasal appears on the surface as a triangular bone the curved base of which forms the posterior boundary of the nostril (figs. 5, 7, & 8), its external angle being produced, in a young specimen of *Anomalopteryx didiformis*, into a short maxillary process. In *Dinornis torosus* this process is continued as a slender bar of bone which passes vertically downwards, in close contact with the anterior border of the lacrymal (preorbital process), completing the lacrymal foramen externally, and articulating by its lower or distal end with the maxilla. In *Emeus*, species  $\alpha$ , and *E. crassus* this process is represented by a distinct ossification which I propose to call the *maxillo-nasal* (figs. 7 & 8, *mx.na.*). I have been unable to ascertain the precise condition of these parts in the other genera, but I am inclined to think there is a distinct maxillo-nasal in *Anomalopteryx*, while in *Pachyornis* there appears to be a maxillary process as in *Dinornis*.

In the skull referred to *Mesopteryx*, species  $\beta$ , the anterior portion of the skull-roof is marked with numerous shallow pits arranged more or less regularly in lines radiating backwards and slightly outwards from the edges of the premaxillary fossa (Plate LX. fig. 20). They appear to indicate the presence of a crest of specially strong feathers, which must have consisted in the present case of paired tufts, since the pits are absent in the middle line. In the type specimen of *Dinornis torosus*, and in the specimen of *D. robustus* (*D. potens*, Hutton) in York Museum, similar pits occur, extending across the middle line and on to the preorbital processes. Similar but less distinct pits occur in two skulls of *Anomalopteryx didiformis*. Since in the two last-named species the pits are absent in certain skulls, it seems probable that the crest was possessed only by the male.

iii. *The base of the skull.* (Plate LVI. fig. 2; Plate LVII. fig. 6; Plate LX. figs. 19, 21, & 22.)

The *basitemporal platform* (*b.temp.pl.*) is a prominent flattened elevation on the base of the skull, having a nearly vertical posterior face separated by a deep groove, the *precondylar fossa* (fig. 2, *pr.con.fos.*), from the occipital condyle; in the fossa two pits, probably venous, occur in *Dinornis*. The middle region of the posterior edge of the platform is usually somewhat excavated, the excavation being bounded on either side by a larger or smaller prominence, the *mamillar tuberosity* (Owen: basioccipital process, Lydekker, *mam.tub.*), which forms the postero-lateral angle of the platform. Owen considers these tuberosities to occur at the junction of the basisphenoid and basioccipital, but the examination of a young skull shows them to lie at the junction of the basioccipital, exoccipital, and pro-otic (figs. 6, 7, & 14). About the posterior third of the platform is formed by the basioccipital, the rest by the basitemporal underlying the basisphenoid; whether the basitemporal extends so far back as I have shown it in fig. 6 is uncertain.

Each mamillar tuberosity is separated from the corresponding paroccipital process by a deep *paroccipital notch*, immediately behind which occur one large and several small foramina. The larger of these is the *vagus foramen* (precondyloid foramen, vagal foramen, Owen, *vag.for.*) for the ninth and tenth nerves; the smaller holes or *condyloid foramina* (*con.for.*) give exit to the twelfth nerve. The notch between the paroccipital process and the mamillar tuberosity is sometimes converted into a foramen by a slender bar of bone bridging it over. Immediately in front of it is the *carotid foramen* (fig. 6, *car.for.*), leading into the canal by which the carotid artery passes to the pituitary fossa. In young skulls the greater part of the carotid canal is an open groove.

The antero-lateral angles of the basitemporal platform are formed by a pair of broad projections, flattened from above downwards, the *basipterygoid processes* (*b.pt.pr.*); they articulate by their distal ends with the pterygoid bones. Between the basipterygoid process and the mamillar tuberosity, the lateral border of the platform is obliquely furrowed by a deep groove for the Eustachian tube (figs. 2 & 6, *eus.gr.*). The edges of the groove are often produced into roughened ridges, but these never meet below so as to convert the groove into a tube; in this respect the adult Moa resembles the Kiwi at the time of hatching.

In the centre of the basitemporal platform and between the inner ends of the Eustachian grooves is usually to be found a more or less well-marked depression of variable form—sometimes short and wide, sometimes long and narrow. At its posterior end there frequently occurs a deep fossa, which in one young specimen was represented by a foramen opening into the cranial cavity a short distance posterior to the pituitary fossa. The aperture (fig. 6) is the *posterior basicranial fontanelle* (median venous foramen, basisphenoidal mid-ventral canal, Owen, *p.b.cr.fon.*), marking the incomplete concrescence of the parachordal cartilages of the embryo (24); the depression apparently marks the incomplete extension mesiad of the basitemporal.

Another interesting embryonic character is the occasional presence of a small pit or foramen situated in the middle line at the junction of the rostrum with the basitemporal platform, and at the level of the anterior borders of the basiptyergoid processes; when patent it leads into the pituitary fossa. This is a remnant of the *anterior basicranial fontanelle* (*a.b.cr.fon.*) through which the pituitary pedicle passes from the pharynx to the cranial cavity. Its retention in the adult is somewhat remarkable, as in *Apteryx* (24) it is completely covered by the rostrum, and only visible when, in the young skull, the latter is stripped from the underlying cartilage.

The rostrum as seen from below has the appearance of a more or less cylindrical rod of bone; actually it is doubtless crescentic in section, as in other birds. It is frequently slightly constricted towards its junction with the basitemporal platform, its middle region is often much compressed and keel-like, and its anterior end is pointed. It will be further considered in connection with the ethmoidal region, but one remark must be made here as to its position. It usually lies nearly or quite in the same horizontal plane as the basitemporal; but in *Dinornis* the two are set at an obtuse angle (about 150°) with one another, thus giving rise to the deflected beak characteristic of that genus.

iv. *The lateral surface of the cranium.* (Plate LVI. fig. 3; Plate LVII. fig. 7; Plate LVIII. fig. 13; Plate LIX. fig. 18; Plate LXI. figs. 35-46).

The *tympanic cavity* is a deep depression bounded behind by the paroccipital process, above by the squamosal prominence, and mesially by a greatly pitted surface furnished by the exoccipital and pro-otic bones. It is continued downwards and forwards into a sort of pocket, the *anterior tympanic recess*, bounded in front by a thin, oblique, quarter-cylinder of bone, the *pretemporal wing* (figs. 6 & 13, *pr.temp.w.*). A young skull shows this process to be part of the combined basisphenoid and basitemporal; probably, as in other birds, it is formed by the latter. In some cases the anterior tympanic recess becomes largely filled up with spongy bone and thus reduced to a quite insignificant cavity; it is best marked in young skulls of *Anomalopteryx didiformis*, but is also large and conspicuous in *Mesopteryx casuarina* and some other species.

The *squamosal prominence* (*sq.prm.*) is a thick outstanding mass, convex above, deeply concave below, and formed by the squamosal bone (mastoid, Owen), which articulates mesially with the parietal, exoccipital, alisphenoid, and pro-otic. It is produced downwards into the *zygomatic process* (mastoid process, Owen, *zyg.pr.*), which, in the entire skull, lies immediately external to the quadrate, is directed slightly forwards, and is sometimes bifid (fig. 3); it varies considerably in length. It is continued upwards on to the lateral surface of the squamosal by a slightly wavy, subvertical *posterior temporal ridge* (*post.temp.r.*), the dorsal end of which joins the inferior temporal ridge described below (figs. 3 and 13).

The margin of the tympanic cavity varies in form: in *Dinornis* (fig. 35) its dorsal edge, furnished by the squamosal, forms an even curve with its posterior edge, furnished

by the paroccipital process, the latter being directed slightly backwards. In *Emeus* (figs. 38, 42, and 46) the two form a slightly acute angle, the paroccipital process being directed forwards; in *E. crassus* there is often a kind of step at the junction of the two, the margin of the cavity being therefore sinuous. In *Anomaloptyryx* (fig. 36) the paroccipital is still more sharply inclined forwards, the dorsal and posterior edges of the tympanic cavity meeting at a very acute angle, and the width of the cavity from before backwards being greatly reduced.

On the roof of the tympanic cavity is the large obliquely-transverse articular facet for the head of the quadrate; its outer end is immediately mesiad of the posterior temporal fossa described below, and is bounded behind by the zygomatic process; from this point it passes inwards and backwards, its inner end being exactly opposite the Eustachian groove. According to my observations the inclination of the quadrate facet (see Lydekker, 12, p. 298) is a point of no classificatory value; a straight line drawn through the axis of the facet makes an angle with the sagittal plane, which rarely sinks below  $130^{\circ}$  or rises above  $140^{\circ}$ , and which is, moreover, very variable, sometimes differing considerably on the two sides of the same skull. The outer two-thirds of the facet is furnished by the squamosal, the inner third in about equal proportions by the exoccipital and pro-otic (Plate LXII. fig. 70).

The zygomatic process is, as it were, bent round the quadrate facet so as to bound its outer end posteriorly as well as externally, and its flattened posterior face is continued backwards into a horizontal *tympanic ledge* (fig. 2), the inner border of which gives attachment to the tympanic membrane, while externally it is produced into a rough horizontal *supratympanic ridge*.

Immediately posterior to the quadrate facet is a large pneumatic foramen leading into the diploë of the pro-otic and squamosal. Mesiad of the inner end of the facet are usually three more or less well-marked depressions in the roof of the tympanic cavity; of these, the one nearest to the quadrate facet is a pneumatic foramen; the hindermost of the other two is a simple depression in the bone, while the foremost is the *fenestral recess*, containing the fenestra ovalis and fenestra rotunda. Just anterior to the recess, and separated from it by a vertical bar of bone, is the small aperture for the facial nerve, immediately dorsad of which is a large pneumatic pit. There is another small but deep pneumatic foramen encroaching on the anterior border of the quadrate facet, and the whole wall of the tympanic cavity is honeycombed with less constant depressions of various sizes.

The *temporal fossa* is a deep depression between the postorbital process in front and the squamosal prominence behind. It is limited above by a strongly marked temporal ridge (*linea semicircularis, temp.r.*) which marks the origin of the temporal muscle; the ridge forms an even curve, passing from the posterior edge of the postorbital process, at first backwards and upwards, and then curving round and passing downwards and forwards (figs. 3 and 13), so that the whole temporal fossa has a strong backward slope; at the base of the zygomatic process it joins the posterior temporal

ridge already mentioned (p. 385), and finally ends in a short, blunt *pretympanic process*, situated immediately in advance of the outer end of the quadrate facet. The ventral portion of the posterior limb of the tympanic ridge, between its junction with the posterior tympanic ridge and its termination in the pretympanic process, is conveniently distinguished as the *inferior tympanic ridge (inf.tymp.r.)*. Between the inferior and posterior ridges thus defined, a more or less triangular space is enclosed which serves for the origin of the second portion of the temporal muscle, and may be distinguished as the *posterior tympanic fossa (post.tymp.fos.)*. Lastly, the main temporal fossa is imperfectly divided, in some species, by a vertical *mid-temporal ridge (figs. 12 & 13, m.temp.r.)* at about the junction of its anterior and middle thirds and just over the lateral portion of the coronal suture.

The temporal fossa varies considerably in width in the different species, being narrowest proportionally in *Mesopteryx casuarina*, widest in *Anomalopteryx didiformis*. But its most striking feature is the different degree of its extension on to the cranial roof; in most species the distance between the right and left ridges is but little less than the diameter of the cranium in the temporal region, while in *Anomalopteryx didiformis* it is hardly more than half that dimension. Moreover, there is usually a flat area between the temporal and lambdoidal ridges (see Plate LXI.); but in *Anomalopteryx didiformis* (fig. 24), *Dinornis*, species *a*, and *Pachyornis*, species *a* (fig. 26), in all of which the temporal fossa is unusually large, the two ridges are in contact. In *Pachyornis elephantopus*, in which there is a wide area between the two lambdoidal ridges, the anterior one often touches the temporal before uniting with the posterior ridge.

The portion of the dorsal region of the temporal fossa lying behind the mid-temporal ridge is formed, as already stated, by the parietal, the part in front of the ridge by the frontal (figs. 7 & 18); its ventral region is furnished by the alisphenoid, which, in the young, joins the parietal by a straight horizontal suture situated at about the level of the roof of the tympanic cavity. Below, the alisphenoid is separated from the basi-sphenoid, in the youngest cranium I have seen, by a gently curved suture (fig. 18) extending forwards and downwards from the trigeminal foramen.

The *trigeminal foramen* (foramen ovale, Owen, *trig.for.*), for the second and third divisions of the fifth nerve, is situated in the side-wall of the cranium below the temporal fossa, and in the same transverse plane as the posterior edge of the basipterygoid process (figs. 3 & 13); it is bounded above by the alisphenoid, below by the pretemporal wing. Sometimes it is partially or completely divided into two passages by a horizontal bar of bone; this duplication of the foramen seems to be constant in *Mesopteryx casuarina*. About 1 cm. below and in front of the trigeminal foramen is a small (*qu. arterial?*) foramen situated just above the base of the basipterygoid process as in *Apteryx*.

The *orbits* are smaller than in the majority of birds, and, as Owen pointed out, there can hardly be said to be an interorbital septum, owing to the backward extension of

the olfactory chambers. There the *Dinornithidæ* show, to a less degree, the state of things which reaches its maximum among birds in *Apteryx*.

As already remarked, the upper margin of the orbit, formed by the supraorbital ledge, may be either evenly curved, sinuous, or right-angled. The roof of the cavity formed by the projecting ledge is almost horizontal from within outwards; its mesial wall slopes from the supraorbital ledge downwards and inwards to the optic and lacerate foramina, the slope being far steeper in the narrow-skulled genera than in the wide-skulled *Dinornis*.

Both roof and mesial wall of the orbit are pierced with vascular foramina, but the first feature of importance met with in this region of the skull is the optic foramen (*op.for.*). This lies in the postero-ventral region of the orbit, slightly in advance of the base of the rostrum. In *Emeus* it is a nearly circular aperture directed from the cranial cavity outwards, forwards, and upwards, and its lower margin is separated from that of its fellow of the opposite side by a distance of about 9 or 10 mm. In *Dinornis* it is proportionally smaller and oval in outline; its lower margin is formed by a thin obliquely horizontal shelf of the presphenoid, represented in the other genera by a mere ridge, and the distance between the two foramina is about 30 mm.

The greater part of the inner wall of the orbit is furnished by the orbital plate of the frontal (fig. 18), which, in the young skull, articulates below with the inferior alioethmoid (*inf.al.eth.*) and the orbitosphenoid (*or.sph.*); the suture passes about 2 mm. above the optic foramen, which is therefore bounded above by the orbitosphenoid, below by the presphenoid.

Bounded above by the shelf or ridge forming the lower margin of the optic foramen, and below by the rostrum, is a depression, the *presphenoid fossa* (fig. 18, *pr.sph.*), very obvious in *Dinornis*, *Pachyornis*, *Anomalopteryx*, rather obscure in *Mesopteryx* and *Emeus*. The vertical plate of bone separating the fossæ of the right and left sides is very thin, and is the only indication of an interorbital septum, thus showing an interesting approximation to the typical avian structure of the presphenoid.

Immediately posterior to the optic foramen is the aperture called by Owen the prelacerate foramen or foramen rotundum, but more conveniently named the *lacerate fossa*, as it is not a simple foramen, but a pit including three perfectly distinct foramina. One of these (Plate LXII. fig. 76, *v*<sup>1</sup>), placed postero-dorsally, is the opening of a tunnel-like excavation in the alisphenoid, and transmits the orbitonasal nerve. The second (*iii*), below and in front of the first, is bounded behind by the alisphenoid and in front by the basisphenoid, and transmits the oculomotor nerve. The third (*vi & a*), situated below and in front of the second, perforates the alisphenoid and probably transmits the internal ophthalmic artery; it has in its hinder margin the aperture of a canal through which the sixth nerve enters the orbit. The fourth nerve (*iv*) enters through a very small foramen placed just above that for the third nerve, and quite outside the lacerate fossa.



v. *The ethmoidal region.* (Plate LVI. figs. 3 & 4; Plate LVII. figs. 7 & 8; Plate LVIII. figs. 11-13; Plate LIX. figs. 16-18.)

The *mesethmoid* (figs. 16 & 18, *meseth.*) is a vertical plate of bone ankylosed in the adult by its whole ventral border to the rostrum, continuous behind with the presphenoid, and having its dorsal border sloping from behind forwards immediately beneath the nasal process of the premaxilla. It is perforated posteriorly by an irregular fenestra of very variable size (fig. 16), which, in the dried skull, places the two olfactory chambers in communication with one another.

The olfactory chambers thus connected form a spacious cavity lying beneath and in front of the anterior portion of the cranial roof and extending nearly as far back as the optic foramen. Postero-dorsally they are perforated, on each side of the middle line, by one or sometimes two rather irregular apertures which serve for the passage of the olfactory nerves. Their roof and side-walls are formed by the *lateral* or *ectoethmoids*, which are divisible into three principal parts. The first, or *superior aliethmoid* (figs. 17 & 18, *sup.al.eth.*) extends almost horizontally outwards on each side from about the posterior half of the dorsal border of the mesethmoid, underlying the nasals and the anterior part of the frontals (fig. 16) and forming the roof of the olfactory chambers. The second portion, or *inferior aliethmoid* (fig. 18, *inf.al.eth.*), is a concavo-convex plate forming the side-wall of the posterior part of the chamber, continuous behind with the pre- and orbitosphenoids, and in the young skull articulating by suture with the orbital plate of the frontal.

These two are the only parts of the ectoethmoid retained in the majority of Moa skulls, but in good specimens there is to be seen more or less of the third portion of the ectoethmoid known as the *antorbital plate* (prefrontal, Huxley), and corresponding with the dilated part of what I have called the fifth portion of the ectoethmoid in *Apteryx* (24). This consists of an upright plate of thin bone (figs. 3 & 7, *a.orb.*) placed somewhat obliquely in the front part of the orbit; its mesial border is continuous with the inferior aliethmoid, and its lateral border is ankylosed to the lacrymal. It is continued forwards (in *Emeus*, species  $\alpha$ ) beyond its ankylosis with the lacrymal by a thin scroll-like bone, the *alinasal* (figs. 3, 4, 7, & 8, *al.n.*), which nearly meets above with the superior aliethmoid and below with the triangular process described on page 390. The ossified posterior turbinal (figs. 6 & 8, *turb.*) is an ingrowth from the posterior end of the antorbital.

The lacrymal (figs. 7 & 8, *lac.*) is completely ankylosed with the lateral border of the antorbital, is deeply notched, or in *Anomalopteryx didiformis* perforated, for the lacrymal duct, and presents below an oblique facet for articulation with the maxilla. The maxillary process of the nasal, or maxillo-nasal of *Emeus*, lies immediately in front of and parallel with the lacrymal, converting the notch into a foramen (*lac.for.*).

In *Dinornis* the antorbital is a much stouter bone than in the other genera, and is, therefore, more frequently found intact. It is much narrower than in the remaining forms, owing to the great size of the supraorbital fenestra (see p. 390), and is sloped

obliquely forwards from its lower edge; it is firmly ankylosed to the inferior aliethmoid as well as to the lacrymal. Its ventral border, instead of being thin and delicate, takes the form of a stout transverse ridge or bar of bone forming the posterior boundary of the aperture between the olfactory chamber and the posterior nasal passage. This *postchoanal bar*, as it may be called, is a very obvious structure when the skull is viewed from below (see Owen, 19, pl. 56, or Ext. Birds of N. Z. pl. 65, fig. 1, *g*), and constitutes a striking difference between *Dinornis* and the smaller genera.

A final ectoethmoidal structure, very characteristic of the whole family, is the *triangular process* (Plate LVI. figs. 2 & 4, *tri.pr.*), a horizontal plate springing by a broad base from the mesethmoid (fig. 18) and extending outwards at the level of the lacrymal foramen. It forms the anterior boundary of the aperture between the olfactory chamber and the posterior nasal passage, and its posterior border is connected by a horizontal ridge with the postchoanal bar. The bar, ridge, and triangular process are together called by Owen the girdle or cingulum olfactorium.

The antorbital plate is perforated dorsally by the *supraorbital fenestra*. This, in *Dinornis torosus*, is a single large aperture, more than 1 cm. in length, and continued dorsad into a shallow fossa on the underside of the lacrymal (preorbital process). Apparently the Harderian gland fitted into both the fossa and the fenestra, the orbito-nasal nerve passing through the anterior part of the latter in its passage from the orbit to the olfactory cavity. Above the posterior end of the dorsal margin of the fenestra is a small foramen also leading into the olfactory chamber.

