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Article XI.— THE SKELETON OF DIATRYMA, A GIGANTIC BIRD FROM THE LOWER EOCENE OF WYOMING.

By W. D. Matthew and Walter Granger.

Plates XX–XXXIII.

Fossil birds are so rare that but little is known about their past history. Four famous discoveries have been made — first the *Archæopteryx* or Reptile-bird of the Jurassic, second the Toothed Birds of the Cretaceous, *Hesperornis* and *Ichthyornis*, third the Moas or Giant Ground-birds of New Zealand, fourth the *Phororhachos* of South America. These are the landmarks of fossil ornithology; they are the only extinct groups which are of any great importance in surveying the records of avian palæontology. There is a long list of names of fossil birds, but the rest all appear to be either near relatives of modern birds or of these extinct types, or are based upon such fragmentary remains that little can be said of their relationships.

To these four landmarks may now be added a fifth no less remarkable, no less important in the past history of birds. This is a gigantic ground-bird, equalling the Moas or the giant *Phororhachos* in bulk and resembling the latter in its huge head and enormous, high, compressed beak, but apparently only distantly related to it, and still more remotely related to the Moas and to the existing ratite birds (ostriches, cassowaries and rheas). It lived during the Lower Eocene, near to the beginning of the Age of Mammals, and was a contemporary and associate of the little *Eohippus* or Four-toed Horse.

In 1874 Professor Cope discovered in the Wasatch formation of New Mexico a few fragments of this gigantic bird, to which he gave the name of *Diatryma gigantea* in 1876,[1] and in 1911 Mr. Granger found certain fragments in the Eocene of Wyoming which were described by Dr. Shufeldt[2] under the name of *Diatryma ajax*. A toe bone from the Eocene of New Jersey, described by Marsh in 1894[3] under the name of *Barornis regens*, is referred by Dr. Shufeldt to *Diatryma*. Last summer Mr. Stein while collecting for the Museum in the Bighorn basin of Wyoming was so fortu-

[1] Cope, 1876, Proc. Acad. Nat. Sci. Phila., p. 10; 1877, Ext. Vert. New Mex., p. 70, pl. xxxii, figs. 23–25.

[2] Shufeldt, 1913, Bull. Amer. Mus. Nat. Hist., Vol. XXXII, p. 287, pll. li–liv; 1915, Trans. Conn. Acad. Sci., Vol. XIX, p. 34, pll. i, ii, v.

[3] Marsh, 1894, Amer. Jour. Sci., Vol. XLVIII, p. 344, text figs.; Shufeldt, 1915, *l. c.*, p. 35, pll. i, v.

nate as to find a nearly complete skeleton of *Diatryma*, so that we now know for the first time what this extraordinary giant bird was like.

The discovery was wholly unexpected. Bird remains are among the rarest of fossils in the American Tertiary formations. During the past twelve years the American Museum has been conducting a systematic and persistent search, in charge of Mr. Granger, for fossil vertebrates in the Eocene and Paleocene formations. The search has been very successful in securing more or less complete skeletons of many of the more characteristic mammals, besides many skulls and thousands of more fragmentary specimens, such as jaws or parts of jaws. A few important specimens of fossil reptiles were also secured. But of fossil birds, great or small, only a very few and very fragmentary specimens were found, the most complete being a hind limb, and nothing so good as a skull, much less a skeleton, of any of them. In four seasons' work in the Bighorn basin of Wyoming, the richest field for Lower Eocene fossils, he obtained two fragments of the *Diatryma*, one consisting of a couple of phalanges or toe bones, the other part of the end of a metatarsus. No traces of it were found in any of the other western formations. The exploration of the badlands of the Bighorn basin had been practically completed, but one or two small areas had not been reached by previous expeditions and it was thought advisable to have Mr. Stein, one of the Museum's staff of experienced collectors, search these areas this past summer, and thus complete the work in this basin. As a result of the season's work he sent in the expected collection of fossil mammals mostly fragmentary, a few important specimens, and in addition this magnificent and quite unexpected bird skeleton.

At first glance it seemed probable that it was an ancestor or relative of the giant birds of the South American Tertiary, *Phororhachos* and its allies. But comparison of the skeleton soon showed that except for the gigantic size and the extraordinary proportions of the head and beak it had very little in common with that singular group. Nor on the other hand did it appear to have any near relationship with any other birds, living or extinct. The nearest in some respects were the emeus and cassowaries of Australia and New Guinea, especially the extinct *Genyornis* of the Australian Pleistocene,[1] although the huge head and short, thick neck contrasted with the small heads and slender necks of all living "ratite" birds, ostriches, rheas, moas etc., and it much exceeded any of them except the moas in bulk of body and massiveness of limbs. Yet its true affinities appeared to be not with the ratites but with the carinate birds, and a consideration of its points

[1] Stirling and Zietz, 1901, 'Fossil Remains of Lake Callabonna.' Mem. Roy. Soc. S. Aust., Vol. I, Pt. II, pp. 41–80, pll. xix–xxiv; 1913, ibid., Pt. IV, pp. 111–126, pll. xxxv–xxxix.

of likeness and unlikeness to *Genyornis*, which is most like it in size and proportions, confirms the view that *Diatryma* is derived from carinate, not from ratite ancestry. There was no suggestion even of remote relationships with the toothed birds of the Cretaceous, either with *Hesperornis* which is said to be remotely related to the modern loons and grebes, or with *Ichthyornis* similarly associated with the modern gannets, cormorants and frigate birds. Nor do the penguins, the auks, the dodo or any of the other outstanding groups of birds afford any nearer basis for comparison.

The only bird with which *Diatryma* seems to show any real affinity is the Cariama or 'seriema' of South America, which is regarded as a very primitive type of carinate and whose affinities have been much disputed, but are now considered as with the cranes (Gruiformes).[1]

The skull and jaws.

The skull is of huge size for a bird, seventeen inches in length as preserved, the greater part made up of an enormous compressed beak six and a half inches high and nine inches long. The lower jaw is correspondingly massive and powerful. It is very different from that of any modern bird, the parrots and other powerful billed types approaching it in some degree, but far from equalling its proportions. The bills of toucans and hornbills are of quite different type. It is superficially like the skull of the extinct *Phororhachos* of the Miocene of South America, but the resemblance apparently does not involve any near relationship.[2] The proportions of the beak are much as in *Phororhachos* except that it lacks the decurved tip. The beak is entirely toothless, and had no groove or pits such as are seen in *Gastornis* of the Cernaysian (Paleocene) of France.[3] In the extinct Australian *Genyornis*[4] the beak is also massive, but not high or compressed, more of the proportions of *Dromœus* to which it was related.

The *anterior nares* are remarkable for their small size, somewhat exaggerated perhaps by crushing but nevertheless unusual. They are situated about two inches in front of the orbit and somewhat nearer to the lower than to the upper border of the beak. The openings are directed forward and a

[1] So adjudged by Stejneger, 1885, Standard Natural History, Vol. IV, p. 119; Pycraft, 1910, 'A History of Birds'; Gadow, Encycl. Brit., art. Bird, etc.

[2] Comparisons made with the figures and descriptions of Ameghino 1895, Bol. Inst. Geog. Arg., Vol. XV, cah. 11, 12, and especially with Andrews, 1899, Trans. Zool. Soc. London, Vol. XV, pp. 55–86, pll. xiv–xvii; also with skeletons of *Pelecyornis* and fragmentary material of *Phororhachos* in the American Museum collections.

[3] See Lemoine, 1878, 'Recherches sur les Oiseaux Fossiles des Terrains Tertiaires Inferieurs des Environs de Reims,' Pt. I, pp. 1–69, pll. i–v; 1881, *ibid.*, Pt. II, pp. 75–170, pll. vi–xi.