In *Emeus*, species  $\alpha$  (fig. 7), the supraorbital fenestra (*sup.orb.fen.*) is quite small and the Harderian pit (*Hard.fos.*) above it very deep; posterior to these is a foramen (*a*) leading into the olfactory chamber, and beneath it a fossa (*b*), sometimes perforated. In *Anomalopteryx didiformis* an intermediate arrangement is found; the supraorbital fenestra is of moderate size and is connected by a wide groove with a fossa in the posterodorsal region of the antorbital—this last answers to fossa *b* in *Emeus*, and to the posterior moiety of the single fenestra in *Dinornis*; above it is a small foramen answering to the similarly placed hole (*a*) in *Pachyornis* and *Dinornis*.

In good specimens a coiled *posterior turbinal* (fig. 6) is seen to spring from the inner surface of the posterior end of the antorbital.

vi. *The cranial cavity.* (Plate LVIII. figs. 10 & 11; Plate LIX. figs. 15 & 16.)

The cavity for the brain has the usual avian form; its length and breadth are nearly equal, the greatest breadth being in the temporal region. The entire cavity may be divided into the following regions:—

- $\alpha$ . The metencephalic fossa for the medulla oblongata.
- $\beta$ . The cerebellar or epencephalic fossa for the cerebellum.
- $\gamma$ . The mesencephalic fossæ for the optic lobes.
- $\delta$ . The pituitary fossa and the optic platform for the pituitary body and the optic chiasma.

ε. The cerebral or prosencephalic fossæ for the cerebral hemispheres.

ζ. The olfactory or rhinencephalic fossæ for the olfactory lobes.

The *metencephalic fossa* is furnished by the post-pituitary part of the basis cranii; it is gently concave both from before backwards and from side to side, and is terminated in front by the dorsum sellæ, while behind it is continued on to the flattened dorsal surface of the occipital condyle. Near its posterior end is seen on each side the large vagus foramen (*va.for.*) and mesiocaudad of this the two small condyloid foramina (*con.for.*).

In front of the vagus foramen and separated from it by a vertical bar of bone about 2 mm. wide is the *internal auditory meatus* (fig. 16, *int.aud.m.*), a shallow pit containing the foramina for the facial and auditory nerves. The minute *abducent foramen* for the sixth nerve lies on a line joining the internal auditory meatus with the middle of the dorsum sellæ (fig. 15, *abd.for.*), and about 5 or 6 mm. from the latter. Between the abducent foramina a median aperture of considerable size is sometimes found, in one instance communicating with the pituitary fossa; this is the internal opening of the posterior basicranial fontanelle.

The *cerebellar fossa* (fig. 11, *cer.fos.*) is in the roof of the cranium and is bounded mainly by the supraoccipital and parietals above and by the pro-otics laterally. It is bounded behind by the dorsal edge of the occipital foramen, and in front by the median portion of the tentorial ridge, while ventrally it passes insensibly on each side into the metencephalic fossa. It is marked by a series of transverse grooves corresponding with the gyri of the cerebellum. On each side, about 3 or 4 mm. above the internal auditory meatus, is the small *floccular fossa*, which varies considerably in size in different individuals.

The *mesencephalic fossa* (*mesen.fos.*) lies in the alisphenoid, laterad of the dorsum sellæ (fig. 10) and is bounded externally by the ventral portion of the tentorial ridge. It is largely occupied by a shallow depression for the root of the trigeminal nerve, and from this depression the trigeminal foramen proceeds directly outwards (fig. 16, *trig.for.*), and the tunnel-like orbitonasal foramen (*orb.na.for.*) forwards and slightly outwards to the lacerate fossa (*vide suprâ*, p. 388).

The *pituitary fossa* or sella turcica (*pit.fos.*) is an almost spherical depression in the middle of the cranial floor. It is bounded behind by a ridge, the dorsum sellæ, which curves forwards on each side and ends at the small oculomotor foramen (*oc.for.*). In front the pituitary fossa is bounded by a transverse *prepituitary ridge* (fig. 16, *pr.pit.r.*), anterior to which is a wide ledge, the *optic platform*, terminating on either side in the optic foramen (*op.for.*). Almost vertically above the prepituitary ridge is a similar transverse prominence, the *preoptic ridge* (fig. 16, *pr.op.r.*), forming the upper boundary of the optic platform and passing laterad into the tentorial ridge.

The optic foramen is bounded behind by a vertical bar of bone separating it from the apertures for the third nerve and the internal ophthalmic artery (fig. 16). The oculomotor foramen (*oc.for.*), which is the uppermost of the two, is continued backwards by a groove placed sometimes just above, sometimes just below the continuation

of the dorsum sellæ: the internal ophthalmic foramen (*int.op.for.*) is also continued by a groove which extends downwards and backwards to the entrance of the internal carotid artery (*car.for.*). The internal opening of the minute pathetic foramen (*path.for.*) is placed about 1 mm. dorso-laterad of the oculomotor. The internal carotid canals (*car.for.*) open by paired apertures placed close together in the posterior wall of the pituitary fossa. And lastly, in occasional instances, the fossa is perforated anteriorly by the anterior basicranial fontanelle.

The *cerebral fossæ* lie altogether in front of the cerebellar fossa, there being no overlapping of the cerebellum by the hemispheres such as occurs in *Apteryx*. They are separated from the cerebellar fossa by the prominent tentorial ridge, which, starting in the centre of the skull-roof, almost exactly above the dorsum sellæ, sweeps at first backwards, outwards, and downwards, and then forwards, downwards, and slightly inwards, and finely comes to an end near the extremity of the preoptic ridge. From the middle of the tentorial ridge a somewhat less prominent median elevation, the bony falx, passes forwards and ends just over the crista galli, marking the separation of the hemispheres dorsally.

The line of separation between the hemispheres on the ventral surface is similarly indicated by a low median ridge which extends from the crista galli backwards to the preoptic ridge. For a distance of about 5 mm. (in *Emeus*) on each side of this ridge the cerebral fossæ are floored by the presphenoid (fig. 15, *pr.sph.*); from it the orbito-sphenoids (*or.sph.*) extend outwards and backwards, forming the dorsal boundaries of the optic foramina. The resemblance of this portion of the Moa's skull to that of an embryo Kiwi is very striking; in the adult *Apteryx* the presphenoid undergoes a remarkable shortening.

The anterior moiety of the roof and side-walls of the cerebral fossa is furnished by the frontal, the posterior portion by the parietal and alisphenoid. A low horizontal ridge running a short distance above the parieto-alisphenoid suture indicates the presence of a similarly-placed sulcus on the cerebrum.

The *olfactory fossæ* are paired oval pits placed vertically at the anterior end of the cerebral fossæ. They are separated from one another by a narrow bony ridge, the *crista galli*, and the floor of each is perforated by a variable number of somewhat irregular apertures for the branches of the olfactory nerve.

#### b. *The Premaxilla.*

The premaxilla is a triradiate bone which may be described in general terms as consisting of a thickened *body* which forms the end of the beak, a median dorsal *nasal process*, paired ventro-lateral *maxillary processes*, and thin ventral *palatine processes* connected in front with the body and externally with the maxillary processes.

The anterior extremity of the body, forming the apex of the beak, is rounded in *Dinornis* and *Emeus*, bluntly pointed in *Pachyornis*, *Mesopteryx*, and *Anomalopteryx*.

Its gently curved alveolar margins are marked, especially in *Dinornis*, with a broad, shallow groove, and are continued horizontally inwards into a flattened ventral plate; from this is given off a strong ascending keel, formed posteriorly of paired plates, but solid in front and gradually diminishing in height towards the tip of the beak. The dorsal edge of the triangular vertical keel thus produced is expanded to form a prominent median ridge passing behind into the nasal process and in front continued more or less distinctly to the apex of the beak; this ridge is best developed in *Dinornis*, in *Emeus* it is almost obsolete. The portion of the vertical keel included between the ridge above and the ventral plate below has a triangular form, and is, as already stated, bilaminar posteriorly; it constitutes the *prenarial septum* (Owen), and is especially well-marked in *Dinornis*; the extremity of the ankylosed rostrum and mesethmoid fits between its laminae.

From the ventral plate of the body the thin, horizontal, palatine processes pass backwards, diverging slightly so as to enclose a median palatine notch, through which in the perfect skull (figs. 2 & 6) the anterior end of the vomer and rostrum are seen. In *Emeus* the posterior end of the inner margin of the palatine plate gives off a somewhat pedate *vomerine process* (*vo.pr.*) which passes inwards and clamps the vomer; this process is small or absent in the other genera. The proportional length of the palatine process and of the body of the premaxilla differs greatly in the various genera.

From the posterior end of the alveolar margin of the body is given off the irregular horizontally-flattened maxillary process, which extends backwards (figs. 3 & 7, *mx.pr.*) dorsad of and in close contact with the anterior end of the maxilla, and ends close to the base of the maxillo-palatine and immediately below the ventral end of the maxillo-nasal.

The nasal process is a flat plate extending backwards and upwards from the body to the fronto-nasal suture, its posterior end lying, as already stated, in a shallow, parallel-sided groove, the premaxillary fossa, furnished by the mesial portion of the nasals. Its anterior or proximal end, where it joins the body of the bone, is slightly thickened in *Dinornis*, considerably thickened and somewhat triangular in section in *Anomalopteryx*, *Pachyornis*, and *Mesopteryx*, greatly thickened and almost cylindrical in *Emeus*.

#### c. *The Maxillo-jugal Arch.*

This consists of the usual three bones, the maxilla, jugal, and quadrato-jugal.

The *maxilla* consists of two parts, a slender external and posterior portion, the maxilla proper, and an irregular expanded antero-mesial portion, the *maxillo-palatine process* (Plate LVII. figs. 6, 7, & 8, *max.pal.*; Plate LXII. figs. 63 & 64). The maxilla proper is a slender rod presenting a flat ventral surface, an oblique lateral surface, a very narrow, smooth mesial surface, and a dorsal surface, to the whole length of which the jugal is applied.

The maxillo-palatine, in *Dinornis*, *Pachyornis*, *Mesopteryx*, and *Anomalopteryx*, is a very irregular shell of thin bone, with a spacious cavity, the *antrum*, opening poste-

riorly by an aperture placed in the angle between the maxilla and the palatine (fig. 63). Its ventral surface forms a nearly flat plate, roughly triangular in form; its lateral border and postero-lateral angle pass insensibly into the maxilla proper; its postero-mesial angle is produced into a short recurrent process which articulates with the palatine; the hinder half of its medial border also articulates with the palatine, and its anterior angle and the fore half of its mesial border with the premaxilla. From this flat ventral plate an irregular hollow mass of bone extends dorsad and fits into a space left between the other facial bones at the base of the beak. Its anterior surface appears in the ventro-lateral corner of the external nostril (figs. 7 & 8), articulating with the palatine process of the premaxilla below, with the rostrum mesiad, and with the maxillary processes of the premaxilla and nasal externally. Its dorsal region articulates with the anterior border of the triangular process of the mesethmoid (fig. 8). Its posterior surface, which is smooth and concave, forms part of the anterior wall of the posterior nasal aperture.

In *Emeus* the structure of the maxillo-palatine is strikingly different; its ascending portion, instead of being a hollow shell, is an irregular flattened plate (fig. 64), either quite solid or presenting a mere vestige of the antrum in the form of a very small pit on the posterior surface. By this peculiarity *Emeus* is sharply distinguished—at least so far as my enquiries go—from the remaining Dinornithidæ

The *jugal* is a slender bone forming the greater part of the dorsal surface of the maxillo-jugal arch (figs. 6 & 7). It articulates by about the anterior half of its ventral surface with the maxilla, by the posterior half with the quadrato-jugal. Near its posterior end the dorsal edge of the bone is raised into a low triangular process which extends upwards towards the postorbital process of the frontal.

The *quadrato-jugal* (figs. 6 & 7) articulates by more than the anterior half of its outer surface with the jugal and maxilla; thus the whole length of the bone is exposed on the mesial side of the maxillo-jugal arch, while less than half appears on the lateral surface. In the greater part of its extent it is flattened from side to side, but posteriorly it is much thickened and presents on its inner surface an oval facet for articulation with the quadrate.

#### d. *The Vomer, Palatine, and Pterygoid.*

The vomer in fully adult specimens of *Emeus*, species *a*, and *E. crassus* is a delicate bone (figs. 2 & 6, *vo.*) formed of paired laminæ united in front but diverging behind, and enclosing an acute dihedral angle. In its whole length it embraces the rostrum;

anteriorly it passes dorsad of the vomerine processes of the premaxilla and articulates with the maxillo-palatines; posteriorly each lamina turns outwards and fits into a groove between the palatine and pterygoid, its lateral border articulating with the mesial border of the palatine, and its posterior extremity being covered ventrally by the vomerine process (*vo.pr.*) of that bone.

In *Mesopteryx*, species  $\beta$  (Plate LX. fig. 21) there are distinct paired vomers; a similar condition appears to obtain in *Anomalopteryx* and in young skulls of *Emeus crassus*. Owen's figure of *Dinornis torosus* (20, pl. 15; Ext. Birds of N. Z. pl. 82) also shows paired vomers; probably their concrescence is a sign of age.

The *palatine* is a delicate, twisted plate of bone, passing from the anterior end of the maxilla in front to the pterygoid behind (fig. 6). Its anterior end is somewhat fan-shaped and underlaps the maxillo-palatine; immediately posterior to this expanded portion it is notched for articulation with the recurrent process of the maxilla. The whole bone is twisted, the inner border of its anterior end becoming ventral in the middle and finally external at the posterior end; at the same time the dorsal border turns mesiad, reaching to within a short distance of the rostrum. The posterior end is obliquely truncated and articulated by all but its ventral extremity with the vomer, becoming ankylosed with it in the adult. The ventral extremity of the posterior border is produced into a thickened squarish *vomerine process* (*vo.pr.*) which underlies the posterior end of the vomer, and laterad of this process the bone presents a short pointed end which underlies the pterygoid.

The *pterygoid* (*pt.*) is a stout irregular bone with a bluntly-pointed anterior and a thickened posterior end. By about the anterior half of its ventral border it articulates with the combined palatine and vomer; by its inner surface it articulates with the basipterygoid process; its outer surface lies parallel to and in close contact with the orbital process of the quadrate; and its posterior end expands into a somewhat pedate surface for articulation with the quadrate.

#### e. *The Quadrate.*

The quadrate consists, as usual, of a *body* bearing the condyle for articulation with the mandible, an upwardly-directed *otic process*, terminating in the *head* for articulation with the tympanic cavity, and a forwardly-directed *orbital process*.

The articular surface on the head is somewhat wider at its outer than at its inner end, and presents no trace of the double facet found in *Apteryx*. The otic process is subtriangular, presenting a *lateral border* running upwards from the quadrato-jugal facet, a *mesial border* from the outer condyle, and an *anterior border* from the orbital process; a *posterior surface* between the mesial and lateral borders, a *mesial surface* between the anterior and mesial borders, and a *lateral surface* between the anterior and lateral borders. On the mesial surface, just where the otic process merges into the body of the bone, is a pneumatic foramen which varies greatly in size in the different species and even in different individuals of the same species; speaking generally, it appears to be large in *Dinornis*, *Anomalopteryx*, and *Pachyornis* as well as in *Mesopteryx*, species  $\beta$ ; smaller in *Emeus*, and smallest of all in *Mesopteryx casuarina*. In *Anomalopteryx didiformis* there is sometimes a second pneumatic foramen on the

posterior surface of the bone at a slightly lower level than the mesial one, and in one specimen of *Dinornis robustus* there are two additional foramina on the posterior surface, one at the level of the mesial aperture, the other close to the head. On the whole the characters of the quadrate appear to be too variable to be of much use for systematic purposes.

The orbital process is laterally compressed and bluntly pointed. On its mesio-ventral border is a small facet (*pterapophysial facet*, Owen) for the pterygoid, and at the base of the same border and extending downwards on to the body of the bone is a larger facet with which the posterior end of the pterygoid articulates.

The ventral face of the body bears the usual two condyles for articulation with the mandible. The *inner condyle* is placed transversely and is separated by a narrow interspace from the *outer condyle*, which is set at an angle of about 45° with the sagittal plane. Immediately above the outer extremity of the external condyle is the deep hemispherical fossa for articulation with the quadrato-jugal.

#### f. *The Mandible.*

The lower jaw consists of two gently curved rami ankylosed with one another in front in a wide symphysis.

Each ramus is expanded at its posterior end to form a cup-like articular surface for the quadrate, the outer border of which projects but slightly beyond the level of the ramus, while internally it is much produced and ends in a triangular *internal angular process*. The surface for the outer condyle of the quadrate forms a long narrow facet running parallel with the outer and posterior edge of the cup: that for the inner condyle is an oval surface, deeply concave from within outwards, situated on the anterior margin of the cup, just mesiad of its junction with the ramus. At the base of the inner surface of the internal angular process is a nearly circular pneumatic foramen, which, however, is sometimes absent in *Emeus* and *Mesopteryx*. At the posterior end of the surface for the outer condyle the bone is produced into a *posterior angular process*, which is small in *Dinornis*, large and prominent in the other genera. Both internal and posterior angular processes are continued on to the ventral surface of the articular cup by ridges which meet each other below: they are especially prominent in *Emeus*.

The ventral edge of each ramus has a sigmoid curve in all genera but *Anomalopteryx*, being convex downwards in its posterior, concave in its anterior half, and the latter being more or less deflected. The curvature of the dorsal follows to some extent that of the ventral border, but is less regular. The deflection is most marked in *Dinornis*, in which, when the mandible is placed upside down on a horizontal surface, the tip of the beak is raised 35–45 mm. above the horizontal. In *Pachyornis*, *Mesopteryx*, and *Emeus* this distance does not exceed 10–15 mm., and in *Anomalopteryx* the jaw is nearly straight. The general plane of the ramus is vertical or nearly so in *Pachyornis*,



*Anomalopteryx*, *Emeus*, and *Mesopteryx*; in *Dinornis* it is inclined, sloping outwards from its lower border. The anterior end of the dorsal edge presents a distinct alveolar groove, like that on the premaxilla; the posterior end is produced into a rough irregular *coronoid process* for the insertion of the temporal muscle.

The form of the symphysis naturally follows that of the premaxilla, being broad in *Dinornis* and *Emeus*, narrow in *Pachyornis*, *Mesopteryx*, and *Anomalopteryx*. The result of this is that the entire mandible is **U**-shaped in the two first-named genera, **V**-shaped in the others. The symphysis itself is almost horizontal, and shows considerable variation in its proportional length. Its ventral or outer surface is marked with a broad ridge, like that on the premaxilla, very well marked in *Dinornis*, less so in *Pachyornis*, *Mesopteryx*, and *Anomalopteryx*, and only just raised above the surface in *Emeus*.

On the inner surface of each ramus, 1–2 cm. in advance of the articular cup, is the *dental foramen* for the mandibular nerve; it perforates the bone, appearing externally at the hinder end of a deep groove along which the nerve runs, entering the ramus, between the two laminae of the dentary, at its anterior end. Two small foramina lie in the groove, one near its lower border, the other towards the anterior end of its dorsal border; they perforate the bone and probably transmit nerves to the tissues on the inner surface of the jaw.

Another pair of foramina, apparently for the symphyseal branches of the mandibular nerve, lie in the posterior edge of the symphysis, usually just in the re-entering angle between the rami. They generally lie side by side, occasionally one above another; in some cases they are united at their origin into a single foramen, and in one instance have moved forwards to near the anterior end of the symphysis.

*Emeus* has, of all genera, the stoutest and most coarsely built jaw, *Anomalopteryx* coming nearest to it in this respect. The mandible of *Dinornis*, in spite of its strong symphysis, has comparatively weak rami, but the most delicate lower jaw of all is that of *Mesopteryx casuarina*.

In young specimens the mandible readily divides into three parts: a symphyseal portion, containing the ankylosed dentaries and the splenials, which latter are separate in still younger skulls; and the posterior portions of the two rami, each containing the articular, angular, supra-angular, and coronary (fig. 7). None of the specimens I have seen show the latter group of bones in the separate condition, but in a young mandible of *Anomalopteryx didiformis* the outlines of the angular and supra-angular can be traced where they overlap the articular. The splenial is well shown in a mandible of *Emeus crassus*; it extends from about the level of the dental foramen forwards to within 4 mm. of the symphysis. Lastly, in the type specimen of *Dinornis torosus*, in which the splenial is absent, the articular is continued forwards into a cylindrical tube of bone lying immediately mesiad of the dental foramen and evidently representing the superficially ossified proximal end of Meckel's cartilage.

g. *The Hyoid.*

In the skull of *Emeus*, species  $\alpha$ , figured on Plate LVI., the posterior cornua of the hyoid—probably the only ossified parts—are present, as well as the larynx and anterior end of the trachea. They consist of gently curved rods of bone, 57 mm. long, 2 mm. in diameter, and expanded at both ends.

Mr. Booth, who found this skull, told Professor Hutton that he saw in the ear a delicate hair-like bone which he was unable to preserve; no doubt this was the columella auris.