[4] Stirling and Zietz, 1913, *l. c.*, pl. xxxvi.

short furrow extends in front of them on the surface of the beak; they are apparently separated by the median septum. They show some analogy to the crows, especially the large billed raven *Corvultur*, in this respect; in the parrots and cockatoos the nares are also restricted and surrounded by

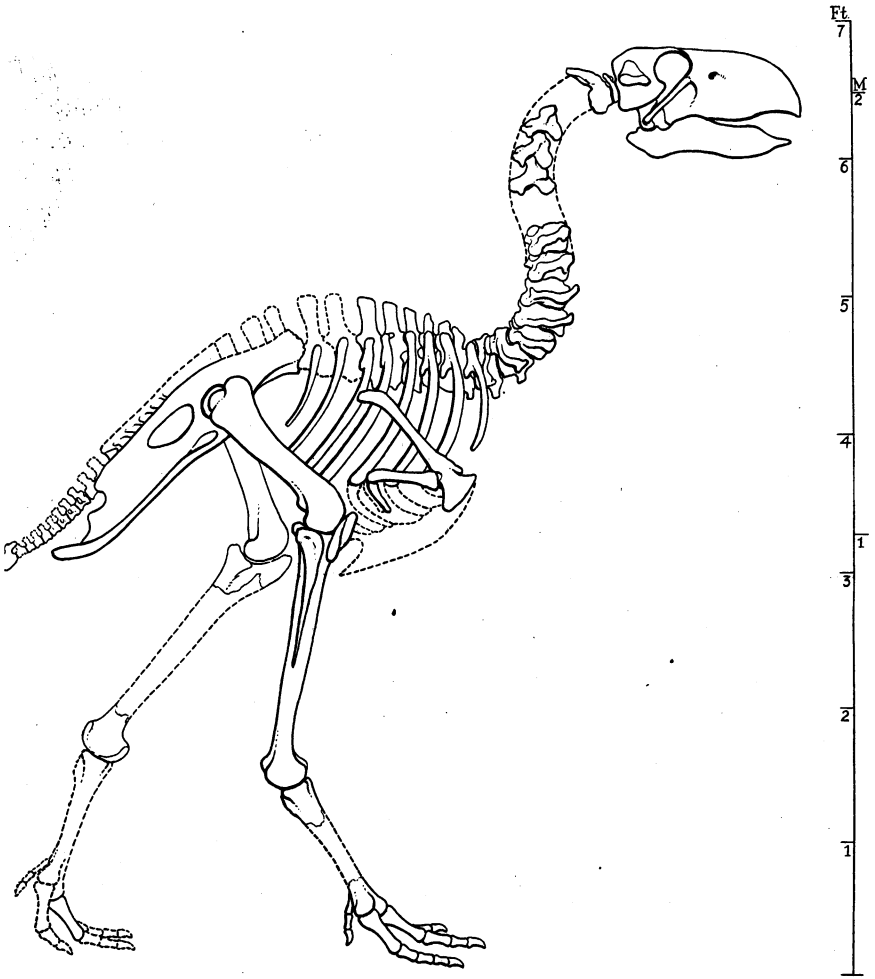


Fig. 1. Reconstructed skeleton of *Diatryma steini*. × $\frac{1}{17}$.

bone, but open more outwardly. In *Phororhachos* the nareal openings are directly in front of the orbit and close to the upper margin of the beak; in *Gastornis* their lower anterior border is much further forward and nearer

the lower margin, but otherwise they are unknown. The upper border of the beak is not thickened in *Diatryma* as it is in *Phororhachos*.

The *orbit* has a heavy, prominent crest of bone above and behind it, not present in *Phororhachos*, and the whole upper half is surrounded by a rather prominent bony ring. This ring does not appear to extend around the lower border of the orbit as it does in the parrots. A broad bony bridge connects the postorbital with the squamosal bone of the skull, making a separate *upper temporal fenestra*, a feature of the skull in many reptiles, but rare in birds. This is also seen in some of the parrot family (cockatoos); but the bridge or "supratemporal arcade" in *Diatryma* is much broader and more massive. It is not regarded as a primitive character inherited from reptilian ancestry, but as a secondary specialization correlated with the development of powerful jaw (masseter) muscles, as is the case with the cockatoos. The *jugal* (quadratojugal) is for a bird rather short and stout with a noticeable sigmoid curvature. It has the usual relations with the quadrate; the maxillary socket is situated at the posterior border of the maxilla but at a considerable distance above its lower border.

The *quadrate* is large, short and stout, with broad, flat orbital process, a single head but with two distinct facets upon it, short, thick neck (otic process) and body, wide and massive articulation for the lower jaw. In the ratite birds the quadrate has but a single head, and is bound in externally by the zygomatic process of the squamosal which overlies it closely so that it is almost immovable. In nearly all other birds it is articulated to the skull by two well separated heads, each upon a distinct neck, and is more free to move, the zygomatic process not overhanging its external face. *Diatryma* appears to be intermediate between the two types, as the two facets for the skull are distinct although conjoined to a single head; and although the zygomatic process does not tie it in as among the ratites the head is buried in a deeply excavated socket surrounded by a heavy border of bone. In *Phororhachos* the quadrate has two well separated heads; in the Cariama the head is single but expanded transversely with two distinct facets on the squamosal, not clearly separated on the quadrate; in neither is the socket so deep as in *Diatryma*. The quadrate of *Genyornis* is single-headed but of quite different type with slender neck and quite small, round head with a single facet for the squamosal. *Genyornis* is typically dromæognathine as *Phororhachos* is typically euornithic; *Cariama* may represent a survival of a very primitive condition among Euornithes, and *Diatryma* a specialization from a somewhat similar stage.

The under side of the skull is much disturbed by crushing so that the exact relations of the bones are not easily distinguished. The palate is very narrow, and almost completely roofed over, by the premaxillæ, the large and

long palatine plates of the maxillæ and the palatine bones. The vomer and pterygoids are not fully recognized but it appears certain that they were reduced in size and that the vomer took no part in the palate roof. The palatines on the other hand are large, stout bones with a heavy inferior border, and their maxillary plates meet in a median suture. They extend forward about five inches in advance of the posterior border of the beak. Posteriorly their articulation for the pterygoids appears to be condylar rather than sutural. The supposed pterygoid is displaced and crushed; it is short and flattened, about two inches long and an inch and a quarter wide with distal articulations at each end which appear to accord with the palatine and quadrate facets for this bone. The maxillopalatines or palatal plates of the maxillæ also meet in a long median suture. The structure of the palate agrees therefore with the Euornithes (Neognathæ) or so-called "Carinate" birds and differs from the Dromæognathæ (Palæognathæ) or "Ratite" birds.[1] It is an extreme example of the desmognathous or roofed palate shown in varying degree by several groups of carinate birds. *Phororhachos* and *Cariama* are both desmognathous, but the latter by no means to this extreme.

The entire postorbital portion of the skull is remarkably short, in contrast to *Gastornis*, and rather in contrast to *Phororhachos*, but as in that genus the occiput is broad and well defined with strong occipital and lambdoidal crests (absent in *Gastornis*). The paroccipital process and posttympanic crest are very prominent, stout and massive; the condyle is large, the foramen magnum small in proportion and the brain-case so far as we can judge from the crushed specimen had the relatively small capacity that one would expect in a bird of such huge size and great antiquity.

The lower jaw is extraordinarily massive, much heavier and deeper than in *Phororhachos* although not so long as in *P. longissimus*. It is comparable in proportions rather with the parrots and cockatoos. The two rami are solidly united into a long spout-shaped symphysis ending in a rather slender tip; the coronoid region is massive and prominent with a large strongly marked muscular scar on its outer side, and the angular process is very large and stout. In *Genyornis* the lower jaw is unusually deep but the symphysis is quite short and the powerful processes of coronoid and angular are not indicated. The few fragments of the jaw of *Gastornis* are of quite different type, with short symphysis, grooved and pitted upper border, etc.

[1] The terms Dromægnathæ and Euornithes of Stejneger are earlier than Palæognathæ and Neognathæ of Pycraft and although not wholly equivalent they are more convenient for the present comparison, as *Ichthyornis*, *Hesperornis* and the penguins are excluded from the Euornithes, but included in Neognathæ. The terms ratite and carinate are used as structural terms, neither corresponding with a primary natural group or evolutionary stage of birds.

The vertebral column.

The vertebræ are short and extraordinarily massive throughout, as the great size of the skull would require. Unfortunately the series is not complete. One vertebra at least is missing behind the axis, and one or more about the middle of the neck. There are probably one or more dorsal vertebræ missing and there may be one caudal lost. Otherwise the series is believed to be complete, but as the vertebræ were disarticulated and somewhat crushed in various directions, there is some uncertainty as to their exact sequence. Eighteen presacrals are preserved and nine caudals besides the pygostyle.

Eleven cervicals or neck vertebræ are preserved, and as at least two more, probably three, are missing, there must have been at least thirteen, probably fourteen. We have the atlas, axis, a series of three anterior cervicals and a series of six posterior cervicals. The axis and anterior cervicals are remarkable for the great reduction of the centrum which is little more than a thick, short plate compressed laterally and not expanded at the articular facets. The chief bulk of the vertebra is composed of the massive spreading zygapophyses with large flat, rounded facets. There are no neural spines and the transverse processes and cervical ribs are quite vestigial, represented only by a small knob below the anterior zygapophysis with a little backwardly directed spine. The posterior cervicals have short, wide centra, flaring moderately at the anterior facets, and expand laterally into great wing-like transverse lamellæ pierced by the large vertebrarterial foramen, the outer and lower part of the wings being formed of the coössified cervical ribs. The zygapophyses are still massive and their facets large, round and plane; they are no longer horizontal, but the anterior pair pitch progressively inward to an angle in the last cervical of about 45° from vertical. The next to the last cervical has a short bifid hypapophysis; the last has a longer single compressed spine-like hypapophysis.

Seven dorsal vertebræ, distinguished as such by having separate ribs, are preserved. The first two are like the cervicals in that they have no spines and large, round, plane, zygapophysial facets. Their rib facets are small, especially the first, and the ribs were undoubtedly unattached to the sternum. The last five dorsals have neural spines, stout and progressively increasing in height, while the transverse processes pitch strongly upward, are stout and carry large rib facets. The hypapophyses are progressively reduced; the last two vertebræ preserved have none. The zygapophysial facets are much smaller, narrow, oval and pitch strongly inward. The centra of all the dorsals are extremely short with widely flaring anterior afects. The articulations of the centra of all the vertebræ behind the axis are of the usual saddle-shaped or heterocœlous type throughout.

The synsacrum is unfortunately much damaged so that the upper portion is mostly gone. It is remarkably short anteriorly, and posteriorly it does not extend more than about three-fifths the length of the postacetabular portion of the pelvis. Apparently it does not include more than two vertebræ in front of the true sacrals; the number behind the true sacrals we have not determined, but the last one is imperfectly coössified, while the first two free caudals appear to be on the verge of coössification to the sacrum. The arches and spines are missing so that we cannot tell whether or not the very considerable height of spine of the last dorsal extended through the sacral vertebræ as it does in the Dromæognathæ;[1] but the shortness anteriorly and tendency to elongate and consolidate posteriorly is a characteristic feature of the ostrich and rhea.

The *caudal vertebræ* are nine besides the pygostyle; one or more may be missing, but the first two, of which only the centra are preserved, are similar to the last sacral, and their facets are imperfect as though they might coössify later in life. The remaining caudals have shorter centra, about as wide as long, short stout spines and vestigial transverse processes. The pygostyle is a flat vertically compressed ovate bone with a large bifid process, antero-superior, if our orientation be correct,[2] much as in the ostrich.

The *ribs* are very flat, thin and wide, with capitulum and tuberculum widely separated and extended upon long necks. Their proportions agree fairly well with those of the cassowary but they are about twice as large in all dimensions. The uncinate processes appear to be either highly vestigial or completely absent — as in *Palamedea.* The sternal segments of the ribs carry about the same relations as in the cassowary.

The *sternum* has not been found. Possibly there may be parts of it unrecognized as yet among the weathered fragments of the skeleton. We may infer from the fact that the coracoids meet in front of it in the median line that it was narrow anteriorly as in *Cariama,* unlike the ratites, and from the great reduction of the wing bones and from the characters of the pectoral girdle that it had no keel, like the ratites and unlike *Cariama.* The sternum of *Phororhachos* has not been described.

The shoulder-girdle and fore limb.

The coracoid and scapula are solidly fused together, meeting end-on as in the ratite birds instead of at a sharp angle as in carinate birds. It is

[1] See Pycraft, 1900, 'Morphology and Phylogeny of the Palæognathæ and Neognathæ,' Trans. Zool. Soc. London, Vol. XV, pp. 211–4, 271.

[2] It is possible that it has been placed upside down. The surface is somewhat damaged by weathering.

remarkably like that of the cassowaries, more so indeed than are the shoulder-girdles of any other ratites. *Phororhachos*, on the other hand, has a fully carinate type of shoulder-girdle; so does *Gastornis*.

The *coracoid* is short, wide and much flattened, its width and length approximately equal. The procoracoid appears to be absent or vestigial; in addition to the usual border for articulation with the sternum there is a small articular facet on the coracoid, apparently for its fellow of the opposite side. In *Cariama* the coracoids almost meet in the median line, being separated only by a narrow splint of bone from the sternum.[1]

The *scapula* has the usual elongate blade, oval in cross-section, flattened and somewhat broadened towards its distal end, and with a rather long, stout, overhanging acromial process.

The *clavicle* may be fused to the tip of the acromial process; if not it is wholly absent as there is no facet for a separate bone.

The resemblance of this shoulder-girdle to that of the emeu-cassowary group is very marked. But in view of the evidence from other parts of the skeleton it would seem that it must be ascribed to parallelism or convergence, not to affinity. If so the resemblances between the shoulder-girdles of the several groups of ratite birds, which are by no means so close, must à fortiori be ascribed to the same agency. This strengthens the case for the polyphyletic origin of the ratite birds.

The *humerus* is reduced to about the same proportion as among the cassowaries; the proximal end is relatively wide and flattened, the distal end narrow and very little expanded at the articular surfaces which are obscurely shown.

The *radius* is doubtfully recognized in a small rod-like bone about as long as one's finger but much slenderer, with the ends not expanded, the facets small and obscure, the supposed distal facet quite oblique.

No other wing bones are recognized.

The pelvis.

The pelvis as a whole is large, very short in front of the acetabulum, broad and long posteriorly. It is articulated in position with the synsacrum but unfortunately the upper part had been much damaged by weathering before fossilization and crushing afterwards, so that some of its important features cannot be determined. It is clear, however, that it is of the euornithic type. The *ilium* and *ischium* are solidly coössified save for the usual

[1] Compare conditions in the several ratite types as contrasted by Pycraft, 1900, Morph. Phyl. Palæognathæ, p. 274.

foramen near the anterior end; they extend much beyond the posterior end of the synsacrum, the lower border of the ischium extending nearly to the posterior end of the pelvis. The *pubis* is a long curving rod-like bone somewhat appressed to the ischium and loosely sutured to it behind the obturator foramen but nowhere coössified, and extending beyond the posterior border of the ischium backwards and inwards towards the median line. Its distal portion is somewhat broadened and thickened. The anterior blade of the ilium is almost wholly lost and its posterior plate is incompletely preserved, so that it is not possible to determine whether the ilia met in the middle line anteriorly, but posteriorly the distinctness of the transverse processes of the synsacral vertebræ seem to indicate that the ilia did not extend wholly over them to the middle line but were separated by a pelvic escutcheon of moderate width.