## 4. A COMPARISON OF THE SKULLS OF THE DINORNITHIDÆ WITH THOSE OF THE OTHER RATITÆ.

The occipital region is usually less clearly marked off from the skull in the other Ratitæ, the lambdoidal ridge being comparatively faint: the fully adult *Apteryx australis* forms, however, an exception; in it the lambdoidal ridge is very strongly marked, and there is a distinct angulation between the roof and the hinder wall of the cranium. There is no indication of the anterior lambdoidal ridge, and although the median occipital region is swollen over the cerebellar fossa, the occipital crest is generally poorly developed or absent; it is most distinct in *Apteryx australis*. The supraforaminal ridge is obvious in all, and is continued to the angle of the paroccipital process; in *Apteryx* it is interrupted, just at the margin of the foramen magnum, by a notch. *Apteryx* is the only genus which resembles the Moas in its pedunculate occipital condyle, as also in the great breadth—in relation to height—of the entire occipital region. In having the plane of the occipital foramen vertical or nearly so the Dinornithidæ stand alone.

The roof of the cranium is more rounded in the other Ratitæ, and in all but *Apteryx* and *Casuarius* the parietal region slopes backwards instead of being nearly flat. As a consequence of this, the temporal fossa has a much stronger backward inclination in *Struthio*, *Rhea*, and *Dromæus*, and the postorbital process is nearly in the same transverse plane as the zygomatic instead of being well in advance of it. In this respect the Cassowary approaches very closely to the Moas.

Another very marked difference in the roof of the cranium is due to the relatively small size of the eyes in the Dinornithidæ. In the Ostrich, Emu, and Rhea, the width of the orbit from the postfrontal process to the lacrymal is about equal to the width of the cranium at the paroccipital processes; in *Casuarius galeatus* it is about four-fifths of the width, in the Moas not much more than half. Moreover, the interorbital region of the skull-roof in the Ostrich, Rhea, Emu, and Cassowary is narrow, while its preorbital region broadens out suddenly owing to the presence of large wing-like orbital processes to the lacrymals. In the Moas this projection is only represented by the comparatively small body of the lacrymal. In *Apteryx* there are no post or pre-orbital processes, and the skull-roof narrows gradually from the occipital to the nasal

region. *Struthio* is peculiar in having a forwardly-directed process, given off from the supraorbital ridge, which meets the lacrymal, enclosing a notch or foramen.

The nasals of the Dinornithidæ differ from those of all the other Ratitæ in the junction with one another of their posterior ends above the ethmoid, so that none of the latter appears on the surface. In the Ostrich, Rhea, Emu, and Kiwi a lozenge-shaped area of the ethmoid appears between the bases of the nasals; in the Cassowary the same arrangement obtains in the young birds (25) at the time of hatching, but in the adult the actual condition of things is hidden by the development of the crest.

The maxillary process of the nasal is well developed in *Struthio* and *Apteryx*, extremely small and delicate in *Dromæus*, absent in *Rhea* and (!) *Casuarius*. It is somewhat remarkable that the absence or vestigial nature of this process should be given as a general character of the Ratitæ by Garrod (4) and Fürbringer (3).

On the base of the skull of the other Ratitæ the basitemporal platform is not raised beyond the general level of the skull-floor to anything like the same extent as in the Moas, and the precondylar fossa is therefore comparatively shallow. It is best defined in *Apteryx*, in which also the mamillar processes are even longer proportionally than in the Dinornithidæ, while in the other genera they are considerably less developed, being fairly prominent in *Casuarius*, small in *Dromæus* and *Struthio*, and obsolete in *Rhea*.

The paroccipital notch may or may not be bridged over by bone. The vagus foramen lies in the notch in *Apteryx*, *Dromæus*, and *Casuarius*, mesiad of it—as in the Moas—in *Struthio* and *Rhea*. In the Australian genera the ventral edges of the Eustachian tubes are prominent and sometimes meet, converting the groove into a canal. In the Ostrich, Rhea, and Kiwi there are actual tubes, the closure of the groove being more complete in the two first-named genera than in *Apteryx*.

Another variable point is the extent to which the carotid canal is closed by bone and the resulting position of its external aperture. In the Ostrich, as in the Moa, the carotid foramen lies in or slightly in front of the paroccipital notch; in the Emu and Cassowary it is on the lateral surface of the basitemporal platform, immediately caudad of the Eustachian groove and laterad of the mamillar tuberosity; in *Rhea* it is in a similar position, but slightly further forward; and in *Apteryx* it is altogether in front of the mamillar tuberosity and fully visible from below.

The basiptyergoid processes are most dinornithic in *Apteryx* and *Dromæus*; in the other three genera they are proportionately longer and more slender. Between their bases the minute anterior basicranial fontanelle sometimes occurs in *Struthio*, *Rhea*, *Casuarius*, and *Dromæus*, but I have never seen any trace of it in the adult *Apteryx*. Amongst my specimens a young *Rhea* is the only one showing any sign of the posterior basicranial fontanelle.

The rostrum of the Ostrich is rounded below; that of all the other genera is keeled, except at the posterior end, the carination being most marked in *Apteryx*.

*Apteryx* is the only genus besides the Dinornithidæ which has a well-marked tympanic ledge; in all the others the cavity is bounded laterally only by the sharp-edged supratympanic ridge.

The quadrate facet on the roof of the tympanic cavity presents some interesting variations in the various genera (Plate LXII. figs. 65–70). In the Dinornithidæ, as we have seen, it is almost regularly oval, its inner third furnished by the pro-otic and exoccipital, its outer two-thirds by the squamosal (fig. 70). In *Struthio* (fig. 65), at about the middle of its anterior or mesial border, it is somewhat deeply notched; as all the specimens at my disposal were adults, the boundaries of the constituent bones could not be made out. A similar notch occurs in *Dromæus* (fig. 67) and *Casuarius* (fig. 68), and the facet is divisible into an inner or prootic-exoccipital and an outer or squamosal region; moreover, in the Cassowary the anterior edge of the external region of the facet is encroached upon by the alisphenoid, which thus takes its share in furnishing the articular surface. In *Rhea* (fig. 66) there is no notch, and the pro-otic portion of the facet appears in an adolescent skull as a wedge of bone near the posterior end of its anterior or mesial margin, and divided into a larger anterior and a smaller posterior portion; the posterior end of the facet is therefore formed mainly by the exoccipital: the alisphenoid enters into the facet as in *Casuarius*. Lastly, in *Apteryx* the facet (fig. 69) is distinctly divided into three portions—a mesial furnished partly by the pro-otic, partly by the exoccipital<sup>1</sup>, a postero-lateral by the squamosal, and an antero-lateral by the alisphenoid.

The anterior tympanic recess is large in all genera but *Apteryx*. The Ostrich differs from the others in having a large (*qu. venous?*) foramen excavated in the postero-ventral region of the pretemporal wing immediately cephalad of the Eustachian groove.

The zygomatic process is more slender in the other Ratitæ than in the Moas, and is directed outwards as well as forwards and downwards. The squamosal prominence is always obscure, and there is never more than the merest trace of the posterior tympanic fossa and ridge. In the Emu there is a distinct facet on the inner surface of the distal end of the zygomatic process for articulation with the quadrate. In *Rhea* the squamosal sends off, posterior to the zygoma, a process which passes forwards and is nearly met by a similar process from the pretemporal wing, the two together forming an almost complete ring round the posterior projection of the head of the quadrate.

The temporal fossa and ridge are far less strongly marked in the Ostrich, *Rhea*, Emu, and Cassowary than in the Moas, and in none of them is there any trace of the mid-temporal ridge. In *Apteryx*, on the other hand, the temporal fossa is very wide from

<sup>1</sup> In my paper on *Apteryx* (24) I incorrectly described this facet as being furnished exclusively by the pro-otic, but a renewed examination of stage M shows a distinct suture passing vertically across it and dividing off a posterior part furnished by the truncated end of a bar-like process of the exoccipital just above the fenestral recess.

before backwards, reaching well in advance of the optic foramen; the temporal ridge is strong, and there is a mid-temporal ridge at about the junction of the middle and posterior thirds of the fossa.

The comparative size of the orbit constitutes, as already remarked, one of the most striking differences between the Moas and Kiwis and the other Ratitæ. In the latter the orbits are separated from one another by a median vertical plate of bone, the interorbital septum, represented in the Dinornithidæ only by the wall between the presphenoid fossæ and wholly absent in *Apteryx*. In an adolescent skull of *Rhea* the posterior third of the septum is formed by the presphenoid, the anterior two thirds by the mesethmoid. There is thus produced an almost straight mesial wall to the orbit, passing above and behind into the arched upper and posterior wall, which is formed above by the orbital plate of the frontal, below by the alisphenoid. In the Dinornithidæ, there is no clear distinction between the mesial and the postero-dorsal wall of the orbit, the two passing insensibly into one another; the anterior part of the mesial wall is formed by the inferior aliethmoid, owing to the backward extension of the olfactory capsules between the eyes, and the presphenoid is limited to a small area below the optic foramen. In *Apteryx* the last trace of the interorbital septum disappears, the swollen aliethmoids reaching back to the optic foramen.

The optic foramina are close together in all the more typical Ratitæ, being separated from one another in front by the edge of the interorbital septum, which is very thin in all but *Struthio*; the adjacent foramina show, however, considerable variations. In the Ostrich (fig. 71) the oculomotor foramen (iii & vi) lies immediately behind the optic and is continued into the interior of the skull by a groove, into the floor of which the canal for the sixth nerve opens, the oculomotor and abducent nerves having therefore a common entrance into the orbit. The internal ophthalmic artery apparently goes out separately by the foramen marked *a*. The small foramen for the fourth nerve (iv) lies just above that for the third, and the orbitonasal foramen (v<sup>1</sup>) is an oblique passage just behind it. In a young specimen the foramina for the third, fourth, and sixth nerves are represented by an oblique cleft communicating with the optic foramen. The trigeminal foramen for the second and third divisions of the fifth nerve may be divided by a narrow vertical bony bar.

In *Rhea* (fig. 72) the oculomotor foramen (iii and vi) is immediately behind and below the optic, and the canal for the sixth opens just within its margin; below and in front of it is an equally large aperture (*a*), which probably transmits the internal ophthalmic artery. The oculomotor and pathetic nerves enter through very oblique foramina (iv, v<sup>1</sup>) in the usual positions. In *Dromæus* (fig. 73) the sixth nerve (vi) has a special foramen below the oculomotor (iii). In *Casuarinus* (fig. 74) the third nerve makes its exit through a notch (iii) in the posterior margin of the optic foramen, the sixth (vi) through a special foramen; a notch (*a*) in the ventral border of the optic foramen possibly transmits the internal ophthalmic artery. In *Apteryx* (fig. 75) there are

distinct orbitonasal, oculomotor, and abducent foramina, but the fourth nerve goes out through the optic foramen. Thus all the Australasian genera agree in having a distinct foramen for the sixth nerve; the Moas are peculiar in having the oculomotor, orbitonasal, and abducent foramina sunk in a fossa (fig. 76).

In the structure of the ethmoid *Apteryx* stands at one end of the series, the Dinornithidæ in an intermediate position, and the remaining Ratitæ at the other end. In the Moas, as we have seen, the lateral ethmoid extends backwards almost to the optic foramen, its posterior part consisting of the gently sloping inferior aliethmoid, which is continued in front into the obliquely set antorbital. In *Apteryx* the place of both these portions is taken by the shell-like aliethmoid, which extends from the optic foramen to the lacrymal, bulging outwards in its whole extent and undergoing a special dilatation immediately caudad of the lacrymal. In the remaining Ratitæ the olfactory cavity is not continued backwards behind the antorbital, the latter springing directly from the mesethmoid and passing outwards and forwards to the lacrymal. In *Struthio* and *Rhea* only the mesial portion of the antorbital is ossified, so that in the dry skull a considerable space is left between its outer edge and the lacrymal. In *Dromæus* and *Casuarius* the ossification extends to the lacrymal, and the dorsal portion of the bone is hollowed by a deep pit for the lacrymal gland. In *Struthio*, *Rhea*, and *Casuarius* the descending process of the lacrymal bone is merely notched for the lacrymal duct; in *Dromæus* and *Apteryx* it is perforated.

The postchoanal bar formed by the ventral border of the antorbital is most distinct in the Ostrich and Emu. The mesethmoid is perforated posteriorly, so as to place the olfactory chambers in communication, in the Ostrich, *Rhea*, and Emu, but not in the Cassowary and Kiwi. In the possession of the triangular process of the mesethmoid the Moas stand alone.

Leaving *Apteryx* aside, the chief difference between the Dinornithidæ and the other Ratitæ as regards the cranial cavity is the greater size of the mesencephalic fossæ in the latter. The pituitary fossa of the Moas is most nearly approached by that of *Struthio*, in which the thickness of the presphenoid gives rise to a broad optic platform, poorly marked in all the other genera. The cerebral fossæ are more pointed anteriorly in the other genera and are continued forwards into deep conical olfactory fossæ; in this point also it is the Ostrich which approaches most nearly to the Moas; its hemispheres are blunter and its olfactory lobes shorter than in the American and Austro-Malayan forms.

*Apteryx* agrees with the Dinornithidæ in the small size of the mesencephalic fossæ, but is quite peculiar in the great proportional size of the cerebral and olfactory fossæ. The hemispheres extend backwards over the cerebellum, the cerebellar fossa being therefore pushed backwards and the tentorial ridge made almost horizontal. Owing to the great size of the olfactory fossæ, the crista galli is nearly as long as the basis cranii from the dorsum sellæ to the occipital condyle.

The premaxilla has the usual structure in all. In the Ostrich alone the palatine

plates are quite vestigial<sup>1</sup>; in the other genera they extend backwards and articulate with the vomer: there is no vomerine process as in some of the Moas. In *Struthio*, *Rhea*, and *Dromæus* the body of the bone is very flat, but in *Casuarius* its median region is elevated into a strong arched keel, from which the nasal process proceeds, and there is a distinct prenarial septum. In *Apteryx* the form of the body is essentially similar: its height is equal to its breadth, and there is a short, thick prenarial septum. The unique form of the beak in this genus is due to the shortening of the body of the premaxilla and to the elongation of the region between the prenarial septum in front and the turbinals behind.

The maxilla shows a wide range of variation. In the Ostrich (Plate LXII. fig. 59) it is a flat bone divided posteriorly into palatine and jugal processes, and sending off from its mesial border an axe-head-shaped maxillo-palatine, which articulates by its thickened inner edge with a facet on the side of the vomer. The lateral half of this process is double, consisting of dorsal and ventral laminae so arranged as to enclose a wedge-shaped cavity, the antrum, open behind. In *Rhea* (fig. 60) the maxillo-palatine is a broad flat plate which gives off from its dorsal surface a nearly vertical, slender, ascending process, which is attached by an outer crus to the maxilla proper and by a long inner crus to the maxillo-palatine. Between the two crura is a small cavity opening behind, apparently the vestige of an antrum. In the Emu (fig. 61) the maxilla is narrow, except at its anterior end, where it broadens out into a maxillo-palatine having the form of a pocket, wide from side to side, narrow from above downwards, and opening behind along its whole width; this cavity is obviously the antrum, resembling pretty closely that of the majority of the Moas (fig. 63), but situated farther forwards. In *Casuarius galeatus* (fig. 62) the maxilla proper is still narrower, but the maxillo-palatine has the form of a long conical pouch, like a jelly-bag, its point directed forwards, dorsad of the palatine process of the premaxilla, and its base widely open behind. Lastly, in *Apteryx* the maxilla is a long flat bone and the maxillo-palatine is represented only by a narrow seam-like projection of its mesial border: there is no dorsal prolongation of the maxillo-palatine, the walls of the antrum being entirely membranous.

It is obvious that in the structure of the maxillo-palatine, upon which Huxley largely founded his classification of birds (10), the Dinornithidæ, with the exception of *Emeus*, approach most nearly to the Australian Ratitæ. Prof. Huxley makes no mention of the antrum, describing the maxillo-palatine of the Emu, Cassowary, Moa, and Kiwi as flat imperforate plates.

In the structure of the vomer it is *Apteryx* which comes nearest to the Dinornithidæ, that genus having a single vomer, deeply cleft posteriorly and ankylosed with the palatines and pterygoids. The maxillo-palatines touch it by a part of their thin mesial edges, but do not articulate with it. In *Casuarius* it has the same general form and

<sup>1</sup> In the skulls in the Otago University Museum, as also in Huxley's (10) and Selenka's (27) figures; but in my father's figures of advanced embryos (25) large palatine processes are shown.

relations, but is proportionally much longer and more slender; it articulates laterally with the maxillo-palatines. In *Dromæus* it is also forked behind, but its anterior end is expanded into a thin, flat plate, which articulates with the maxillo-palatine and is underlaid by the palatine process of the premaxilla. In *Rhea* it is deeply forked in front, each limb of the fork being underlaid by the corresponding palatine process of the premaxilla. In *Struthio* it is flattened anteriorly, and on each side presents a facet for articulation with the maxillo-palatine; although shorter than in the other Ratitæ, it is considerably longer in the specimens in the Otago Museum than in Huxley's figure, reaching as far forward as the anterior end of the nasals, and its forked posterior end being connected on each side by ligament with the corresponding palatine.

In the characters of the palatines also *Apteryx* is the nearest ally of the Dinornithidæ. In it they are short bones, about the same length as the vomer, and having much the same twist as was described above in the Moas. They are also expanded posteriorly, where they unite with the vomer and pterygoids, and are overlaid in front by the maxillo-palatines. Each is, however, clamped along its whole lateral edge by the long palatine plate of the maxilla, and does not reach so far forward as the palatine plate of the premaxilla. In *Struthio* the palatines are long, flat rods, their posterior ends expanded for union with the pterygoids, and their anterior ends passing ventrad of the maxillo-palatines and reaching nearly as far forward as the anterior end of the vomer. In *Rhea*, *Dromæus*, and *Casuaris* the palatines are short, thin plates, more or less curved, which pass from the pterygoids behind outwards and forwards to the palatine processes of the maxillæ; they are not ankylosed with either the vomer or the pterygoids in the *Rhea* and *Emus* in the Otago Museum, but are firmly united to both in *Casuaris galeatus*.

The pterygoid is a rod-shaped bone in all but *Struthio*, in which it is expanded in front. Without the opportunity of examining good specimens of adolescent skulls, it is impossible to enter into a detailed account of the modifications of this bone in the various genera.

In all the other Ratitæ except *Apteryx*, the head of the quadrate resembles that of the Moas, bearing an elongated oval articular surface broader at its lateral than at its mesial end, and showing no trace of division into two facets. In *Apteryx*, as I have pointed out elsewhere (24), the quadrate is practically double-headed; the details of its form are, however, subject to considerable variation. In an adult *A. oweni*, the mesial end of the head bears a very distinct, nearly circular surface for articulation with the facet furnished by the pro-otic and exoccipital (Plate LXII. fig. 69); passing outwards from this it narrows considerably and at its lateral end is greatly expanded, forming a surface, very convex from before backwards, for articulation with the concave surface furnished by the squamosal and alisphenoid. In an adult *A. australis* there is a perfectly distinct facet on the anterior surface of the outer end of the head for articulation with the alisphenoid; in another specimen of the same species the usually distinct



facets are so close together that the head is virtually single. In *Dromæus* alone there is a facet on the base of the otic process, just anterior to the lateral ridge, for articulation with the surface already mentioned on the zygomatic process.

It was pointed out that in all the Moas there is a pneumatic foramen on the mesial surface of the otic process, while a second foramen occurs on the posterior surface in certain instances. The only other case in which I have found the mesial foramen is that of *Struthio*, in which there is an extremely small aperture in the corresponding position, looking, however, more like a vascular or nervous than a pneumatic foramen. The posterior foramen is of moderate size in the Emu and Cassowary, and is situated near the base of the otic process; in the Ostrich it is higher up and proportionally smaller; in *Rhea* it is on the posterior margin of the head, immediately below the articular surface. In the adult Kiwi there are several small foramina in the same position, but at the time of hatching there is a single large foramen in the same position as in *Anomalopteryx*. The otic process in *Apteryx* is peculiar for sending off small mesial and lateral processes just below the head.

In the orbital process the Cassowary presents the closest resemblance to the Moas, but is more compressed and blunter at the apex than in the latter. In the Emu it is blunt and thick, and takes a more nearly horizontal direction than usual. In the Ostrich it is also compressed and the apex truncated. In *Rhea* it is extremely short and blunt. In *Apteryx* it is unusually long and strongly compressed, so as to have the form of a thin vertical plate with a thickened ventral rim.

In the mandible the internal angular process and ridge are best developed in *Apteryx* and to a less degree in *Rhea*, but are also well marked in *Dromæus* and *Casuarius*. The posterior angular process and ridge are large in the Ostrich, Emu, and Cassowary, obscure in the Rhea and Kiwi. In the general form of the jaw the Moas come nearest to the Cassowary, in which the rami are moderately stout and slightly deflected distally. The comparative weakness of the mandible in the other large Ratitæ is very marked, and in *Apteryx* the immense length of the symphysis separates it at once from all the other genera; in the strength and solidity of the jaw and in the size of the coronoid process *Apteryx australis* is, however, the only form which approaches the Dinornithidæ.