This type of pelvis differs notably from that of any of the dromæognathine birds in construction, although affording some points of resemblance in proportions. The Dromæognathæ all have the ilium well separated from the ischium and the pubis usually from both.[1] The Euornithes have the ilium and ischium solidly coössified beyond the short ilio-ischiadic foramen, and the pubis slender, closely applied to the ischium and either extending beyond it backward and inward or else more or less vestigial and closely coössified with it.

The nearest ally in structure of the pelvis that we have been able to find among modern birds is the South American *Cariama.* The *Diatryma* pelvis might well be a derivative of this type except that in *Cariama* the anterior portion is decidedly longer, the synsacrum having been extended forward, while the pubis is vestigial, almost thread-like, and the whole post-acetabular portion is shorter. In the essentials, however, the agreement is fairly close, and it is important to note that *Cariama* is regarded as representing an extremely primitive type of the Euornithes, although related to the cranes and in a lesser degree to the Accipitres. The long heavy pubis suggests *Palamedea,* but in that genus the pubis is much more separate from the ischium, and there is little else to suggest any especial relationship to *Diatryma.*

The shortness of the anterior and elongation of the posterior regions of the pelvis are comparable with the ostrich and rhea, but in structure they are wide apart from *Diatryma. Phororhachos* has a quite different type of pelvis, which while euornithic in structure, and also compared by Andrews with that of *Cariama,* differs from the modern genus in almost an opposite direction from the differences seen in *Diatryma;* the anterior and posterior

[1] See Pycraft, *l. c.*, p. 276, for details.

portions are more evenly balanced, the posterior portion is very narrow and the pubis quite vestigial. The pelvis of *Gastornis*, on the other hand, judging from the few fragments preserved, may have been of somewhat similar proportions to that of *Diatryma*, but the ischium is widely different.

The hind limb bones.

In general the hind limb bones compare with the more massive types of the moas in size and proportions, and especially with *Genyornis* the giant extinct emeu of Australia.[1] They are of much the size of the largest species of *Phororhachos* and of *Gastornis*, and considerably smaller than *Dinornis maximus*.[2] We have both femora complete, one tibia complete and both ends of the other, both fibulæ, one lacking the distal end, both ends of one metatarsus and all the phalanges of one foot. The only doubtful point in the reconstruction of the hind limb is the exact length of the metatarsus.

The *femur* is massive, fifteen inches long, six inches across the head (this measurement is probably exaggerated by crushing) and five inches across the condyles. The trochanter is very high and robust, the condyles massive, the outer one decidedly heavier and projecting considerably beyond the inner one. It is longer than in *Genyornis* and the moas, but hardly as massive; in *Phororhachos* the trochanter is not nearly so high or prominent; it agrees better with *Gastornis* than with any other type and allowing for the effects of crushing it may have agreed closely with *G. klaasseni* and *parisiensis*, less nearly with *G. edwardsi*.[3]

The *tibia* is nearly two feet in length, the cnemial ridge rising proximally into a high bifid process, the ectocnemial crest very prominent, compressed, and thickened at its border, the procnemial crest smaller, compressed and unusually distinct. The shaft is straight and the distal end nearly symmetrical, the tendinal bridge almost median, the distal condyles subequal. This tibia agrees very well with that of *Genyornis* in length, robustness, and the prominent cnemial crests, but the shaft is somewhat straighter in *Diatryma* and the cnemial crests more compressed and more deeply separated. These differences may, however, be exaggerated by crushing. In the moas the cnemial crests appear to be still less prominent or distinct, the extensor bridge more internal in position. In *Phororhachos*, as also in *Cariama*, the crests are much compressed but the procnemial is the more prominent of

[1] As described by Stirling and Zietz, *l. c.* (footnote 4) and also by comparison with hind limb bones of this genus in the American Museum.

[2] Compared with the mounted skeleton in the American Museum collection.

[3] See Lemoine, *l. c.*, and Newton, 1886, Trans. Zool. Soc. London, Vol. XII, pp. 143–157, pll. xxviii, xxix, for comparison with hind limb bones of *Gastornis*.

the two and the tibia is longer. The agreement with *Gastornis klaasseni* and *parisiensis* appears to be again quite close, allowing for the crushing of the *Diatryma* tibia.

The *fibula* is slender and comparatively long, comparable with the Dinornithidæ; in *Genyornis* it is shorter, only nine inches in length and thickened beyond the middle of the shaft. In *Phororhachos* the fibula is much shorter in the shaft.

The *metatarsus* is unfortunately incomplete, the shaft being lost through weathering. The proximal and distal ends have been pieced together from fragments, so that they are almost complete. Cope's type of *Diatryma gigantea* consisted of the proximal end and two distal condyles of the metatarsus and it is upon the close agreement with this type that we base our reference of the skeleton to his genus. The perforation of the shaft near the proximal end by which the name *Dia-tryma* was suggested is shown in our specimen, and the form and relations of the tibial facets are in close agreement. The distal condyles also agree in proportions, the shallow grooving, and various details, and the third (inner) condyle which was associated with the type by Shufeldt also agrees with ours except that it is more reduced in size. This feature with slightly larger size and other minor differences are the grounds for regarding the skeleton as a distinct species from *D. gigantea.* It comes from a rather distant locality, Cope's type being from the New Mexican Wasatch, and our skeleton belongs in a somewhat older faunal zone, so that the less reduction of the lateral digits might be expected.

In the moas the three digits are of almost equal size. In *Genyornis* the relative size of the three digits is much as in *Diatryma,* but the lateral digits are not grooved while the median digit is more deeply grooved. In *Phororhachos* the metatarsus is much longer, the two lateral digits about equally reduced.

The *phalanges* are of moderate length and somewhat flattened, especially those of the third digit. The third digit is the largest, the fourth a little smaller, the second smaller than the fourth, while the first is much smaller than the second. The vestigial first metatarsal is doubtfully identified, the corresponding first phalanx and claw more certainly so. The unguals are rather short, triangular in cross-section, pointed and moderately curved; they are of quite different type from the longer, more curved unguals of *Phororhachos,* which are round in cross-section, and they are no less different from the short, rather flattened unguals of the moas.

On the whole, the structure of the hind limb and foot, while presenting many differences of detail from all the great ground birds living or extinct, affords very little to indicate the broader affinities of *Diatryma.* It would take a more thorough knowledge than we possess of the osteology of birds to decide from the hind limb bones alone where its nearest relationships lay.

Summary of Characters.

Diatryma was a gigantic bird, ground-living and with vestigial wings. In bulk of body and limbs it equalled all but the largest of the moas and surpassed any living bird, but was not so tall as an ostrich. The height of the reconstructed skeleton is nearly seven feet. The neck and head were totally unlike any living bird, the neck short and very massive, the head of enormous size with a huge compressed beak much like that of the extinct *Phororhachos* but very different from that of any living bird, and in striking contrast to the small head and slender neck of the living ratite birds.

The construction of the skeleton indicates that despite some resemblances to the ratite birds, *Diatryma* is more nearly related to the Euornithes, and in particular to the modern *Cariama* of South America. It may perhaps be regarded as a very ancient offshoot from the primitive carinate birds of which *Cariama* is a modern survival. Although it resembles the extinct South American *Phororhachos* in size and proportions and was probably of similar habits it does not appear to have been at all nearly related to it and was certainly not in any degree ancestral. Both were gigantic ground birds with enormous heads and high compressed beaks, and the proportions throughout are considerably alike, but they appear to have been independent specializations from primitive carinate birds, *Diatryma* a much more ancient one, *Phororhachos* arising at a much later date. The modern *Cariama* may represent broadly the primitive carinate type from which both were derived. *Phororhachos* although a much later type than *Diatryma* has not gone so far in its adaptive specialization; that is, its convergent resemblances to the ratite birds are not so close, and it shows less departure from the typical carinate birds, in shoulder-girdle, pelvis, hind limb characters, etc. It must be derived from a much later and presumably higher stage in the evolution of the typical euornithine stock. If *Cariama* accurately represented that normal stock, then *Phororhachos* should be in all respects nearer to it than *Diatryma;* but aside from its less extreme adaptive specialization this does not seem to be the case. More probably *Phororhachos* is a derivative of some extinct Eocene type of normal adaptation allied to the Eocene ancestors of *Cariama,* while *Diatryma* would be a derivative of normal Cretaceous Euornithes allied perhaps more closely to the ancestral line of *Cariama.*

The relations of *Diatryma* to *Gastornis* are a more difficult problem. *Gastornis* is a gigantic ground bird whose remains have been found in the Lower Eocene and Paleocene of France, England and Belgium. It was first described from limb bones found in the Suessonian or Lower Eocene, where it is accompanied by fossil mammals very nearly related to those

found with *Diatryma.* But it is chiefly known from the referred species *G. edwardsi* of which a fragmentary skull and various skeleton bones were described from the older Cernaysian formation by Doctor Lemoine.[1] The skull is of gigantic size, like those of *Diatryma* and *Phororhachos,* but is widely different from either in construction, so far as one can judge from the fragments preserved. The skeleton, if Dr. Lemoine has correctly associated the various bones, is also widely different, especially in the shoulder-girdle, from our Wasatch genus. If these skull and skeleton fragments are truly related to the Suessonian *Gastornis* limb bones, then the genus has no affinity to *Diatryma.*

But it is possible that the Cernaysian *G. edwardsi* is not nearly related to the Suessonian *G. parisiensis* and *klaasseni,* and it is also possible that the various bones associated by Lemoine under the name of *G. edwardsi* do not all belong with the hind limb bones which form the type of his species. They come from various localities near Rheims, and were referred apparently upon the basis of suitable size and character, no two of them belonging to one individual, save that the fragments of skull and jaws are believed to be all of one individual.

It is very desirable that the *Gastornis* remains be revised with a view to a possible reconstruction of the skull and reconsideration of the associations as above suggested. We hope that our European confrères may find this practicable in the near future. But it is quite clear that the *Gastornis* skull represents a gigantic ground bird, similar in adaptation to *Diatryma,* and only slightly older, but not nearly related; and that *Phororhachos* represents a third similar adaptation, also independent and of much later age.

Systematic Position.

Cariama is placed by all modern authors in the Gruiformes, but considered evidently as a primitive and marginal member of the order. The systematic position of *Phororhachos* is disputed; some authors appear disposed to place it in the Gruiformes on account of its relationship to *Cariama;* others are disposed to maintain the Order Stereornithes in an amended sense to include *Phororhachos* and its allies. But it does not appear reasonable to us to include a type of such extreme specialization and great antiquity as *Diatryma* with the Gruiformes merely because of a necessarily remote relationship to a primitive member of that order. The common ancestral stock must necessarily date far back in the Cretaceous, very likely

[1] The Cernaysian mammal fauna is not closely related to that of the Suessonian and Wasatch, and is regarded as of equivalent age to the Torrejon fauna of the American Paleocene.

antedating the earliest separation of various other orders from the primitive euornithic stock. And the extreme specialization affords obvious structural distinctions which are elsewhere considered as of high rank in the classification of birds.

It appears necessary therefore to place *Diatryma* in a new order and family, as it differs too fundamentally from the Gastornithes and Stereornithes to fall into either order and is but remotely related to any other known group of birds. They may be defined provisionally as follows:

Order DIATRYMÆ.

Euornithine birds, holorhinal, with desmognathous palate; the quadrate with imperfectly double head; pterygoid short, movably articulated to palatine and quadrate; palatines large, taking part in palatine roof; vomers reduced or vestigial; the zygomatic process of the squamosal not overhanging quadrate but united with postorbital bar into a superior temporal arcade; orbits open inferiorly. Wings more or less vestigial; scapula fused with coracoid and scapulo-coracoid angle approximating 180°; coracoid a short, broad, expanded plate; no procoracoid; clavicle vestigial or absent. Pelvis wide and long posteriorly; ischium united to ilium save for a short foramen; pubes long, appressed to lower border of ischium, arching inward beyond its posterior tip. Feet tetradactyl; the first digit reduced, ?opposed.

Family DIATRYMIDÆ.

Skull greatly enlarged with powerful compressed beak; heavy jaw; broad supratemporal arcade; quadrate head socketed in a deep fossa; occiput broad with prominent crest; palate narrow, very completely roofed over. Neck short and very powerful. Wings greatly reduced; coracoids meeting in front of scapula. Pelvis very short anteriorly, broad and long posteriorly with heavy pubes nearly meeting behind. Hind limbs large and stout; feet with vestigial first digit; second digit smaller than fourth; third the largest. Unguals rather short and moderately curved, triangular in cross-section with a deep groove upon one side.

Genus **Diatryma** *Cope.*

Gigantic and massively proportioned, the beak like that of *Phororhachos* but lacking the decurved tip. Anterior nares small, situate about two inches in front of orbit and midway between top and bottom of skull. Lower jaw

much heavier than in *Phororhachos* with powerful coronoid and angular processes, long symphysis rather slender anteriorly. Anterior cervicals articulating mainly through their zygapophyses, the centra much reduced. Posterior dorsals with massive and moderately high spines. Limb bones comparable to those of the moas in size and proportions.

The above analysis of the ordinal, family and generic characters is necessarily tentative as no other genus than *Diatryma* is known. Four described species.

D. gigantea Cope. Lower Eocene (Lower Wasatch) of New Mexico. Type, proximal and distal ends of metatarsus. Outer digit considerably reduced.

D. ajax Shufeldt. Lower Eocene (Basal Wasatch) of Wyoming. Type, part of distal end of metatarsus. Size one-fourth greater than *D. gigantea.*

D. steini sp. nov. Lower Eocene (Lower Wasatch) of Wyoming. Type, a skeleton nearly complete. Lower Eocene, Gray Bull horizon, Wasatch formation, S. Elk Creek, Bighorn basin, Wyoming. Found by William Stein of American Museum Expedition of 1916. Amer. Mus. No. 6169. Size of *D. gigantea,* outer digit less reduced.

?*D. regens* (Marsh). Eocene, New Jersey. Type, a proximal phalanx. Referred provisionally on authority of Shufeldt, but practically indeterminate.

General Conclusions.

In conclusion a few words may be permitted as to the bearing of this new discovery upon the general lines of avian evolution.

It has been made sufficiently clear that *Diatryma* stands well apart, widely separated from any other group of birds. It shows a number of unique features, some adaptive, some more probably primitive, in the skull and skeleton. Although paralleling *Phororhachos* in adaptation it is evidently quite unrelated, and its resemblances to the ratite birds appear to be largely, if not wholly, conditioned by similar adaptation.

But its isolated position would hardly have been suspected had we known only the limb and foot bones. Such authorities as Cope regarded it as a relative of the rhea, and Shufeldt of the ostrich, and neither had any suspicion of its extraordinary characters — nor does it seem likely that a complete knowledge of the hind limb bones would have materially altered their concept of its form and near affinity to the ratites. Lucas suggested its affinity to *Phororhachos* partly upon the ground of faunal dispersal,[1] but

[1] Lucas, 1903, Proc. U. S. Nat. Mus., Vol. XXVI, p. 556.

this suggestion, while implying a view of probable skull proportions and adaptation that has been strikingly verified, appears also wide of the mark as regards any real affinity. Yet a plausible argument could have been maintained for this view too, had we known no more than the hind limb of *Diatryma;* and had we had to deal with an incomplete and badly preserved skull it would have been regarded as well proven.