##### 5. MEASUREMENTS OF THE SKULLS OF THE RATITÆ.

Measurements of the skulls of Moas are given by Owen, Haast (5), and Hutton (9). It is, however, desirable for purposes of comparison that a more complete set of measurements should be given, and that the precise way in which they are taken should be accurately defined.

Owing to the early ankylosis of the bones of the cranium, it is impossible to determine

such points as the bregma, lambda, pterion, &c., and as the main object of the measurements is to serve as a means of identification, it is important to select standard points which can be readily made use of in any fairly well preserved skull. Moreover, as a matter of convenience it is desirable that the measurements should be made with some common and readily procurable instrument. I have therefore taken them all with callipers, so that in the case of curved surfaces, such as the roof of the skull, the chord is given, not the arc. All measurements are given in millimetres; the standard being so small, fractions are neglected.

The measurements given are defined as follows:—

1. *Total length of skull*: from centre of occipital condyle to anterior extremity of premaxilla.
2. *Length of cranio-facial axis*: from centre of occipital condyle to tip of rostrum.
3. *Length of basis cranii*: from centre of occipital condyle to base of rostrum, *i. e.* to the centre of a line joining the anterior ends of the bases of the basi-ptyergoid processes.

It will be seen that the expression *basis cranii* is here used in a special sense: the dimension chosen nearly corresponds with the length of the base of the skull as measured from the condyle to the preoptic ridge. The entire basicranial axis, *i. e.* from condyle to junction of presphenoid and ethmoid, can only be got at by bisecting the skull, and even then, owing to the ankylosis of the bones named, cannot be determined with precision.

4. *Length of roof of cranium*: from the centre of the supraforaminal ridge to the middle of a line joining the anterior borders of the lacrymals (preorbital processes).

Hutton takes the naso-frontal suture as the anterior boundary of this line, but in old skulls the suture is obliterated, and the posterior end of the premaxillary groove which coincides with it is frequently obscure.

5. *Width of cranium at paroccipital processes*: the length of a straight line joining the dorsal ends of the paroccipital processes, immediately below the supratympanic ridges. Occasionally there is a sort of step where the supratympanic ridge passes into the paroccipital process; the measurement should then be taken below the step.
6. *Width of cranium at squamosal prominences*: length of a straight line joining the most projecting portions of the squamosals.
7. *Width of cranium at temporal fossæ*: length of the longest straight line joining the right and left temporal fossæ.

This measurement gives an indication of the width of the brain-case, the walls of the skull being much thinner at the temporal region than elsewhere.

8. *Width of cranium at postorbital processes*: length of a straight line joining the most prominent parts of the right and left postorbital processes.

9. *Width of cranium at preorbital processes*: length of a straight line joining the posterior borders of the lacrymals.
10. *Distance between temporal ridges*: length of the shortest straight line joining the right and left temporal ridges.
11. *Height of cranium*: length of a perpendicular from the highest part of the cranial roof to the basitemporal platform.
12. *Width of tympanic cavity*: length of the longest horizontal straight line joining the posterior temporal ridge and the edge of the paroccipital process.
13. *Width of temporal fossa*: length of the longest horizontal straight line joining the anterior and posterior limbs of the temporal ridge, above the junction with the latter of the posterior temporal ridge.
14. *Width of orbit*: length of the longest horizontal straight line joining the posterior border of the lacrymal and the anterior border of the postorbital process.
15. *Distance between optic foramina*: length of a straight line joining the lower borders of the foramina.
16. *Greatest length of premaxilla*: from apex of body in a straight line to posterior end of nasal process.
17. *Length of premaxilla to end of maxillary process*: from apex of body in a straight line.
18. *Length of body of premaxilla*: length of a straight line between apex and posterior border of prenasal septum.
19. *Width of body of premaxilla*: length of a straight line between the right and left alveolar borders at the level of the posterior edge of the prenasal septum.
20. *Length of maxillo-jugal arch*: the greatest length in a straight line.
21. *Length of vomer*: the greatest length in a straight line.
22. *Length of palatine*: the greatest length in a straight line.
23. *Length of pterygoid*: the greatest length in a straight line.
24. *Length of quadrate*: length of a straight line from the articular surface of the head to the most prominent part of the internal condyle.
25. *Length of mandibular ramus*: from middle of anterior border of symphysis to extremity of posterior angular process.
26. *Greatest height of mandible*: length of a perpendicular from the coronoid process to the ventral border.
27. *Least height of mandible*: a similar measurement of the anterior part of the ramus a short distance posterior to the symphysis.
28. *Length of mandibular symphysis*: length of a straight line passing from the middle of the anterior to the middle of the posterior border of the symphysis.
29. *Width of mandibular symphysis*: length of a straight line between the right and left alveolar borders at the level of the posterior edge of the symphysis.

Absolute measurements, as defined on pp. 406–407, of the various species examined, are given in Table A.

But, as an aid to the determination and definition of the genera, the proportions of the skull are more important than absolute measurements, a fact recognized by Hutton, who gives (9, p. 107) the proportion between length and breadth, and between breadth and height, in his eight genera. I have come to the conclusion, however, that a more convenient method is to take as a standard the length of the basis cranii as defined above (p. 406, § 3), and to express various other important dimensions as percentages. In this way a number of indices are obtained, many of which are of great importance in the definition of the genera: they are given in Table B.

Table C gives what may be called the temporal index; *i. e.* the width of the cranium at the temporal fossa as compared with the distance between the right and left temporal ridges.

## 6. SUMMARY OF THE CRANIAL CHARACTERS OF THE RATITÆ.

### STRUTHIO.

Occipital plane inclined backwards; occipital condyle sessile; a broad occipital crest. Length of cranial roof nearly three times that of basis cranii.

Width at paroccipital processes about one and a half times length of basis cranii.

Width at squamosals about double length of basis cranii.

Height of cranium nearly double length of basis cranii.

Temporal fossæ continued mesiad on to parietal region; distances between temporal ridges about one third less than width of cranium at temporal fossæ.

Zygomatic process outstanding; no squamosal prominence.

Width of orbit about equal to breadth of cranium at paroccipital processes, or one and a half times length of basis cranii; interorbital septum present; a projecting supraorbital ledge notched in front and produced behind into a short blunt, post-orbital process.

Lacrymal produced into a broad, backwardly-directed orbital process, and a strong descending process passing mesiad of the lacrymal duct.

Nasal has a well-developed maxillary process, and is separated posteriorly from its fellow by an interval in which the mesethmoid appears.

Ossified portion of antorbital does not extend outwards to lacrymal.

Premaxilla weak; body flat, having no prenasal septum; no palatine processes; width of body about equal to length of basis cranii.

Maxilla narrow; extends forwards to body of premaxilla; maxillo-palatine a hatchet-shaped process given off from its mesial border; antrum small.

No.	Sex.	EMEUS				APTERYX	DROMEUS	CASARIUS	STRUTHIO	RHEA
		Species β. 1 specimen.	Species α.	<i>crassus</i> .	Species γ. 1 specimen.	<i>australis</i> .	<i>novæ-hollandiæ</i> .	<i>galeatus</i> .	<i>camelus</i> .	<i>americana</i> .
1.	Total length	233	122	134-140	..	186	150	170	188	173
2.	Length of culmen	96?	..	110	102-112	..	90	76	?95	122
3.	Length of bill	31	?35	37	37-41	40	18	29	33	30
4.	Length of cere	73	71	73-85	80-94	75	49	80	?85	93
5.	Width of cere	54	54	54-59	61-72	?67	39	43	53	48
6.	Width of cere	63	70	70-73	76-80	75	33	57	60	53
7.	Width of cere	44	47	45-51	50-52	52	30	51	54	45
8.	Width of cere	72	80	79-85	84-86	80	..	66	70	62
9.	Width of cere	41	39	37-43	40-45	47	16	34	31	35
10.	Distance between nostrils	26	42	42-49	41-50	50	30	50	54	41
11.	Height of cere	44	43	45-50	46-50	48	26	47	?55	62
12.	Width of tip of bill	15	20	19-24	17-21	20	9	21	24	22
13.	Width of tip of bill	26	20	16-23	16-28	17	15	13	20	20
14.	Width of orbit	29	30	30-31	29-33	32	..	45	41	53
15.	Distance between eyes	9	12	9-11	10	12	4	2	2	9
16.	Greatest length of tarsus	68	..	72	80-88	..	144	80	?90	109
17.	Length of phalanx	56	..	54	60-66	..	?120	71	93	115
18.	Length of bill	28	..	28-31	27-33	..	5	23	24	28
19.	Width of bill	22	..	28-31	37-41	..	4	25	14	35
20.	Length of middle toe	70?	..	67-72	69-73	..	?77	87	127	139
21.	Length of ventral toe	..	..	46	49	..	36	74	86	76
22.	Length of palmar toe	..	..	43	45	..	?31	32	?41	?87
23.	Length of palmar toe	..	..	21-25	23-26	..	?20	?32	?32	?40
24.	Length of middle toe	32?	..	35	36-40	..	12	25	26	31
25.	Length of middle toe	20	..	111	122-127	..	183	141	165	184
26.	Greatest height of tarsus	20	..	20-21	20-22	..	9	9	12	17
27.	Least height of tarsus	2	..	12-13	12-13	..	7	8	8	8
28.	Length of middle toe	23?	..	14-19	16-20	..	101	21	22	11
29.	Width of middle toe	21	..	28-31	35-38	..	12	26	12	24



Table A.—ABSOLUTE MEASUREMENTS OF THE SKULLS OF RAHILE (*in millimetres*)

	Males					Females					Young					Total
	1 specimen	4 specimens	2 specimens	3 specimens	1 specimen	7 specimens	2 specimens	2 specimens	1 specimen	1 specimen	1 specimen	1 specimen	1 specimen	1 specimen	1 specimen	
1. Length of skull	226	105-265	1165-175	156		132	141	135-148	141	122	156-149	186	159	175	188	174
2. Length of rostrum to base		2135	2	2	199			111	103-116	96	119	102-112	91	78	95	102
3. Length of orbit		46	38-40	37-41	41	38	27-35	32	33	32-35	31	35	37	37-41	39	39
4. Length of cranial roof	118	105	94-97	90-98	94	85	70-81	59	83	85-87	73	74	78-85	80-91	75	79
5. Width of cranium at paroccipital processes	93	90-105	81-83	82-78	84	57	45-55	44	59	59-62	54	54	44-59	61-72	57	60
6. Width of cranium at squamosal promontories	118	104-115	94	82-92	85	74	58-67	72	76	64	70-74	65	70	70-74	76-80	75
7. Width of cranium at temporal fossae	73	65-82	50-63	52-57	55	50	43-50	41	48	47	42-44	44	47	45-71	50-52	52
8. Width of cranium at postorbital processes	91	129-136	105-110	92-96	92		77	61	60	69	77-82	72	80	70-85	84-86	80
9. Width of cranium at preorbital processes		84	80	56-67	60	54	47-42	38	54	40	47-49	41	39	37-44	40-45	47
10. Distance between temporal ridges	58	46-59	40-46	37-44	45	39	30-49	37	41	41	27-34	26	42	42-49	41-50	39
11. Height of zygoma	49	50-61	48	51-55	52	51	41-44	45	47	44	44-45	44	44	45-50	46-50	48
12. Width of tympanic cavity	25	25-29	22-25	23-30	25	22	17-21	18	21	17	16	15	20	18-24	17-21	20
13. Width of temporal fossa	2	8-17	23-31	26-32	28	20	13-17	16	23	14	18-24	26	20	16-24	16-28	17
14. Width of orbit		35	34-38	32-37	37	33	28-31	24	32	26	32	29	30	30-34	29-33	32
15. Distance between optic foramina		30-35	26-30	15-21	14	14	8-11	9	14	9	9-10	9	12	9-11	10	2
16. Greatest length of premaxilla	157	110-129	108-110	81-90	73	74	63-74	64	84	73-76	68	72	80-88	74	80	80
17. Length of premaxilla to end of maxillary process		97	785-93	68-82	70	63	50-63	64	64	60-62	56	54	60-66	72	71	64
18. Length of body of premaxilla	82	60	440-92	37-43	50	43	31-36	28	43	31-36	28	28-31	27-33	5	24	24
19. Width of body of premaxilla	11	5-71	55-57	30-35	24	27	30-35	22	27	30-35	22	28-31	37-41	4	5	14
20. Length of maxillo-jugal arch		63		94	70	74	78	73	77	72	69-73	77	87	87	130	92
21. Length of palatine					54				54			46	49	46	74	68
22. Length of pterygoid					12				43			43	45	41	42	44
23. Length of quadrate		53	41	41	45	44	35	32	35	32	35	35	34	42	35	26
24. Length of mandibular ramus	211	179-208	164-164	141-155	117	88	125	127-135	129	111	122-127	183	141	165	184	173
25. Greatest height of mandible	24	25-28	20-23	20-21	16	12	17	19-21	20	20-21	20-22	17	17	17	17	12
26. Least height of mandible	9	16-20	13-19	11-12	8	7	10	11-12	12	12-13	12-13	7	8	8	8	9
27. Length of mandibular symphysis	27	27-31	22-23	17-20	14	10	16	16-20	20	14-15	13-20	19	21	20	11	27
28. Width of mandibular symphysis	30	1-52	35-42	24-25	21	14	21	23-25	21	28-31	25-28	12	26	12	24	25





tages of length of basis cranii).

[To face p. 408.

	APTERYX	DROMÆUS	CASUARIUS	STRUTHIO	RHEA
<i>crassus.</i>	<i>australis.</i>	<i>novæ-hollandiæ.</i>	<i>galeatus.</i>	<i>camelus.</i>	<i>americana.</i>
100	100	100	100	100	100
204-247	272	275	? 293	281	293
148-180	216	148	182	151	160
185-216	183	196	206	196	176
121-137	166	175	186	160	150
121-132	144	162	? 189	187	156
51-70	83	44	68	60	70
78-89	..	155	141	160	153
200-237	800	275	? 310	330	316
67-89	27	79	82	84	96
100-110	22	86	48	106	80
132	200	255	296	230	206
121	171	111	? 141	263	96
309-335	1016	486	568	557	576
92-100	66	89	41	72	83

	APTERYX	DROMEUS	CASUARIUS	STRUTHIO	RHEA
<i>crassus.</i>	<i>australis.</i>	<i>novæ-hollandiæ.</i>	<i>galeatus.</i>	<i>camelus.</i>	<i>americanus.</i>
100	100	100	100	100	100
100-120	100	100	110	130	140







Vomer more than double length of basis cranii; flattened in front, trough-like and forked behind; articulates with maxillo-palatines; connected with palatines by ligament.

Palatine slender; expanded posteriorly and ankylosed to pterygoid; about two and a half times length of basis cranii.

Mandible weak; symphysis flat, with very obscure median ventral ridge.

#### RHEA.

Occipital plane inclined backwards; occipital condyle sessile; occipital crest obscure.

Length of cranial roof nearly three times that of basis cranii.

Width at paroccipital processes about one and a half times length of basis cranii.

Width at squamosals less than double length of basis cranii.

Height of cranium about one and a half times length of basis cranii.

Temporal fossæ continued on to parietal region; distance between temporal ridges about one third less than width of cranium at temporal fossæ.

Zygomatic process slender, outstanding; no squamosal prominence.

Width of orbit about equal to width of cranium at paroccipital processes, or one and a half times length of basis cranii; interorbital septum present; supraorbital ledge narrow, not notched in front, produced behind into short blunt post-orbital processes.

Lacrymal produced into pointed, backwardly-directed orbital process and curved descending process which passes mesiad of lacrymal duct.

No maxillary process to nasal; mesethmoid appears on dorsal surface between posterior ends of nasals.

Antorbital quite unossified in the skulls examined.

Premaxilla weak; body flat, with no prenasal septum; long palatine processes; width of body rather less than length of basis cranii.

Maxilla broad; anterior end does not reach to body of premaxilla; maxillo-palatine a broad, thin plate, perforated by small and variable apertures, and produced dorsad into a narrow vertical plate, at the base of which is a vestige of the antrum.

Vomer about double length of basis cranii; flattened and deeply forked in front, carinate and deeply forked behind; not ankylosed to palatines.

Palatine a broad, thin, curved plate, not ankylosed to pterygoid, and shorter than basis cranii.

Mandible weak; symphysis flat, with a median ventral ridge.

## DROMLEUS.

- Occipital plane inclined backwards; occipital condyle sessile; occipital crest obscure.  
 Length of cranial roof less than three times length of basis cranii.  
 Width at paroccipital processes less than one and a half times length of basis cranii.  
 Width at squamosals nearly twice length of basis cranii.  
 Height of cranium about one and a half times length of basis cranii.  
 Temporal fossa nearly vertical; distance between temporal ridges equal to width of cranium at temporal fossæ.  
 Zygomatic process strong and outstanding; bears facet for quadrate on the inner surface of its distal end; no squamosal prominence.  
 Width of orbit rather greater than width of cranium at paroccipital processes, and about one and a half times length of basis cranii; interorbital septum present; supraorbital ledge narrow, not notched in front, produced behind into a short postorbital process.  
 Lacrymal produced into a pointed, backwardly-directed orbital process, and a slender descending process, which is perforated for the lacrymal duct.  
 Antorbital well ossified and ankylosed laterad with the descending process of the lacrymal; a deep Harderian fossa.  
 Maxillary process of nasal vestigial; mesethmoid appears dorsally between posterior ends of nasals.  
 Premaxilla weak; body flat, with a very short prenasal septum; palatine processes long, width of body rather less than length of basis cranii.  
 Maxilla rather broad; anterior end does not reach to body of premaxilla; maxillo-palatine thin and pocket-like, containing a wide antrum.  
 Vomer nearly two and a half times length of basis cranii; broad, flat, and longitudinally grooved in front, narrow and deeply forked behind; ankylosed to pterygoids.  
 Palatine a thin, oblique plate, somewhat longer than basis cranii, articulating in front with maxilla and behind with pterygoid.  
 Mandible weak; symphysis flat with a narrow ventral ridge.

## CASUARIUS.

- Occipital plane inclined backwards; occipital condyle sessile; occipital crest obscure.  
 Cranial roof produced into a large crest; nearly three times length of basis cranii.  
 Width at paroccipital processes nearly double length of basis cranii.  
 Width at squamosals double length of basis cranii.  
 Height of cranium, not counting crest, nearly double length of basis cranii.

Temporal fossa nearly vertical; distance between temporal ridges about equal to width of cranium at temporal fossæ.

Zygomatic process narrow and outstanding; no squamosal prominence.

Width of orbit considerably less than width of cranium at paroccipital processes, and about one and a half times length of basis cranii; interorbital septum present; supraorbital ledge continued into cranial crest and produced behind into a broad, nearly vertical, postorbital process.

Orbital process of lacrymal united with cranial crest, only its posterior end projecting as a short, backwardly-directed process; descending process notched for lacrymal duct and sending off, ventrad of the latter, a short upwardly-directed process from its lateral margin, which partly converts the notch into a foramen.

Antorbital well ossified and ankylosed laterad with descending process of lacrymal; a deep Harderian fossa.

No descending process to nasal; the specimen examined does not show whether the mesethmoid is covered by the nasals, but it appears to be so<sup>1</sup>.

Premaxilla strong; body high and strongly ridged, with a distinct prenasal septum; narrow palatine processes; width of body about half length of basis cranii.

Maxilla reaches nearly as far forward as prenasal septum; maxillo-palatine an elongated cone with the apex directed forwards, and contains a spacious antrum opening behind by a wide aperture.

Vomer nearly three times length of basis cranii; flattened and obscurely grooved in front, deeply forked behind; ankylosed to palatines and pterygoids.

Palatine a short oblique plate, nearly one and a half times length of basis cranii, articulating anteriorly with the maxilla and ankylosed posteriorly with the vomer and pterygoid.

Mandible weak; symphysis narrow, pointed, and keeled below.

#### APTERYX.

Occipital plane inclined at an angle of 45° to the basis cranii; occipital condyle pedunculated; occipital crest variable.

Length of cranial roof less than three times that of basis cranii.

Mamillar processes very large and prominent.

Width at paroccipital processes about double length of basis cranii.

Width at squamosals nearly double length of basis cranii.

Height of cranium less than one and a half times length of basis cranii.

Temporal fossa very wide and nearly vertical; distance between temporal ridges equal to width of cranium at temporal fossæ.

<sup>1</sup> See, however, 25, p. 428.

- Zygomatic process directed forwards and strongly compressed; no squamosal prominence.
- Orbit small and ill-defined; no interorbital septum, supraorbital ledge, or post-orbital process.
- Lacrymal ankylosed to aliethmoid and perforated for lacrymal duct; no orbital process.
- Antorbital not clearly marked off from rest of aliethmoid, which is strongly convex, completely ossified, and extends backwards to the optic foramen.
- Nasal has maxillary process ankylosed to lacrymal; mesethmoid appears dorsally between posterior ends of nasals, but complete ankylosis of the bones in this region takes place in the adult.
- Premaxilla strong and greatly elongated; body short but high, with a very short prenasal septum; narrow palatine processes; width of body not more than one-fifth length of basis cranii.
- Maxilla broad and flat; articulates in front with maxillary and palatine processes of premaxilla; maxillo-palatine represented by the thin mesial border of the bone; no bony antrum.
- Vomer about twice length of basis cranii; flattened and narrow in front; broad, keeled, and deeply cleft behind; ankylosed to palatines and pterygoids.
- Palatine a thin, twisted plate with pedate posterior end; about one and three quarters length of basis cranii; ankylosed in front and by its entire outer border to maxilla and behind to vomer and pterygoid.
- Mandible strong; symphysis occupies more than half its length, narrow, strongly keeled below.

#### DINORNITHIDÆ.

- Occipital plane vertical or very slightly inclined backwards or forwards; occipital condyle pedunculate; occipital crest variable.
- Length of cranial roof from two to two and a half times length of basis cranii.
- Mamillar tuberosities usually prominent; basitemporal platform always well defined and separated from occipital condyle by a deep precondylar fossa.
- Width at paroccipital processes from less than one and a half to more than twice length of basis cranii.
- Width at squamosals from about one and three quarters to two and a half times length of basis cranii.
- Height of cranium about one and a quarter times length of basis cranii.
- Temporal fossa extends mesiad to a greater or less extent on to parietal region; distance between temporal ridges varies from about width of cranium at temporal fossæ to half that width.



Zygomatic process short, pointed, and nearly parallel to median plane; auditory region of skull produced into a strong squamosal prominence.

Width of orbit about half width of cranium at paroccipital processes, and almost invariably less than length of basis cranii; interorbital septum absent or greatly reduced; a broad supraorbital ledge, produced behind into a strong, broad, post-orbital process.

Lacrymal ankylosed with frontal, forming a preorbital process; no orbital process; a descending process ankylosed with outer border of antorbital and notched or perforated for lacrymal duct.

Mesethmoid produced into paired horizontal triangular processes.

Antorbital well ossified; ankylosed to descending process of lacrymal; perforated dorsally by a supraorbital fenestra of variable size.

Nasal either has a slender maxillary process, or there is a distinct maxillo-nasal bone; meets its fellow of the opposite side in the middle line above the ethmoid, so that the latter does not appear on the dorsal surface; premaxillary groove on upper surface of nasals extends backwards to or beyond naso-frontal suture.

Premaxilla strong; body more or less elevated, and with a distinct premaxillary septum; palatine processes broad and produced into more or less definite vomerine processes; width of body always more than half and sometimes one and a half times length of basis cranii.

Maxilla short and narrow; maxillo-palatine a short, flat plate, produced dorsad either into an irregular shell of bone containing a large antrum, or into a thick, oblique plate, containing no, or but little, trace of the antrum.

Vomer less than one and a half times length of basis cranii; consists of thin paired plates meeting each other ventrad in an acute dihedral angle, and either quite free or partially ankylosed with one another in front; firmly ankylosed behind, in fully adult specimens, with palatines and pterygoids.

Palatine a thin twisted plate, about one and a fifth times length of basis cranii; pedate posterior end produced into short mesial vomerine process; articulates at anterior end with maxilla, and posteriorly with vomer and pterygoid, with which, in fully adult specimens, it becomes ankylosed.

Mandible very strong; symphysis short, more or less flattened and ridged below; distal end more or less deflected downwards.

#### 7. THE CLASSIFICATION OF THE DINORNITHIDÆ.

At an early period of his investigations—in 1846—Owen was led to the conclusion that the differences between certain of the Moas were of more than specific value, and instituted the genus *Palapteryx* for the reception of species (*ingens* and *dromioides*) in which the hallux was present. Further investigations, however, convinced him that the retention of a purely vestigial structure was not, even if constant, of sufficient

importance to distinguish a genus, and he therefore returned to his earlier practice of placing all the species in the single genus *Dinornis*.

Reichenbach (26) was the first, in 1850, systematically to divide the family into genera, proceeding upon the simple plan of erecting into a genus each of the seven species known to him. His material must necessarily have been very imperfect, and two of his genera (*Moa* and *Movia*) are undoubtedly synonyms of a third (*Dinornis*).

Von Haast (6) was the next, in 1873, to attack the problem. He divided the Moas into two families, each containing two genera; but the characters upon which the definition of the families was based were shown by Hutton (8) to be quite unreliable; many of the generic characters are incorrect and others inconstant; and in at least three instances, in the Canterbury Museum, the skull of one species was assigned to the skeleton of another. Moreover, the brief account of the proposed classification, given in a Presidential address, was never followed up by a detailed statement, and was unsupported by measurements or figures. Under these circumstances the wide acceptance of Von Haast's views is rather remarkable: they are adopted without remark by Wallace (28) in 1876, and with a qualifying note by Newton (14) in 1885; and Lydekker (15) in 1889 discusses the question and comes to the conclusion that the distinction between the two families is a valid one,—a decision which this author's later enquiries (12) have led him to reverse. Fürbringer (3) has a long discussion in his usual judicial manner, and concludes that there is no evidence for the establishment of more than one family.

Last year two classifications were propounded, unfortunately independently: one in England by Lydekker (12), the other by Hutton in New Zealand (9). Both agree in recognizing only a single family, which Lydekker divides into five genera—or four if *Megalapteryx* be excluded—and nineteen species, Hutton into seven genera and twenty-six species. In both schemes the definitions of certain of the genera are wanting in exactness, especially as regards the skull, which Prof. Hutton rightly considers the most important part of the skeleton for generic distinctions. Mr. Lydekker supplies valuable corrections of many of Owen's determinations, but he has only examined the British Museum collection, which is evidently deficient in many important respects. Prof. Hutton, on the other hand, besides examining the large public and private collections in New Zealand, has himself collected Moa-bones in various parts of the colony, and was the first to recognize the important bearing of the geographical distribution of the species.

The table on p. 415 gives a comparison of the arrangement of the Dinornithidæ by the four authors referred to with that adopted in the present paper.

It will be seen that Haast, Lydekker, and Hutton are all agreed as to the limits of *Dinornis*, and that Reichenbach's *Anomalopteryx* corresponds with the similarly-named genus of Hutton and with Haast's *Meionornis*. Lydekker's *Anomalopteryx* includes four of Hutton's genera and part of a fifth. Hutton's *Euryapteryx* includes species from two of Haast's and from two of Lydekker's genera, and so on.

REICHENBACH, 1850.	VON HAAST, 1873.	LYDEKKER, 1891.	HUTTON, 1891.	PARKER, 1892.
	<i>Dinornis</i> maximus.	<i>Dinornis</i> maximus.	<i>Dinornis</i> altus. maximus. excelsus. validus. giganteus. firmus.	<i>Dinornis</i> maximus.
<i>Moa</i> giganteus.		novæ-zealandiæ.	robustus. ingens. potens. gracilis. torosus. struthioides.	robustus. potens (?). torosus. species a.
<i>Movia</i> ingens.	robustus. ingens.			
<i>Dinornis</i> struthioides.	gracilis. struthioides.	gracilis. struthioides.		
		<i>Anomalopteryx</i> dromioides.	<i>Palapteryx</i> plena. dromioides.	
<i>Anomalopteryx</i> didiformis.	<i>Meionornis</i> didiformis.	didiformis. parva.	<i>Anomalopteryx</i> didiformis. antiqua.	<i>Anomalopteryx</i> didiformis. parva (?).
<i>Cela</i> curta.		geranoides. curta. oweni. didina.	<i>Cela</i> geranoides. curta. <i>Mesopteryx</i> didina.	<i>Mesopteryx</i> species a. species β. species γ.
<i>Syornis</i> casuarinus.	casuarinus.	casuarina.	<i>Syornis</i> casuarinus.	casuarina.
<i>Emeus</i> crassus.	<i>Euryapteryx</i> rheides.  gravis.	<i>Emeus</i> crassus.  gravipes.	rheides. crassus.  <i>Euryapteryx</i> gravis.	<i>Emeus</i> crassus. species a. " β. " γ.
	<i>Palapteryx</i> elephantopus.	<i>Pachyornis</i> elephantopus. immanis. species a. " b.	ponderosa. elephantopus. pygmaea.	<i>Pachyornis</i> species a. elephantopus. species β. " γ. " a. " b.

My own observations have led me to the following conclusions, which, it must be remembered, are founded mainly upon a study of the skull, and take no cognizance of several of Hutton's and of one or two of Lydekker's species:—

1. The tall, comparatively slender-limbed forms, with broad skull and long, wide,

deflected beak, constitute a very natural and highly specialized group. It may be called the *maximus*-group, and, so far as I can make out, includes all the species placed by Haast, Lydekker, and Hutton in the genus *Dinornis*, which name should therefore be retained.

2. A second highly specialized or culminating group is constituted by heavy-limbed forms with strongly-built narrow skull, short broad beak, and stout mandible. This may be called the *crassus*-group: its type species is also the type of Lydekker's *Emeus*. I adopt this name.

3. The remaining species together form a comparatively generalized group, including forms of small or moderate height and of varying bulk, having narrow skulls and pointed beaks. This assemblage is divisible into three subdivisions:—

*a.* The *elephantopus*-group, characterized by a larger and relatively broader cranium than is possessed by either of the following groups, large temporal fossæ, and a wide V-shaped mandible. It corresponds with Lydekker's *Pachyornis* and with Haast's *Palapteryx*, and is placed under *Euryapteryx* by Hutton. The name *Pachyornis* should be retained, *Palapteryx* having been wrongly applied by Haast.

*b.* The *casuarina*-group, so-called from its type species. The skull resembles that of the *elephantopus*-group in general features, but is smaller and more delicate, and has considerably smaller temporal fossæ. This section includes Hutton's *Mesopteryx* and *Cela*, with part of *Syornis*; it corresponds with Haast's *Meionornis*, with Reichenbach's *Syornis*, and with Lydekker's typical group of *Anomalopteryx*. *Casuarinus* being the type species, Reichenbach's name has priority, but, as Lydekker has shown, it clashes with *Synornis* of Hodgson. The group is certainly not congeneric with either the preceding or the following one, and I therefore adopt Hutton's name *Mesopteryx*, the type species of which (*didina*) is here considered to be a variety of *casuarina*<sup>1</sup>.

*c.* The *didiformis*-group, in which *parva*, if really distinct, should be included. It is characterized by an unusually straight beak and immense temporal fossæ. This section corresponds with *Anomalopteryx* of Reichenbach and Hutton, doubtfully with Haast's *Meionornis*, and with Lydekker's Celine group of *Anomalopteryx*. There seems to be no doubt that the name *Anomalopteryx* probably belongs to this group.

I see no evidence favouring the retention of the genera *Palapteryx* and *Cela*. Hutton retains *Palapteryx* for the reception of *dromioides*, Owen, and *plena*, Hutton, the main ground of generic distinction being, as I understand, that the posterior view of the skull of *dromioides*, as figured by Owen (17, pl. 54), shows an undoubted approximation to that of *Dinornis* in its great relative breadth and short rounded paroccipital processes. Lydekker, however, with the skull itself at his disposal, places this species near *casuarina*. As to *Cela*, the type species is *curta*, of which *oweni* is, according to Hutton, a synonym. Judging from Haast's figure of a fragmentary skull, I am disposed to agree with Lydekker in placing this species under *Anomalopteryx*.

<sup>1</sup> *Megalapteryx* probably belongs to this group. See Note above, p. 378.—June 1895.

These conclusions may be summarized by stating that the Dinornithidæ are divisible into three groups, two of highly specialized forms and one of more generalized forms, which last may be again split up into three subgroups. These facts might be expressed equally well by making three genera, and subdividing one of them into three subgenera, or by making three subfamilies, two of them containing a single genus apiece, and the third including three genera. The latter appears to me the more convenient method. Agreeing, as I do, with Hutton and Lydekker, that the differences between, say, *elephantopus* and *didiformis* are of generic value, it appears to me quite clear that those between *robustus* and *elephantopus* or between *didiformis* and *crassus* are something more than generic.

Arranging the groups as nearly as possible according to their affinities as determined by cranial characters, we get the following scheme:—

### Family DINORNITHIDÆ.

#### Subfamily *a.* DINORNITHINÆ.

##### Genus 1. DINORNIS.

#### Subfamily *b.* ANOMALOPTERYGINÆ.

##### Genus 2. PACHYORNIS.

##### ,, 3. MESOPTERYX.

##### ,, 4. ANOMALOPTERYX.

#### Subfamily *c.* EMEINÆ.

##### Genus 5. EMEUS.

### 8. SUMMARY OF CRANIAL CHARACTERS OF THE SUBFAMILIES AND GENERA OF THE DINORNITHIDÆ.

#### Subfamily DINORNITHINÆ.

Width of cranium at paroccipital process nearly always more than twice length of basis cranii.

Distance between optic foramina about two thirds length of basis cranii.

Orbit right-angled.

Greatest length of premaxilla more than two and a half times that of basis cranii.

Body of premaxilla deflected, bluntly rounded; its length and width about one and a half times length of basis cranii.

Maxillo-palatine contains a large antrum.

Nasal has a slender maxillary process.

Mandible much deflected, with bluntly rounded symphysis, width of which is at least three quarters of, and is usually more than, length of basis cranii.  
Length of mandible more than four times that of basis cranii.

#### Genus DINORNIS.

Occipital plane inclined forwards, condyle projecting beyond middle of supra-foraminal ridge; occipital crest usually indistinct.

Paroccipital process short, and evenly rounded below; projects beyond occipital condyle.

Width of cranium at squamosals from two and a third to two and a half times length of basis cranii.

Mamillar tuberosities very large and prominent; a large precondylar fossa.

Margin of tympanic cavity forms a continuous curve.

Temporal fossa large; distance between temporal ridges about two thirds of width of cranium at temporal fossæ; width of temporal fossa more than half length of basis cranii: no mid-temporal ridge.

Temporal and lambdoidal ridges usually distinct, but occasionally in contact.

Posterior tympanic fossa wide; inferior temporal ridge prominent, usually stops short of pretympenic process.

Zygomatic process very short.

Postorbital process angled, consisting of horizontal and descending portions.

Antorbital strong, deeply excavated above by a large supraorbital fenestra; its ventral edge forms a strong transverse postchoanal bar.

Prenarial septum very distinct.

Maxillo-jugal arch compressed, gently curved.

Quadrate has a rather long and compressed orbital process; pneumatic foramen of variable size, but usually very large, on mesial surface of otic process; occasionally two additional foramina on posterior surface.

Posterior angular process of mandible small or obsolete.

#### Subfamily ANOMALOPTERYGINÆ.

Width of cranium at paroccipital processes less than twice length of basis cranii.

Distance between optic foramina usually less than one third and never much more than one half length of basis cranii.

Orbit evenly curved, sinuous, or obtuse-angled (right-angled in *Mesopteryx*, species  $\gamma$ ).

Greatest length of premaxilla less than two and a half times that of basis cranii.

Body of premaxilla narrow and pointed; its length rarely and its breadth never more than length of basis cranii.

Maxillo-palatine contains a large antrum.

Nasal has a slender maxillary process (*qu.* except in *Anomalopteryx*, where there is a distinct maxillo-nasal bone?).

Mandibular symphysis pointed; its width always considerably less than three fourths of length of basis cranii.

Length of mandible nearly always less than four times that of basis cranii.

#### Genus PACHYORNIS.

Occipital plane vertical or slightly inclined backwards; occipital crest prominent; supraoccipital fossæ well marked; anterior and posterior lambdoidal ridges enclose a wide lozenge-shaped area.

Paroccipital process short, bluntly pointed.

Width of cranium at paroccipital processes from one and a half to nearly twice length of basis cranii.

Width at squamosals more than double length of basis cranii.

Cranial roof strongly and evenly arched; an irregular shallow depression at base of postorbital process.

Mamillar tuberosities large.

Margin of tympanic cavity evenly curved.

Temporal fossa large; distance between temporal ridges about one and a third times width of cranium at temporal fossæ; width of temporal fossa about three fourths length of basis cranii; mid-temporal ridge small or absent.

Temporal and lambdoidal ridges may or may not be in contact.

Posterior temporal fossa narrower than in *Dinornis* and *Anomalopteryx*, but wider than in *Mesopteryx* and *Pachyornis*; inferior temporal ridge strong; pretympanic process short.

Zygomatic process long, bluntly pointed.

Margin of orbit rather sinuous; postorbital process angled, consisting of horizontal and descending portions.

Distance between optic foramina about one half length of basis cranii.

Antorbital very thin; supraorbital fenestra moderate; postchoanal bar strongly curved outwards and forwards and more prominent than in any genus except *Dinornis*.

Rostrum broad and flattened in about its posterior 15 mm., then moderately compressed as far as the triangular processes, where it becomes broad and rounded below (the anterior extremity is lost in all the specimens I have examined).

Width of body of premaxilla nearly equal to its length, and about three fourths of the length of the basis cranii.

Prenarial septum distinct.

Maxillo-jugal rather slender, compressed posteriorly, and strongly curved.

Orbital process of quadrate compressed and bluntly pointed; a single pneumatic foramen of variable size on the mesial surface of the otic process.

Mandible strong, **V**-shaped, moderately deflected; posterior angular process of moderate size.

#### Genus MESOPTERYX.

Occipital plane vertical or inclined backwards; occipital crest usually distinct; supraoccipital fossæ present.

Occipital condyle often projects beyond paroccipital processes.

Paroccipital process pointed; width of cranium at paroccipital processes about one and a half times length of basis cranii.

Width at squamosal prominences double length of basis cranii.

Mamillar tuberosities small; posterior border of basitemporal platform nearly straight.

Margin of tympanic cavity right-angled (evenly curved in species  $\alpha$ ).

Temporal fossa small; distance between temporal ridges about equal to width of cranium at temporal fossæ; width of temporal fossa about one half length of basis cranii.

Temporal and lambdoidal ridges never confluent.

Posterior temporal fossa narrow; inferior temporal ridge moderate.

Margin of orbit evenly curved or slightly sinuous (right-angled in species  $\gamma$ ); post-orbital process evenly curved.

Trigeminal foramen usually double (single in species  $\beta$ ), consisting of apertures placed one above the other and separated by a narrow horizontal or oblique bar.

Distance between optic foramina about one third length of basis cranii.

Antorbital very thin; supraorbital fenestra rather small; postchoanal ridge very thin or barely discernible.

Rostrum dilated but not flattened towards its posterior end, usually much compressed and carinate in its intermediate portion, and slightly dilated between and in front of the triangular processes.

Body of premaxilla narrow and pointed; its width nearly equal to its length and about three fourths length of basis cranii; a distinct prenarial septum.

Maxillo-jugal arch slender and gently curved.

Orbital process of quadrate compressed and bluntly pointed; a single pneumatic foramen of variable size on mesial surface of otic process.



Mandible slenderer than in any other genus, moderately deflected ; posterior angular process well developed.

Genus ANOMALOPTERYX.

Occipital plane distinctly inclined backwards, the condyle being hidden in a view from above by the supraforaminal ridge and also in a view from the side by the paroccipital process.

Occipital crest slight, but whole median supraoccipital region dilated to form a wide transversely convex ridge.

Width at paroccipital process about one and three quarters length of basis cranii.

Anterior and posterior lambdoidal ridges usually widely separated.

Width at squamosals about double length of basis cranii.

Mamillar tuberosities large.

Margin of tympanic cavity sharply angled.

Temporal fossa very large ; distance between temporal ridges about half width of cranium at temporal fossæ ; width of temporal fossa more than three fourths length of basis cranii.

Posterior limb of temporal ridge confluent with lambdoidal ridge ; mid-temporal ridge well marked and often prominent.

Posterior temporal fossa wide ; inferior temporal ridge strong ; no pretympenic process.

Zygomatic process short and blunt.

Margin of orbit obtusely angled ; postorbital process evenly curved.

Distance between optic foramina less than one third length of basis cranii.

Presphenoid fossa unusually well defined.

Antorbital very thin ; a large supraorbital fenestra ; no definite postchoanal bar.

Lateral contour of premaxilla much straighter than in any other genus ; body narrow and pointed, its width about two thirds of its length and three fourths of length of basis cranii ; a distinct prenarial septum.

Maxillo-jugal arch stout and nearly straight.

Orbital process of quadrate long, compressed, and rather pointed at the tip ; a large pneumatic foramen on the mesial surface of the otic process and often a second foramen on its posterior surface.

Mandible stout and nearly straight ; symphysis narrow, with a moderately prominent ventral ridge ; posterior angular process strong.