Now with very few exceptions all our knowledge of the older Tertiary and Cretaceous birds is based upon very fragmentary material, most of it upon fragments of the hind limb or foot or of the humerus. These fragments have been named and compared to modern forms, referred to modern families, often to modern genera. The recorded geological range of these genera is thus supposed to extend backward into the early Tertiary or even into the Cretaceous. In one instance a bird from the marine Cretaceous is referred by Shufeldt to an existing species of grouse. The modern types of birds thus have apparently an antiquity of origin in striking contrast with the modern types of Mammalia. No modern genus of mammals extends back further than the Miocene; most of them originated later. Most of the modern families originated in the middle or later Tertiary; with the possible exception of the Didelphidæ and Centetidæ none are of pre-Tertiary origin. Setting aside *Archæopteryx,* the five types among the older birds which are adequately known — *Hesperornis* and *Ichthyornis* of the late Cretaceous, *Gastornis, Diatryma* and *Gallinuloides* of the Eocene, are very far from being nearly related to the modern birds which they resemble in adaptation. But nevertheless the fragmentary evidence has apparently given a widespread impression of the antiquity of differentiation of the modern bird types. This appears to have no sound foundation. Theoretically it ought not to be so. It is true that certain well known reptilian and lower types, such as crocodiles, turtles, etc., have persisted from the beginning of the Tertiary to the present day with very little alteration, the changes hardly amounting to generic, much less family value. These, however, are, so-to-speak, dead groups. They are and have been during that time strictly limited to a narrowly circumscribed range of adaptation and environment. On the contrary the birds are, like the mammals, of widely varying adaptation, a highly progressive, adaptable class of animals, and we should expect them to exhibit a good deal of parallelism to mammals in the broad features of their evolutionary history. It seems probable that this was the case, that the modern genera of birds did not in reality appear earlier than the modern genera of mammals, and that if we knew more about the early Tertiary birds we should find that they were not nearly so close to modern genera as they have been supposed to be. So far as we can judge from the analogy of fossil mammals, we would suspect that

fragmentary remains of Eocene birds referred to the modern cranes, grouse, eagles or owls, were more probably similar adaptations no more related to the modern types than *Didymictis* to *Viverra* or *Patriofelis* to *Felis*, while the true lines of ancestry of modern bird types may well involve as wide a change in structure and habits as separates *Eohippus* from *Equus* or *Miacis* from *Canis*.

Shufeldt's recent revisions of the fossil birds of North America are of the greatest value in providing for the first time competent descriptions and excellent photographs of the numerous Tertiary and Cretaceous types which have hitherto been nothing but names. But he has shown very clearly the wholly provisional nature of all these identifications and the fragmentary and inadequate character of all the material. It is by no means desirable to change the provisional identifications, provided they are understood always as comparisons and not as positive references. But they afford no ground for concluding that the antiquity of modern groups of birds is greater than that of modern groups of mammals. Nor, on the other hand, does it appear that they were notably less ancient. *Diatryma* shows that the characters and differentiation of the Euornithes were already well established by the beginning of the Tertiary period, and they had passed decidedly and irrevocably beyond the more primitive stages preserved in the struthious birds, just as the placental mammals at the beginning of the Tertiary were already clearly differentiated from the marsupials. While the orders of birds, or some of them, may have originated in the Tertiary, the primary divisions must date well back into the Mesozoic as they unquestionably do among mammals. Gadow's conclusion (Encycl. Brit., art. Birds) that "The Ratitæ branched off, probably during the Eocene period, from that still indifferent stock which gave rise to the Tinami + Galli + Gruiformes, when the members of this stock were still in possession of those archaic characters which distinguish Ratitæ from Carinatæ" if it be accurate as to phylogenetic relations, places the differentiation at much too recent a date.

On the whole the evidence of the *Diatryma* seems to support the view that the evolution and differentiation of mammals and birds was largely similar in time and manner and conditioned by similar causes. That is to say, the Cenozoic was the era of the great expansion and dominance of euornithic birds as it was of placental mammals, of the progressive differentiation of the modern orders, then of the modern genera, finally of modern species. The Tertiary was the Age of Birds as it was also the Age of Mammals — only we shall never in our day have the evidence to prove it conclusively. But like the mammals, the birds originated long before the dawn of the Tertiary, probably very early in the Mesozoic, and the Euornithes, like the Placentals, were fully differentiated from the older groups by the end of the Cretaceous.

EXPLANATION OF PLATES XX TO XXXIII.

Diatryma steini, type specimen, Amer. Mus. Coll. No. 6169.

The quadrate and ?pterygoid are figured ½ natural size; all other figures are ¼ natural size.

The presacral vertebræ are arranged and numbered in what is considered their proper sequence.

Photographs are by Mr. Albert Thomson; the restoration by Mr. Erwin S. Christman.

PLATE XX. *Skull:* Fig. 1a, right side; 1b, left side; 1c, palatal view.

PLATE XXI. *Mandible:* Fig. 1a, viewed from above; 1b, from right side; 1c, from below.

PLATE XXII. Fig. 1. The *skull*, viewed from behind. Fig. 2a. *Quadrate*, anterior view; 2b, external view; 2c, inferior view; 2d, superior view. Fig. 3. *?Pterygoid.* Fig. 4a. *Atlas vertebra*, viewed from in front; 4b, from left side; 4c, from behind.

PLATE XXIII. Fig. 1a. *Axis vertebra*, viewed from the front; 1b, from left side; 1c, from behind. Fig. 2a. *Anterior cervical vertebra*, viewed from above; 2b, from left side; 2c, from the front. Fig. 3a. *Anterior cervical vertebra*, viewed from above; 3b, from left side; 3c, from the front. Fig. 4a. *Anterior cervical vertebra*, viewed from above; 4b, from left side; 4c, from the front.

PLATE XXIV. Fig. 1a. *Anterior cervical vertebra*, viewed from the front; 1b, from left side. Fig. 2a. *Posterior cervical vertebra*, viewed from in front; 2b, from behind. Fig. 3a. *Posterior cervical vertebra*, viewed from front; 3b, from behind; 3c, from below; 3d, from above.

PLATE XXV. Fig. 1a. *Posterior cervical vertebra*, dorsal view; 1b, left side view; 1c, anterior view; 1d, posterior view. Fig. 2a. *Posterior cervical vertebra*, anterior view; 2b, posterior view. Fig. 3a. *Posterior cervical vertebra*, viewed from the front; 3b, from behind.

PLATE XXVI. Fig. 1a. *Anterior dorsal vertebra*, viewed from the front; 1b, from behind. Fig. 2a. *Anterior dorsal vertebra*, viewed from the front; 2b, from behind. Fig. 3a. *Anterior dorsal vertebra*, viewed from the front; 3b, from left side; 3c, from behind. Fig. 4a. *Anterior dorsal vertebra*, viewed from the front; 4b, from left side; 4c, from behind. (The photographs for figures 4a and 4b were made before the hypophysis was attached).

PLATE XXVII. Fig. 1a. *Posterior dorsal vertebra*, viewed from the front; 1b, from left side. Fig. 2a. *Posterior dorsal vertebra*, viewed from the front; 2b, from left side. Fig. 3a. *Posterior dorsal vertebra*, viewed from the front; 3b, from left side. Fig. 4a. *Caudal vertebra*, viewed from the front; 4b, from left side. Fig. 5a. *Caudal vertebra*, viewed from the front; 5b, from left side. Fig. 6a. *Pygostyle*, viewed from the front; 6b, from left side.