## Subfamily EMEINÆ.

- Width of cranium at paroccipital processes less than twice length of basis cranii.  
 Distance between optic foramina less than one third length of basis cranii.  
 Orbit evenly curved or slightly sinuous (right-angled in *Pachyornis*, species  $\alpha$ ).  
 Greatest length of premaxilla rarely more than twice, and never more than two and a half times length of basis cranii.  
 Body of premaxillæ bluntly rounded in front; its length always less, its breadth either less or slightly more than length of basis cranii.  
 Maxillary process of nasal represented by a distinct maxillo-nasal bone.  
 Maxillo-palatine devoid of an antrum.  
 Mandibular symphysis bluntly rounded; its width at least three fourths of length of basis cranii.  
 Length of mandible usually more than three and less than three and a half times length of basis cranii.

## Genus EMEUS.

- Occipital plane inclined backwards; occipital condyle hidden in a view from above by supraforaminal ridge, and in a view from the side by paroccipital process.  
 Occipital crest prominent; supraoccipital fossæ well marked.  
 Anterior and posterior lambdoidal ridges distinct, but close together.  
 Width of cranium at paroccipital processes usually about once and a half, but occasionally (in *E. crassus*) once and three quarters length of basis cranii.  
 Width at squamosals rarely more than double length of basis cranii.  
 Mamillar tuberosities large.  
 Temporal fossæ small; distance between temporal ridges but little less than width of cranium at temporal fossæ; width of temporal fossa usually about half length of basis cranii.  
 Temporal and lambdoidal ridges do not touch; mid-temporal ridge usually well marked.  
 Posterior temporal fossa narrow; inferior temporal ridge strong.  
 Zygomatic process long, often bifid.  
 Postorbital process evenly curved, sometimes slightly inturned at distal end.  
 Antorbital thin; supraorbital fenestra small; no definite postchoanal bar.  
 Nasal process of premaxilla very thick, its anterior end not flattened but rod-like; prenasal septum often obscure.  
 Maxillo-jugal arch strong and nearly straight; maxillo-palatine gives off dorsally an oblique vertical plate, with sometimes the merest vestige of an antrum at its base.

Orbital process of quadrate bluntly pointed; a large pneumatic foramen on mesial surface of otic process.

Mandibular symphysis broader than long, with a very obscure ventral ridge; posterior angular process better developed than in any of the other genera.

#### 9. THE PHYLOGENY OF THE RATITÆ<sup>1</sup>.

The most definite opinion I have met with as to the phylogeny of the Ratitæ is that expressed in the elaborate genealogical tree which illustrates Fürbringer's great work. He ascribes a common origin to the Moas and Kiwis and to the Emus and Cassowaries, but derives his four main groups of Ratitæ—the *Struthioniformes*, *Rheiformes*, *Casuariiformes*, and *Apterygiformes*—separately from a primitive stock.

Mivart, in his memoir on the axial skeleton of the Ratitæ (13), gives no definite opinion as to the phylogeny of the group, but his diagram illustrating the mutual relationships of the various genera seems to indicate his belief in their monophyletic origin. He shows a main stem dividing into two branches; one of these divides again for *Struthio* and *Rhea*; the other forks a second time, one branch dividing again for *Casuarius* and *Dromæus*, the other for *Dinornis* and *Apteryx*.

The monophyletic origin of the Ratitæ is also supported by Newton, who, in his luminous article "Ornithology" (14), says "that these forms—Moa, Kiwi, Emu and Cassowary, Rhea, and finally Ostrich—must have had a common ancestor nearer to them than is the ancestor of any carinate form seems to need no proof." Prof. Newton's classification indicates no closer affinity between any of the genera except the Emu and Cassowary, which together constitute his order *Megistanes*; each of the other genera has an order to itself.

A study of the skull certainly confirms the view that the nearest ally of the Dinornithidæ is *Apteryx*, and that the four families of Australasian Ratitæ are more nearly related to one another than is either of them to the Asio-African and South-American forms. *Struthio* and *Rhea* differ so much from the Australasian members of the subclass as to lend strong support to Fürbringer's view that they arose separately from a primitive stock; but whether the Cassowaries and Emus on the one hand and the Moas and Kiwis on the other had a distinct or a common origin is a very complex question.

The main difficulty lies in deciding what characters should be considered as of phylogenetic importance and what merely adaptive, but it appears to me that in the following particulars the Emu and Cassowary show an undoubted relationship to the Moas:—

The general characters of the maxilla, maxillo-palatine, and antrum in both genera.

<sup>1</sup> As my conclusions are based upon a study of the skull, I have omitted all reference to *Æpyornis*, *Dromornis*, *Megalapteryx*, and *Palæocasuarius*.

The general relations of the vomer, palatines, and pterygoids in both genera.

The presence of a vestige of the maxillary process of the nasal in *Dromæus*.

The well-ossified antorbital ankylosed to the descending process of the lacrymal in both genera.

The elevated body of the premaxilla with its distinct prenasal septum in *Casuarius*.

Dr. Forbes's discovery (1) of a dinornithine bird which he calls *Palæocasuarinus* will, if the detailed account of his very interesting researches bears out the opinions expressed in his preliminary note, lend strong support to this view. The tibiæ upon which the genus is founded have, as the name implies, a remarkable resemblance to those of the Cassowary.

On the other hand I know of no character in the skull of *Rhea* by which it definitely approaches the Moas, and the presence of a maxillary process to the nasal, the form of the cerebral fossæ, and the position of the pneumatic foramen of the quadrate seem the only particulars in which the Ostrich comes in any way near them. *Struthio* and *Rhea* are, in fact, sharply separated both from one another and from the Australasian Ratitæ as well by the characters of the bony palate as by those of the pelvis. The characters possessed by them in common with the other Ratitæ are of two kinds: ancestral characters, such as the form of the vomer, the basi-ptyergoid processes, and the single-headed quadrate, which, according to the view taken in this paper, are accounted for by the hypothesis of common descent from a group of generalized flying birds or Proto-Carinatæ; and adaptive characters, such as those of the sternum, shoulder-girdle, and wing, which they share to a greater or less degree with all flightless birds.

The marked differences between the Moas and Kiwis are certainly for the most part adaptive: the two families resemble one another in the increased size of the olfactory organ and the reduced size of the eye; but both processes have gone so much further in *Apteryx* that the differences between the two, in this respect alone, give their skulls the appearance of being more widely separated than those of any other two ratite birds. The real affinities underlying these differences are, however, shown by the striking similarity of the bones of the palate in the two forms. The absence of a maxillary antrum in *Apteryx* seems at first sight a difference of great importance, but the fact that this cavity has disappeared or become vestigial in one of the most specialized genera of Moas seems to indicate that its complete atrophy in the Kiwi is simply to be looked upon as an instance of the extreme specialization of that genus.

As to the origin of the various genera of Dinornithidæ, I am not altogether in accordance with Prof. Hutton (9, p. 428). I think there can be no doubt that *Dinornis* and *Emeus* have diverged furthest from the ancestral stock, but in opposite directions; and that the narrow-beaked forms are the most generalized. Of the three narrow-beaked genera, *Mesopteryx* appears to me to deviate least from the ordinary type of the Ratitæ, its comparatively lightly-built skull and slender mandible bringing it nearer

than any other genus to *Dromæus* and *Casuarius*<sup>1</sup>. On the other hand, the relative size of the orbit is greatest in *Anomalopteryx*, and the presphenoid fossa or vestige of the interorbital septum is most marked in that genus and in *Dinornis*: I am disposed, therefore, to derive *Mesopteryx* and *Anomalopteryx* from a common ancestor.

*Pachyornis* appears undoubtedly to spring from the *Mesopteryx*-stock: these two genera are more nearly allied than any other two, *Pachyornis* being the more differentiated in virtue of its greater bulk, broader skull, larger temporal fossæ, more widely separated optic foramina, and stronger beak.

*Emeus* is derived by Hutton from *Mesopteryx*, a view which I am strongly inclined to adopt. The cranium of *Emeus* undoubtedly comes nearest to that of *Mesopteryx*,

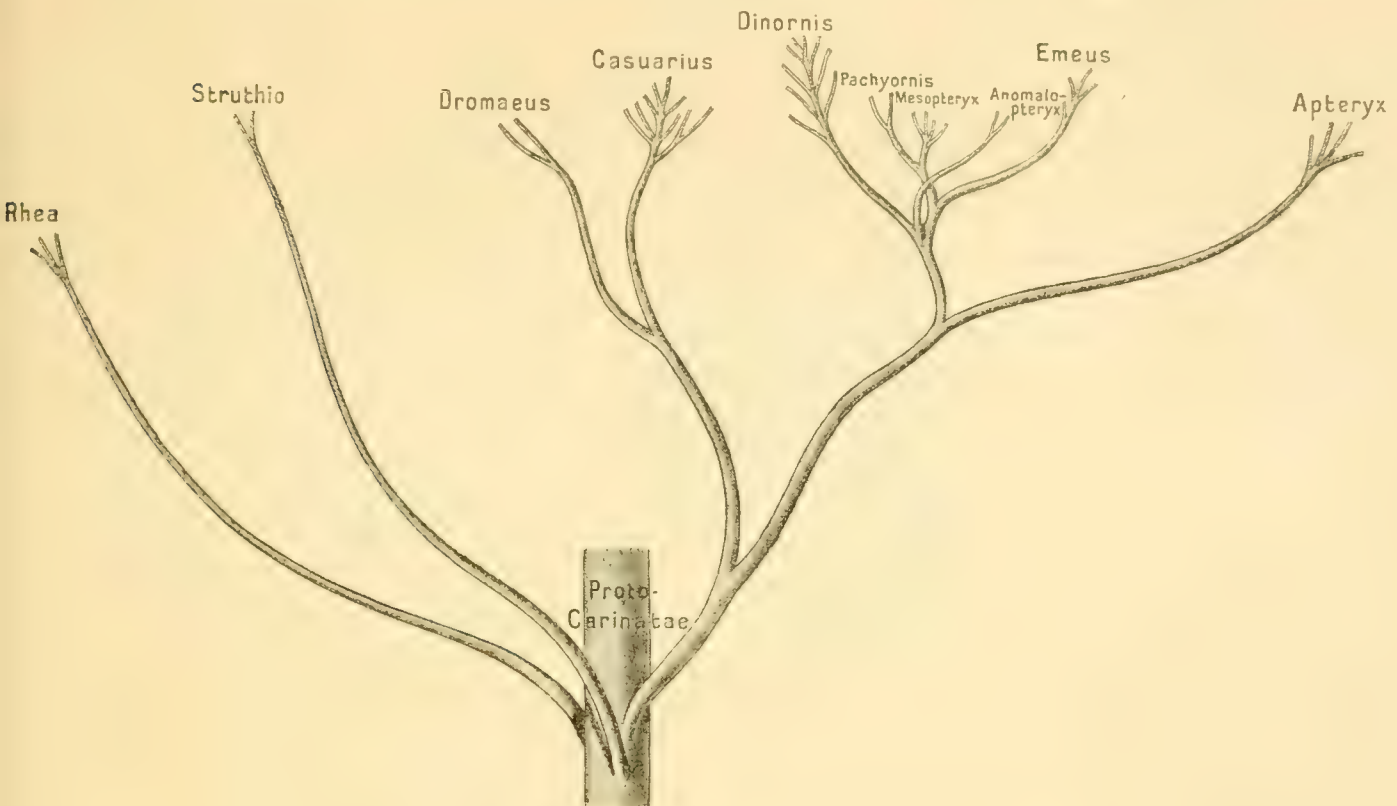


Fig. 1.—Phylogenetic diagram showing the mutual relations of the Ratitæ.

the differences between the two skulls depending mainly on the stronger and coarser character of the whole skull, the broader beak, and the stronger mandible of *Emeus*. I think, therefore, that the latter genus should be considered as springing from the *Mesopteryx*-stock—not, of course, from *Mesopteryx* itself, but from an older member of the line of descent which culminated in that genus.

*Dinornis* agrees with but goes beyond *Pachyornis* in its widely separated optic

<sup>1</sup> The striking resemblance of the dried head of *Mesopteryx casuarina* (*Didornis didinus*, Owen) to that of an Emu is noticed by Owen (23).

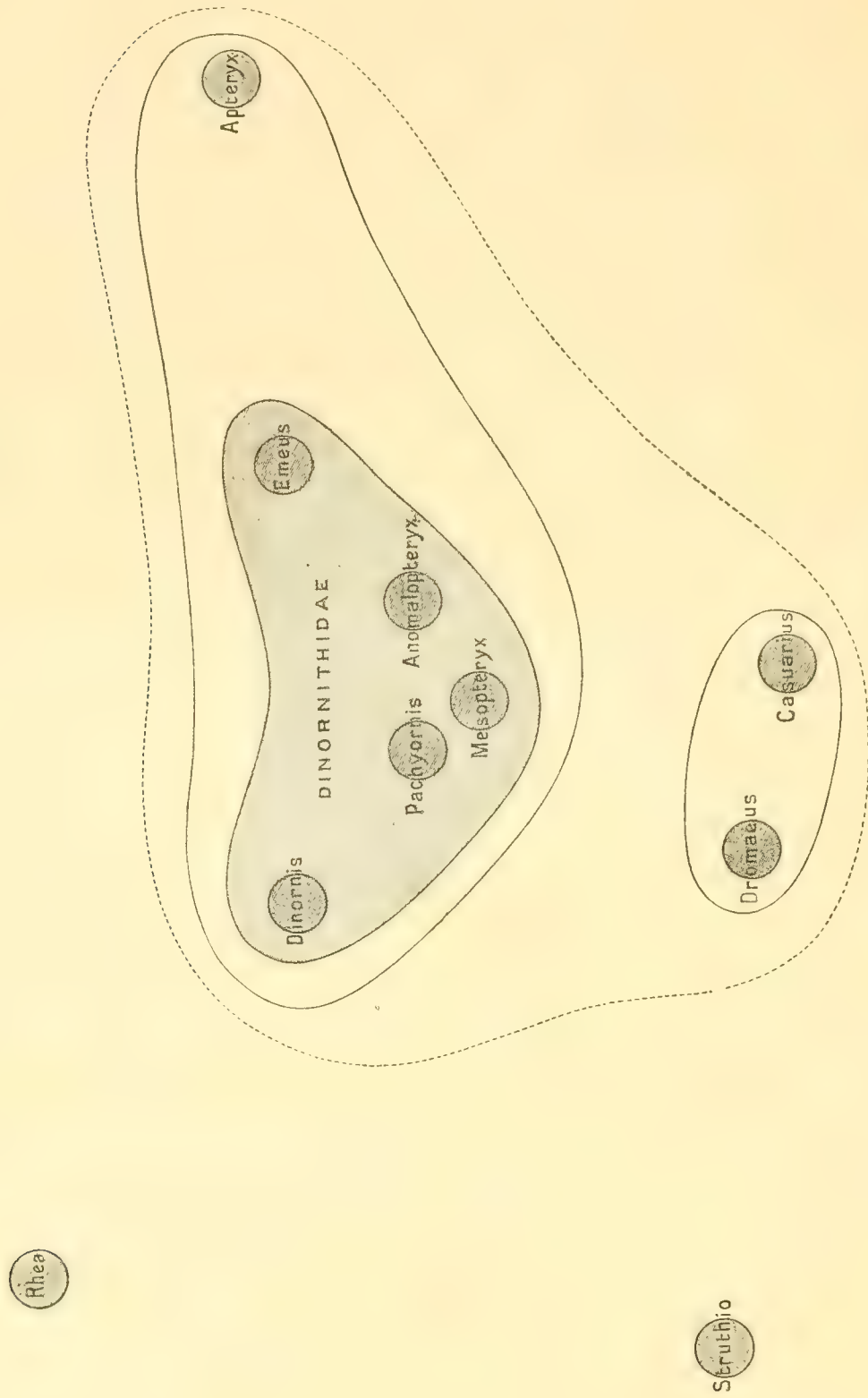


Fig. 2.—A similar diagram in horizontal projection.

foramina and its broad skull, but in other respects—the form of the orbit, the length, breadth, and strong deflection of the beak, &c.—is quite peculiar. I think that on the whole it is reasonable to suppose this most specialized of the Moas to have sprung from the common ancestor of the family independently of all the other existing genera. It is, however, quite possible that future research may show Hutton to be right in placing *Palapteryx* on or near the line connecting *Dinornis* with the generalized ancestor of the group.

The accompanying diagrams (pp. 425, 426) express these views in a graphic form. The first figure has the tree-shape adopted by Fürbringer, which, after several trials, I find more suitable to the present purpose than the usual straight-line diagram. The second figure shows the same thing in horizontal projection: the various genera of Dinornithidæ are included in a tinted area indicating the limits of the family: the Dinornithidæ and *Apteryx* on the one hand, and the Emu and Cassowary on the other, are enclosed by an even line indicating the limits of two groups, probably of subordinal value, including respectively the New Zealand and the Australian forms: finally all these are enclosed within a dotted line to show that the Australasian forms may be included in a natural group, perhaps of ordinal value, clearly separated from the isolated Asio-African and South-American genera.

These conclusions may be further expressed by a table of Classification as follows:—

Subclass **RATITÆ**, Merrem.

Order I. STRUTHIONES, Newton.

Fam. STRUTHIONIDÆ. Genus *Struthio*.

Order II. RHEÆ, Newton.

Fam. RHEIDÆ. Genus *Rhea*.

Order III. MEGISTANES, Newton.

Suborder I. CASUARIFORMES, Fürbringer.

Fam. 1. CASUARIIDÆ. Genus *Casuarus*.

2. DROMEIDÆ. Genus *Dromæus*.

Suborder 2. APTERYGIFORMES, Fürbringer.

Fam. 1. DINORNITHIDÆ.

Subfam. *a.* Dinornithinæ. Genus *Dinornis*.

Subfam. *b.* Anomalopteryginæ. Genera *Pachyornis*, *Mesopteryx*, *Anomalopteryx*<sup>1</sup>.

Subfam. *c.* Emeinæ. Genus *Emeus*.

Fam. 2. APTERYGIDÆ. Genus *Apteryx*.

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<sup>1</sup> And probably *Megalapteryx*. See Note, p. 378.—June 1895.

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## EXPLANATION OF THE PLATES.

## PLATE LVI.

Figs. 1-4. Four views of a perfect skull of *Emeus*, species  $\alpha$ , in the Otago University Museum. Natural size.

## PLATE LVII.

Figs. 5-8. Outline sketches of figs. 1-4, with the various bones distinguished by colour.

## PLATE LVIII.

Fig. 9. Back view of the skull shown in Plate LVI.

Fig. 10. Cranium of *Emeus*, species  $\alpha$ , in horizontal section.

Fig. 11. The same in sagittal section.

Figs. 12 & 13. Two views of an immature cranium of *Anomalopteryx didiformis*, Owen.

All natural size.

## PLATE LIX.

Figs. 14-18. Outline sketches of figs. 9-13, with the various bones distinguished by colour.

## PLATE LX.

Fig. 19. Skull of *Mesopteryx casuarina*, in Dr. H. O. Forbes's Collection.

Figs. 20 & 21. Two views of the skull of *Mesopteryx*, species  $\beta$ , in the Colonial Museum, Wellington.

Both natural size.

Fig. 22. Skull of *Pachyornis elephantopus*, in Dr. H. O. Forbes's Collection.

Five-sixths natural size.

## PLATE LXI.

Figs. 23-34. Outlines of the crania of various species of Dinornithidæ, from above.

Drawn to the same absolute size with the camera lucida.

Figs. 35-46. A similar series of outlines from the left side.

## PLATE LXII.

Figs. 47-58. A similar series of outlines from behind.

Figs. 59-64. The maxillo-jugal arch (maxilla only in *Rhea*) of various Ratitæ.

Natural size.

Figs. 65-70. The quadrate facet on the roof of the tympanic cavity, in various Ratitæ.  
Drawn to the same absolute size.

*als.*, alisphenoid; *pr.o.*, prootic; *sq.*, squamosal; *ex.oc.*, exoccipital.

Figs. 71-76. The optic and adjacent foramina in various Ratitæ. Drawn to the same absolute size.

ii, optic foramen; iii, oculomotor foramen; iv, pathetic foramen;  
v<sup>1</sup>, orbitonasal foramen; vi, abducent foramen; *a*, foramen for internal  
ophthalmic artery.

#### LIST OF ABBREVIATIONS.

<i>a.b.cr.fon.</i> Position of anterior basicranial fontanelle.	<i>Hard.fos.</i> Harderian fossa.
<i>abd.for.</i> Abducent foramen.	<i>inf.al.eth.</i> Inferior alioethmoid.
<i>a.lamb.r.</i> Anterior lambdoidal ridge.	<i>inf.orb.for.</i> Inferior orbital foramen.
<i>al.n.</i> Alinasal.	<i>inf.temp.r.</i> Inferior temporal ridge.
<i>al.sph.</i> Alisphenoid.	<i>int.aud.m.</i> Internal auditory meatus.
<i>ang.</i> Angular.	
<i>a.orb.</i> Antorbital.	<i>ju.</i> Jugal.
<i>art.</i> Articular.	
	<i>lac.</i> Lacrymal.
<i>b.oc.</i> Basioccipital.	<i>lac.for.</i> Lacrymal foramen.
<i>b.pt.pr.</i> Basipterygoid process.	
<i>b.sph.</i> Basisphenoid.	<i>mam.tub.</i> Mamillar tuberosity.
<i>b.temp.</i> Basitemporal.	<i>mesen.fos.</i> Mesencephalic fossa.
<i>b.temp.pl.</i> Basitemporal platform.	<i>mes.eth.</i> Mesethmoid.
	<i>m.temp.r.</i> Mid-temporal ridge.
<i>car.for.</i> Carotid foramen.	<i>mx.</i> Maxilla.
<i>cer.fos.</i> Cerebellar fossa.	<i>mx.ju.ar.</i> Maxillo-jugal arch.
<i>con.for.</i> Condylar foramen or foramina.	<i>mx.na.</i> Maxillo-nasal.
	<i>mx.pal.</i> Maxillo-palatine.
<i>d.</i> Dentary.	<i>mx.pr.</i> Maxillary process.
<i>dor.sell.</i> Dorsum sellæ.	
	<i>na.</i> Nasal.
<i>eth.</i> Ethmoid.	<i>na.pr.</i> Nasal process.
<i>eus.gr.</i> Eustachian groove.	
<i>ex.oc.</i> Exoccipital.	<i>oc.con.</i> Occipital condyle.
	<i>oc.cr.</i> Occipital crest.
<i>for.a.</i> Foramen <i>a</i> .	<i>oc.for.</i> Oculomotor foramen.
<i>foss.b.</i> Fossa <i>b</i> .	<i>olf.ch.</i> Olfactory chamber.
<i>fr.</i> Frontal.	<i>op.for.</i> Optic foramen.

- op.pl.* Optic platform.  
*orb.na.for.* Orbitonasal foramen.  
*orb.pr.* Orbital process.  
*or.sph.* Orbitosphenoid.  
*ot.pr.* Otic process.
- pa.* Parietal.  
*pal.* Palatine.  
*pal.pr.* Palatine process.  
*par.oc.pr.* Paroccipital process.  
*path.for.* Pathetic foramen.  
*p.b.cr.fon.* Posterior basicranial fontanelle.  
*pit.fos.* Pituitary fossa.  
*p.lamb.r.* Posterior lambdoidal ridge.  
*p.mx.* Premaxilla.  
*post.orb.pr.* Postorbital process.  
*post.temp.fos.* Post-temporal fossa.  
*post.temp.r.* Post-temporal ridge.  
*pre.con.fos.* Precondylar fossa.  
*pre.orb.pr.* Preorbital process.  
*pre.temp.w.* Pretemporal wing.  
*pr.lacer.fos.* Prelacerate fossa.  
*pr.op.r.* Preoptic ridge.  
*pr.ot.* Prootic.  
*pr.pit.r.* Prepituitary ridge.  
*pr.sph.* Presphenoid.  
*pr.sph.foss.* Presphenoid fossa.  
*pt.* Pterygoid.
- q.* Quadrate.  
*q.j.* Quadrato-jugal.
- rost.* Rostrum.
- s.ang.* Supra-angular.  
*.oc.* Supra-occipital.  
*s.oc.fos.* Supra-occipital fossa.  
*sq.* Squamosal.  
*sq.prm.* Squamosal prominence.  
*sup.al.eth.* Superior alieithmoid.  
*sup.for.r.* Supra-foraminal ridge.  
*sup.orb.fen.* Supra-orbital fenestra.
- temp.fos.* Temporal fossa.  
*temp.r.* Temporal ridge.  
*tent.r.* Tentorial ridge.  
*trig.for.* Trigeminal foramen.  
*tri.pr.* Triangular process.  
*turb.* Turbinal.
- vag.for.* Vagus foramen.  
*vo.* Vomer.  
*vo.pr.* Vomerine process.
- zyg.pr.* Zygomatic process.



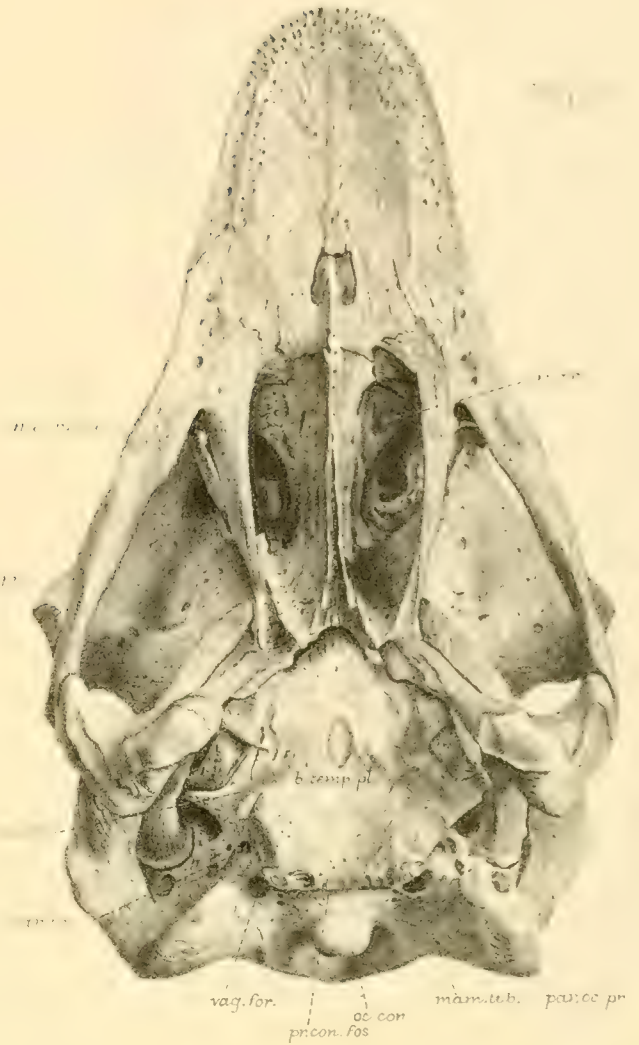
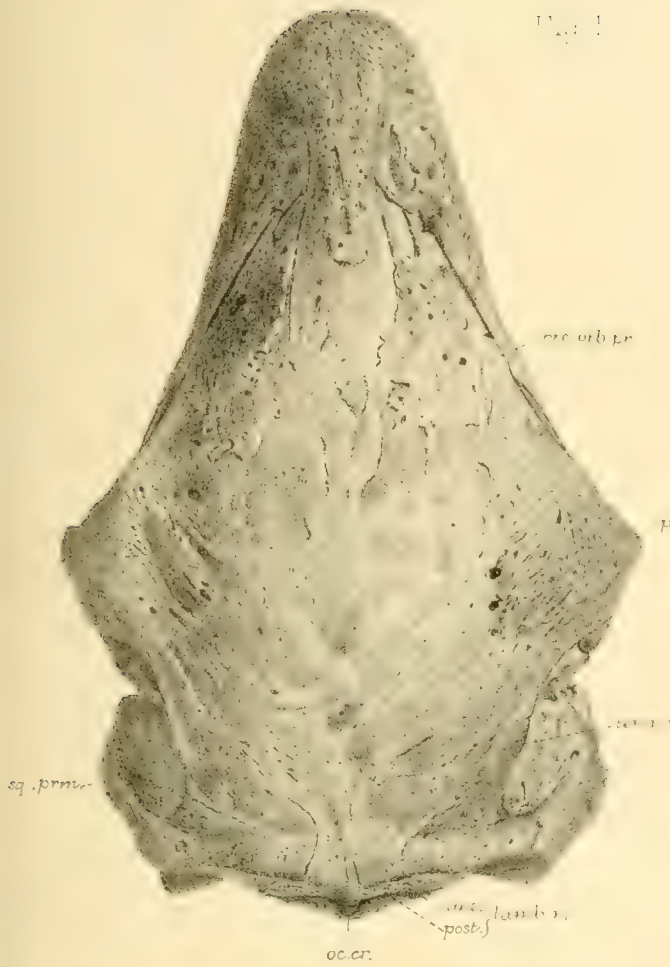
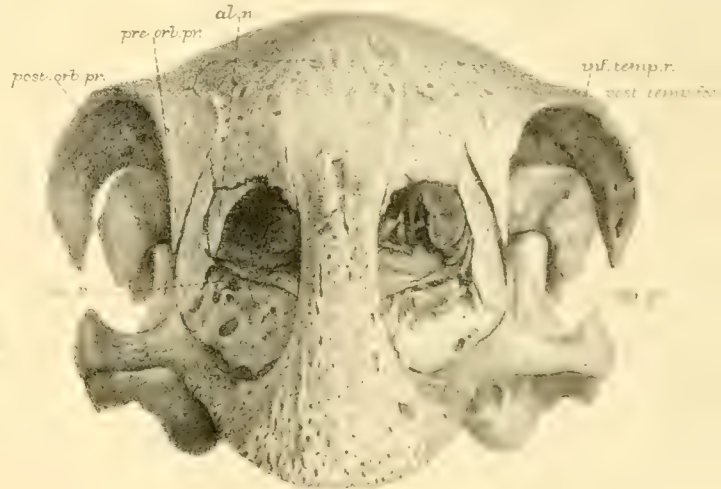
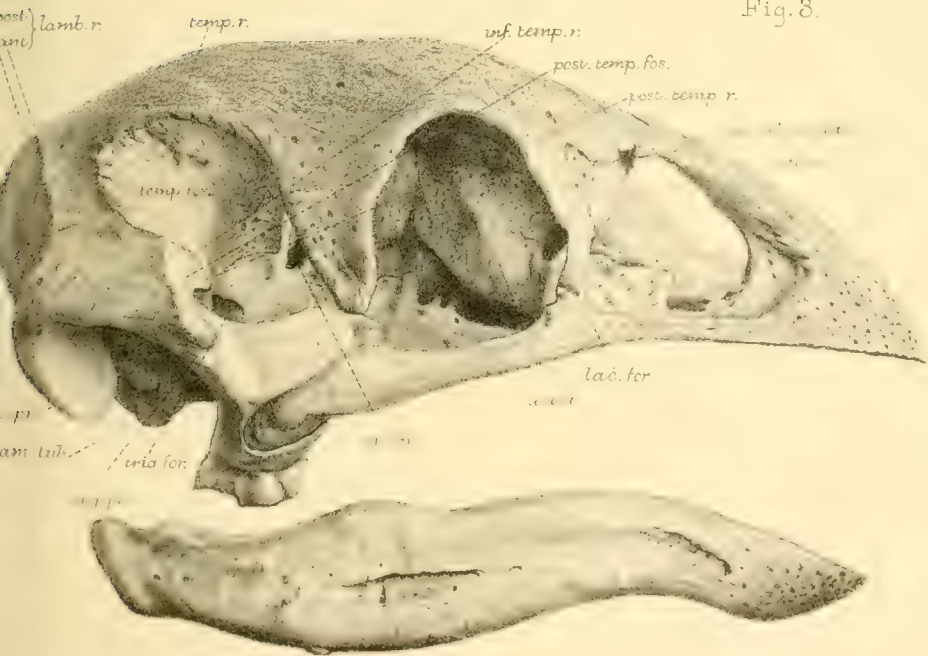
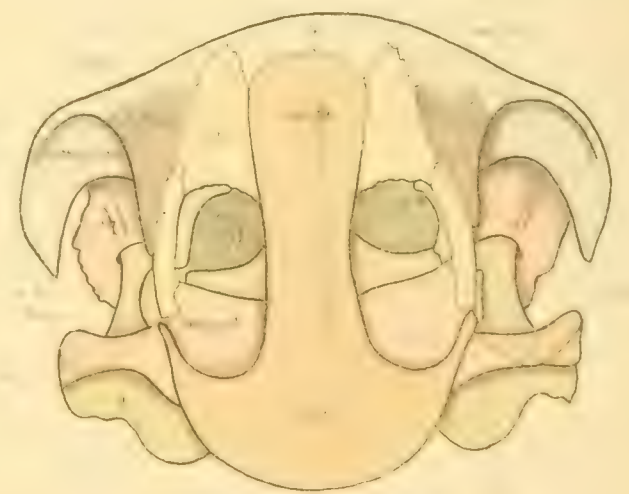
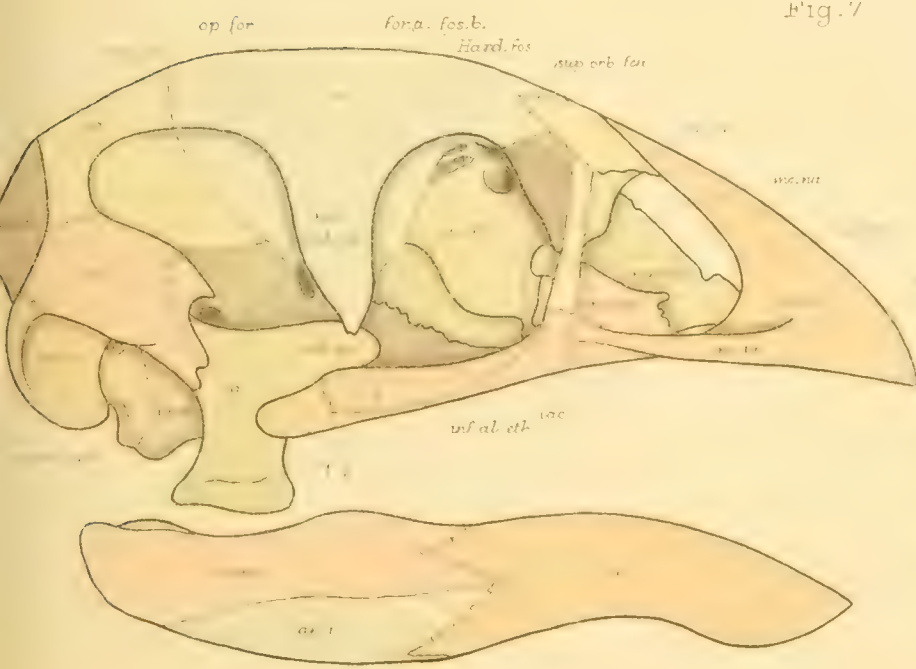
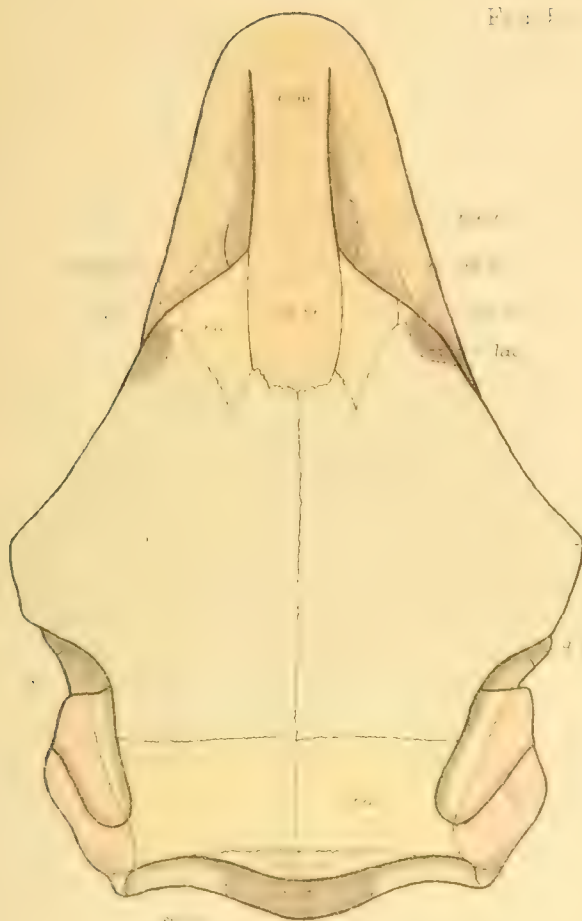


Fig. 3.

Fig. 4.







T.J.P. del.  
M.P. Parker Chrono.

EMBUS sp. a

Wm. M. Edwards del.





Fig 9

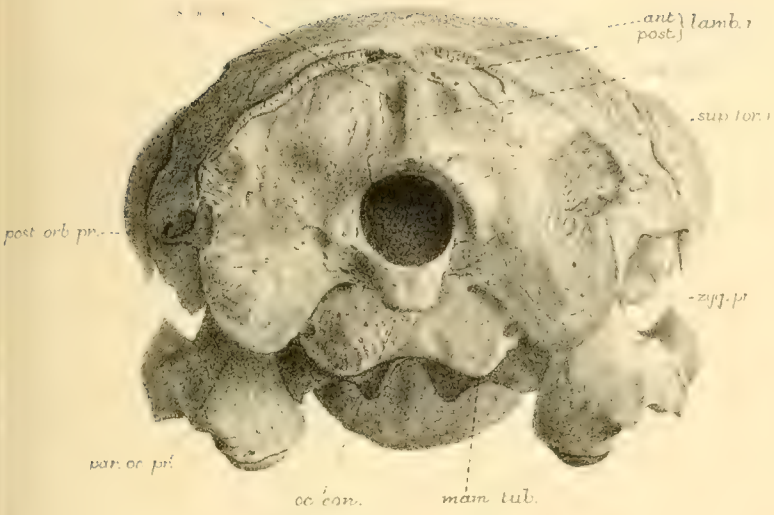
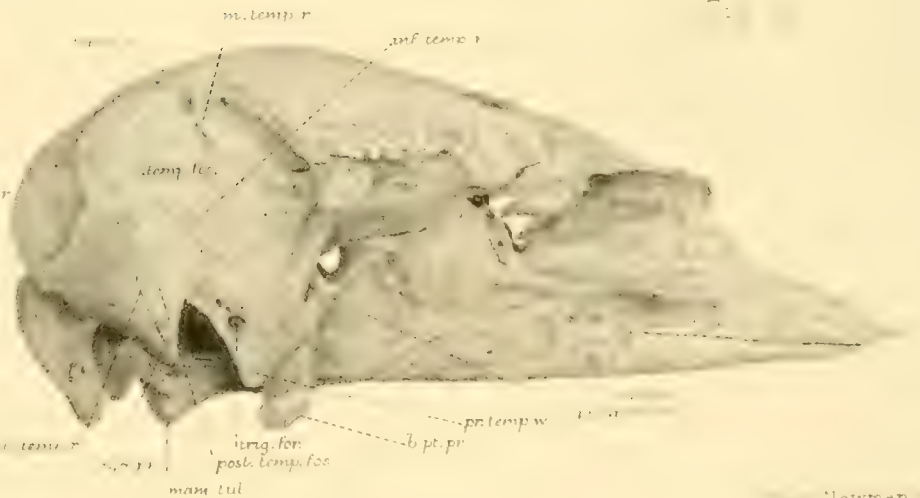
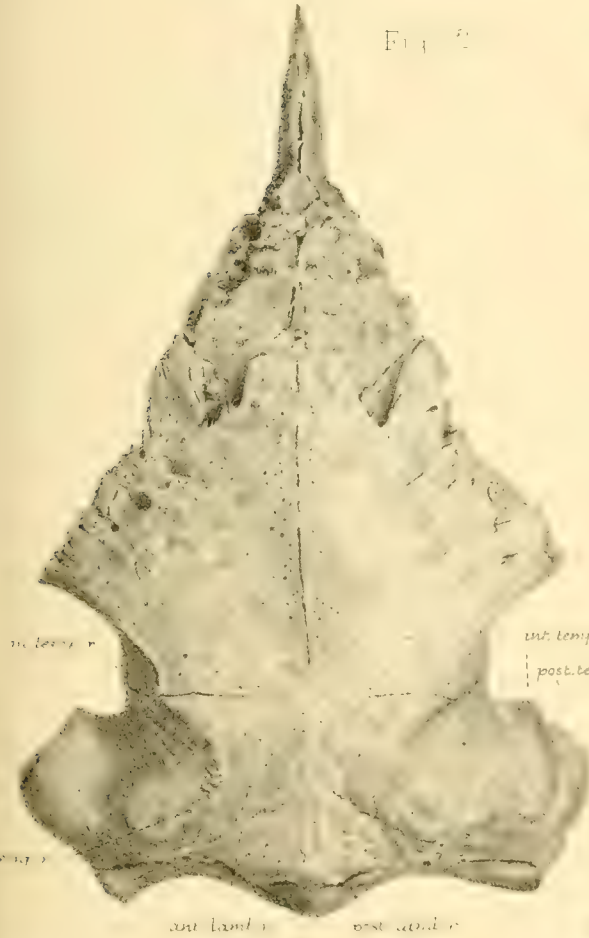
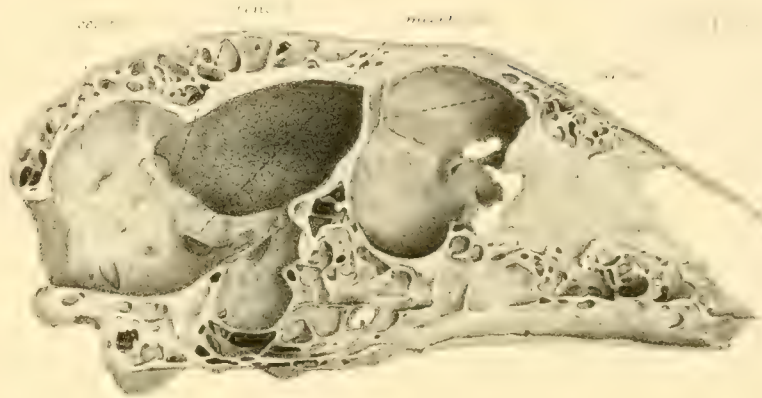


Fig 10



Fig 11



J. Thomson. Photo.  
M.P. Parker. Lith.

Hayman R.