PLATE XXVIII. Six *dorsal ribs* of the right side and (lower figures) the distal ends of four *sternal ribs*.

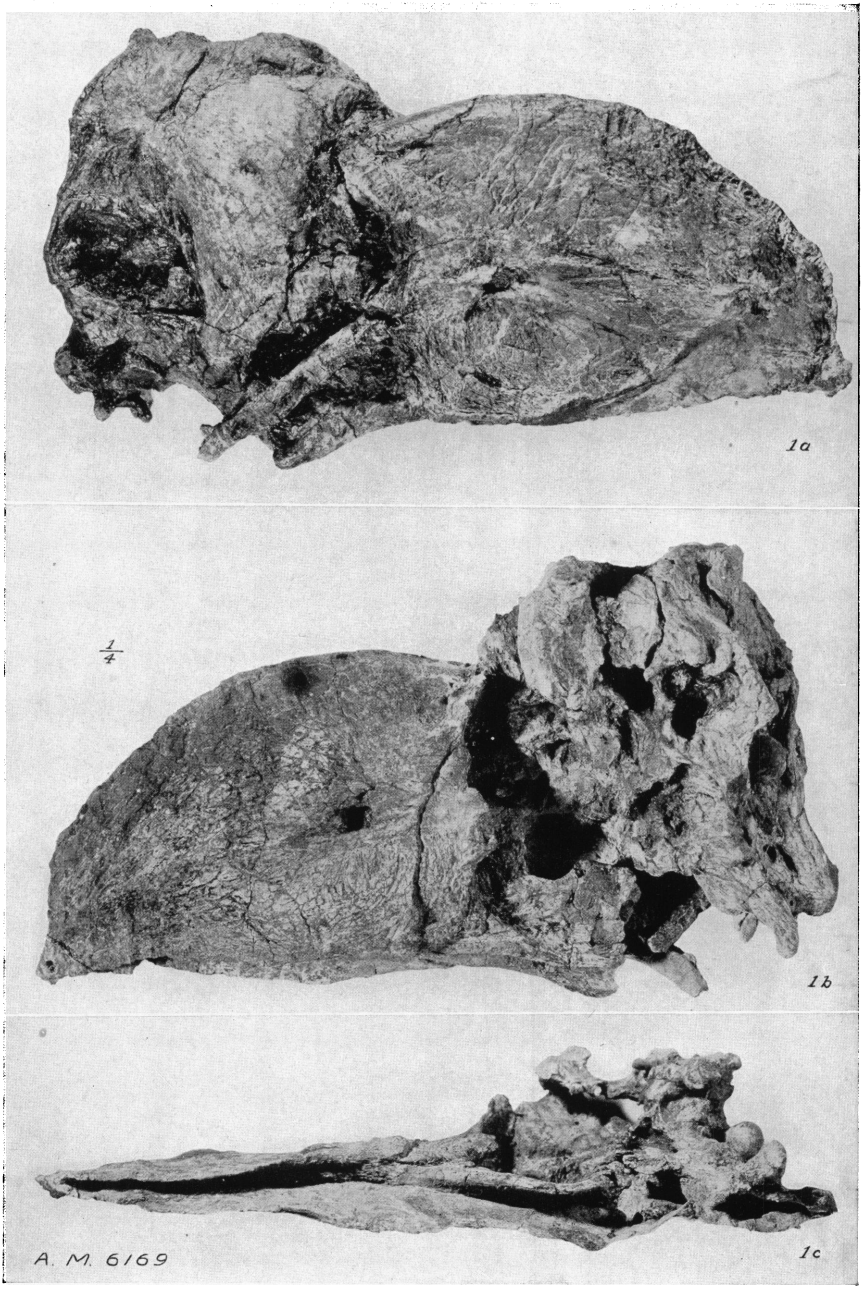
PLATE XXIX. *Pelvis* and *sacrum*: Fig. 1a, ventral view. Fig. 1b, view of left side.

PLATE XXX. *Pelvis* and *sacrum*: Fig. 1a, dorsal view. Fig. 1b, view of right side.

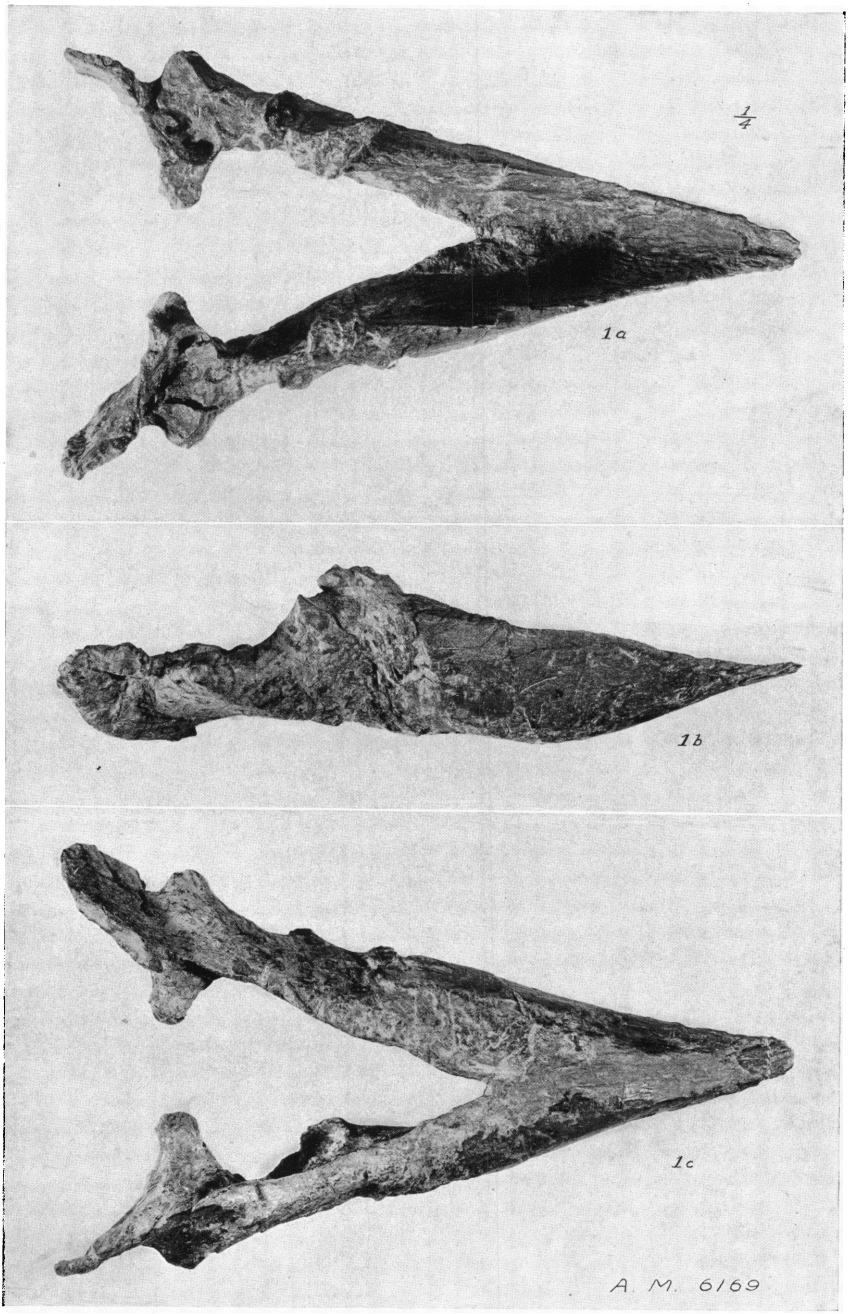
PLATE XXXI. Fig. 1. Right *scapulo-coracoid*, outer view. Fig. 2. *Humerus* of ? right side. Fig. 3. *?Radius*. Fig. 4. Front view of left *femur*. Fig. 5. Hind view of right *femur*.