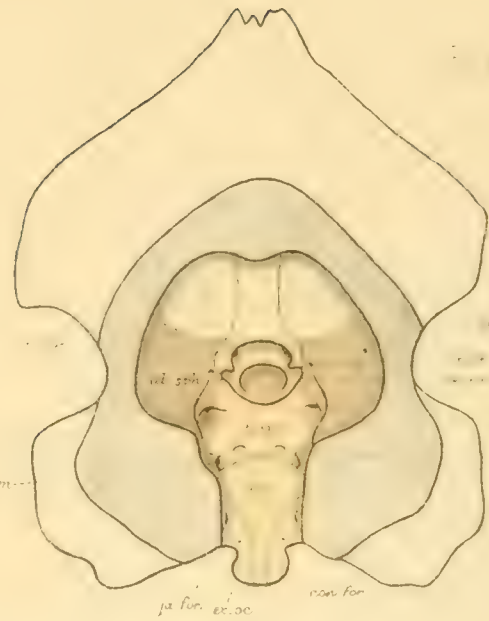
Figs. 9-11 EMEUS sp. a.  
Figs. 12 & 13, ANOMALOPTERYX DIDIFORMIS.



Fig. 14.



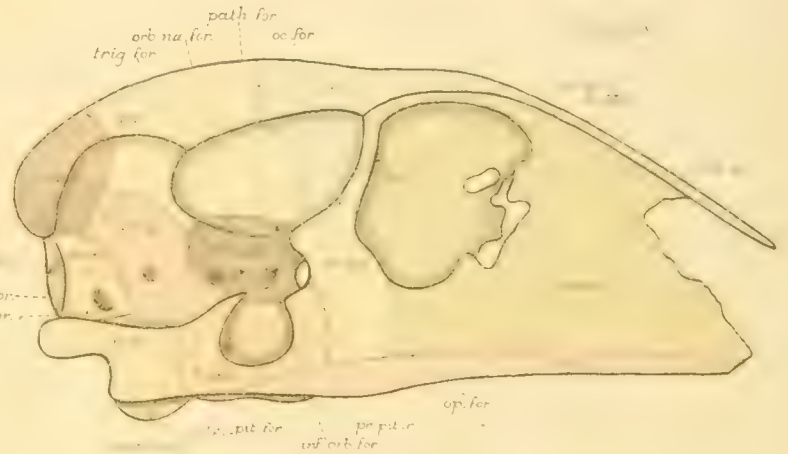
post. orb. pr.



int. aud. m.

ja. fur. ex. oc.

con. for.



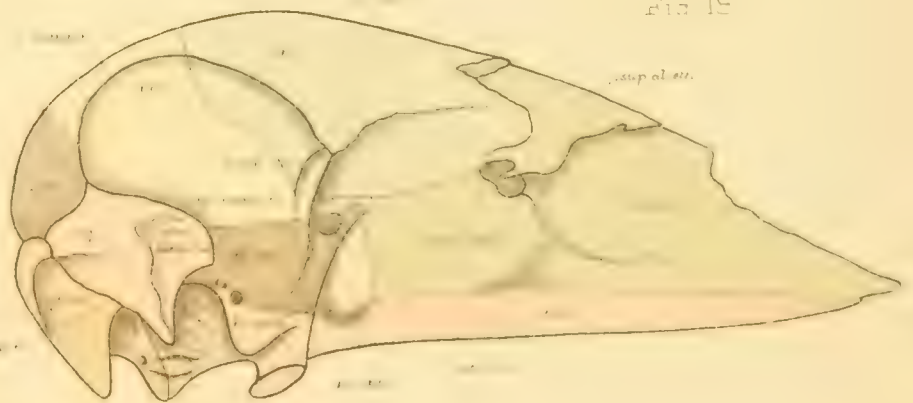
orb. na. for. path for oc. for. trig. for.

na. for. cen. for.

op. for.

pit. for. pre. pit. inf. orb. for.

Fig. 18.



sup. al. for.



Fig. 19.



Fig. 20.

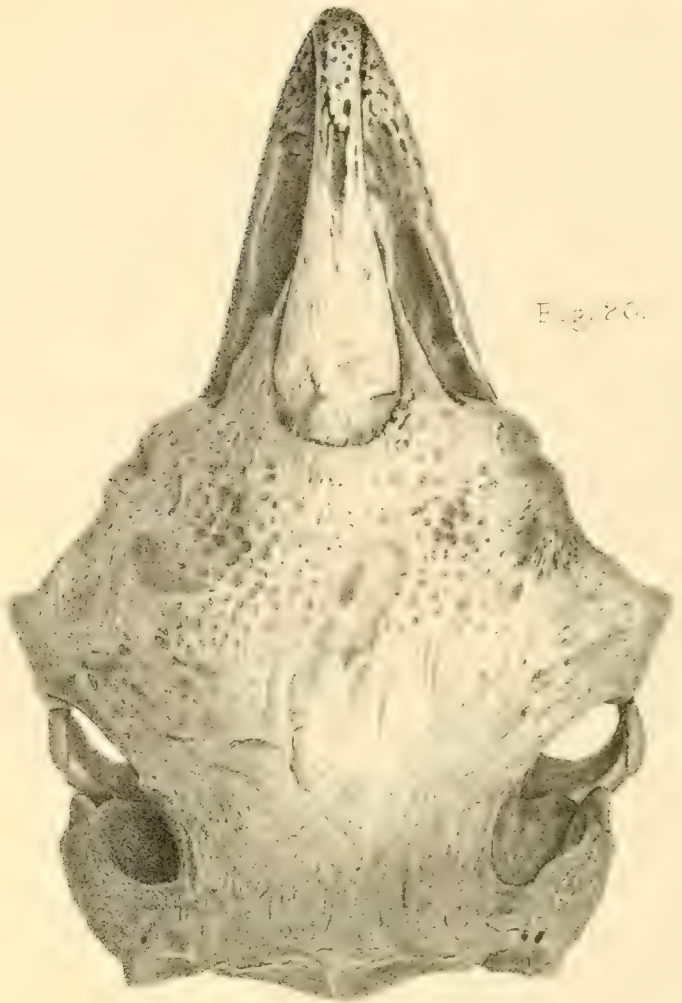


Fig. 22.

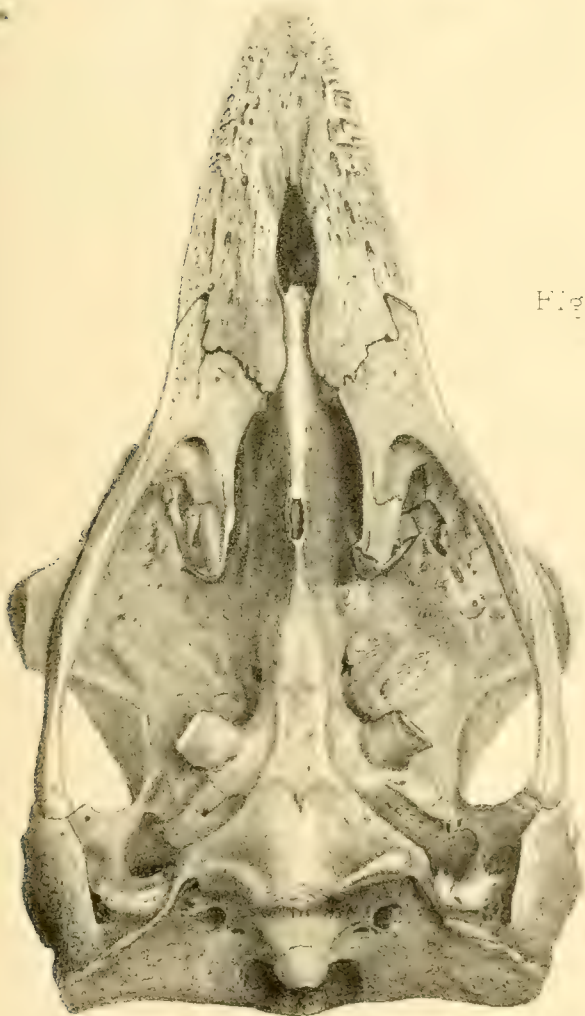
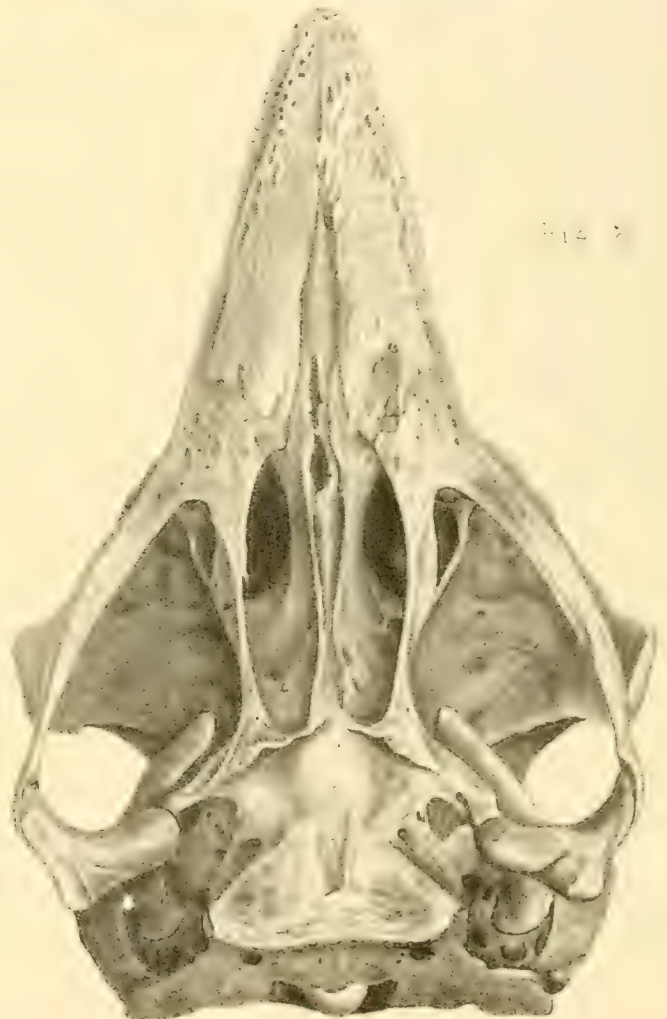
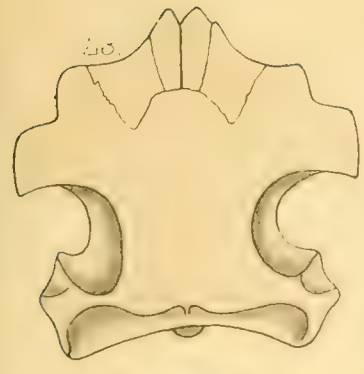


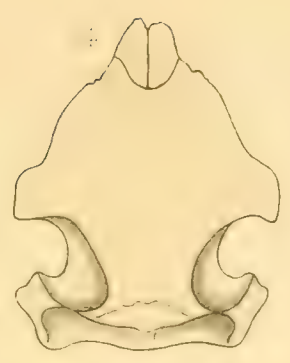
Fig. 21.







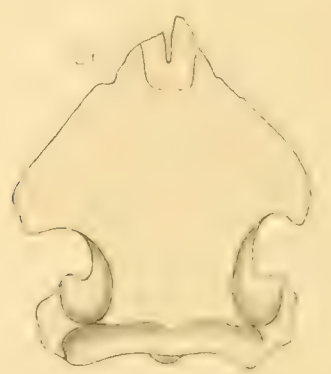
*D. torosus*, Hill



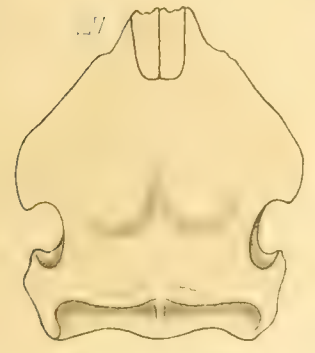
*A. didiformis*, Ow.



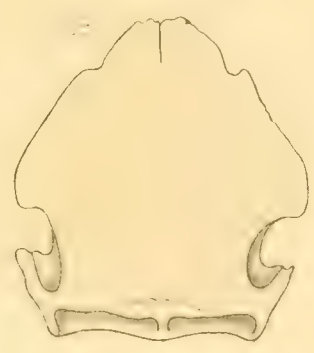
*A. casuarina*, Ow.



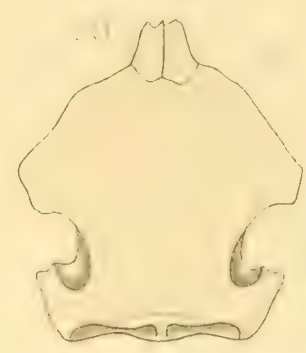
*Emeus*, sp.  $\alpha$ .



*H. isidoreus*, Hill



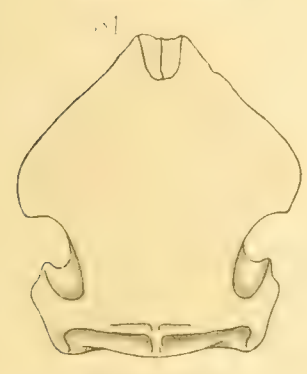
*Mesopteryx*, sp.  $\alpha$ .



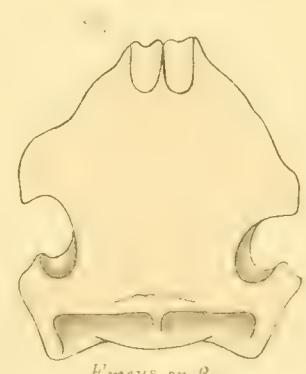
*Mesopteryx*, sp.  $\beta$ .



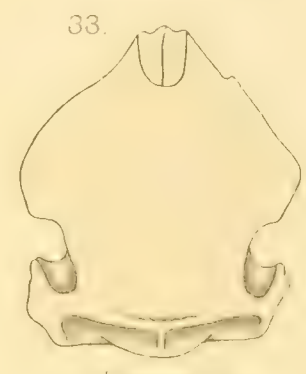
*H. isidoreus*, sp.  $\gamma$ .



*Emeus*, sp.  $\alpha$ .



*Emeus*, sp.  $\beta$ .



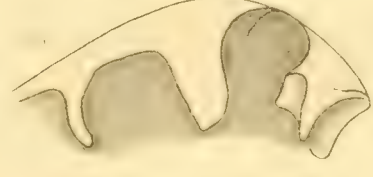
*Emeus*, sp.  $\gamma$ .



*Emeus*, sp.  $\gamma$ .



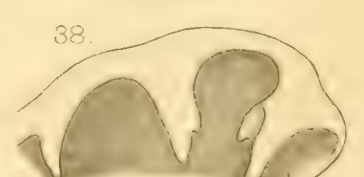
*D. torosus*, Hill



*A. didiformis*, Ow.



*A. casuarina*, Ow.



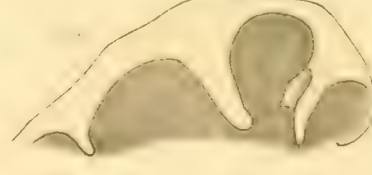
*Emeus*, sp.  $\alpha$ .



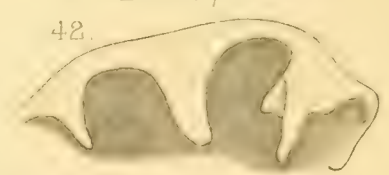
*Pachyornis*, sp.  $\alpha$ .



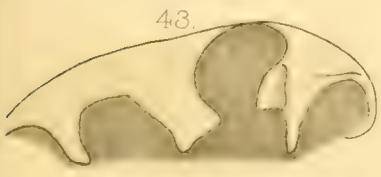
*Emeus*, sp.  $\gamma$ .



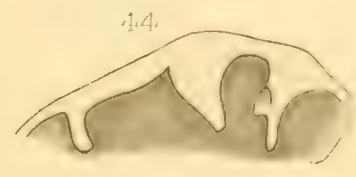
*Mesopteryx*, sp.  $\alpha$ .



*Emeus*, sp.  $\beta$ .



*Pach. elephantopus*, Ow.



*Mesopteryx*, sp.  $\gamma$ .



*Mesopteryx*, sp.  $\beta$ .



*E. crassus*, Ow.

T.J.P. del.  
M.P. Packee lith.







A. Hamilton & T.J.P. del.  
M.P. Parker. lith.

Vest, Newmar. exp.

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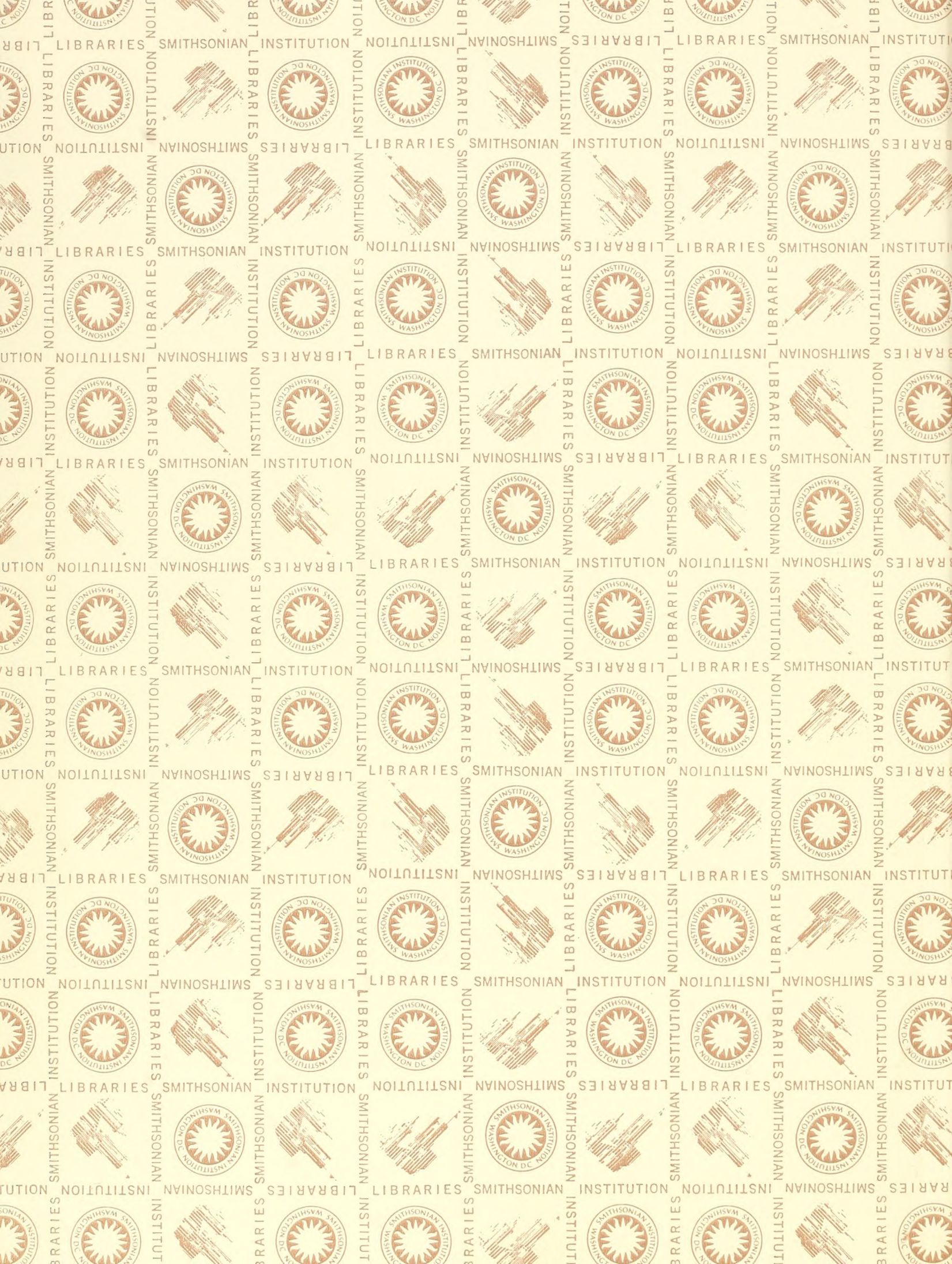
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