PLATE XXXII. Fig. 1. Front view of right *tibia*. Fig. 2. Outer view of right *fibula*. Fig. 3. Front view of *pes*.

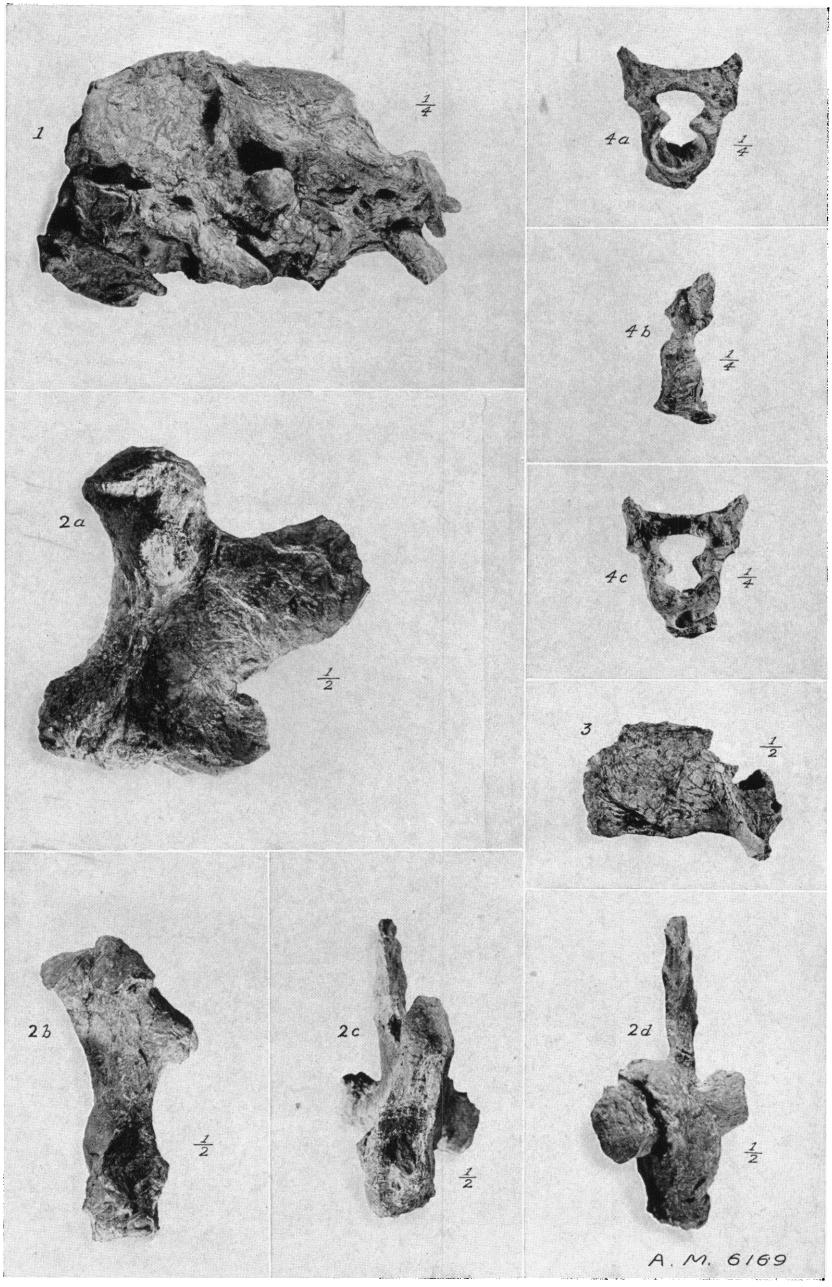
PLATE XXXIII. Restoration of *Diatryma steini*, one twenty-fifth natural size. In this restoration the cassowary has been used as a guide for the external characters, as it affords the nearest parallel among living birds in general proportions and adaptive specializations of the skeleton. Except as to size, proportions, and the characters of head and feet, the restoration is of course, conjectural.



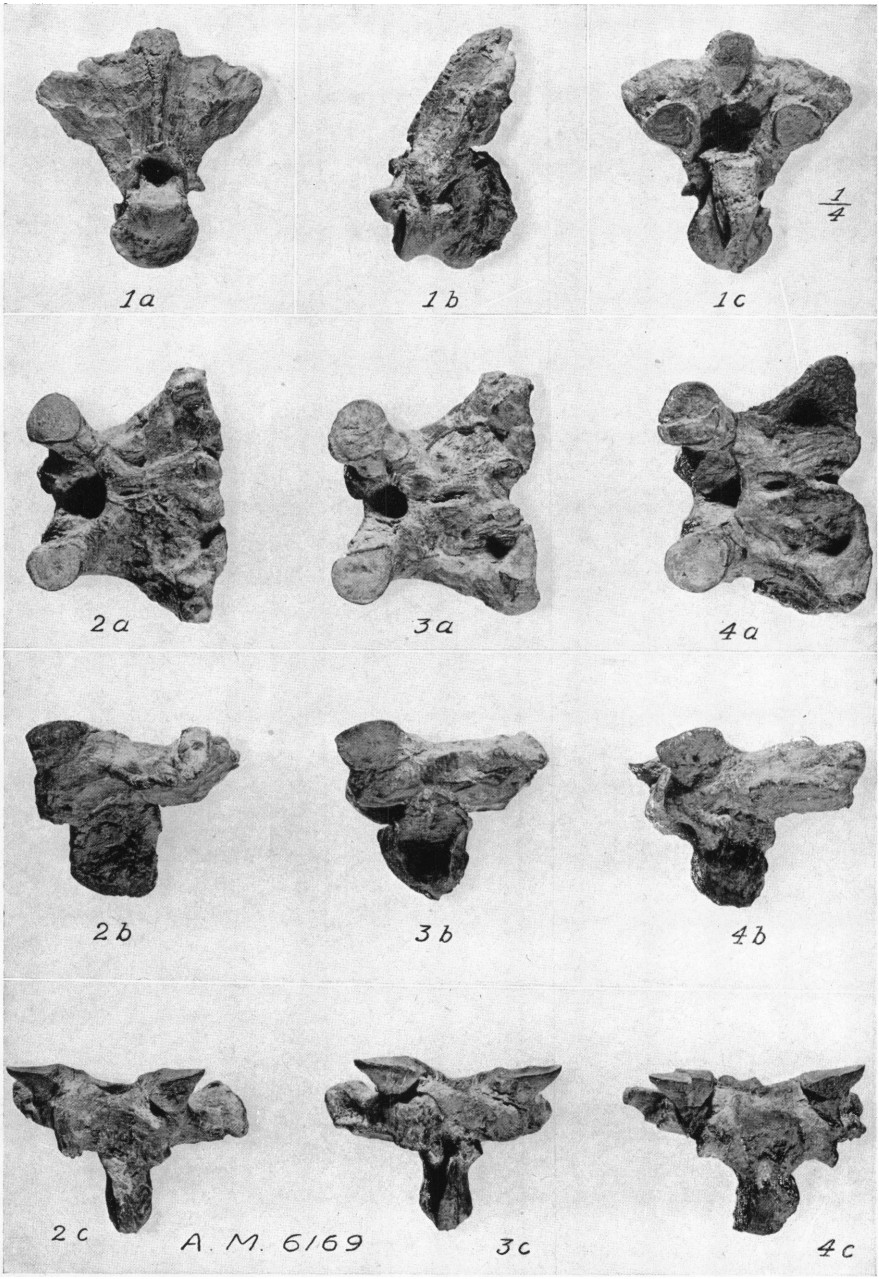
DIATRYMA STEINI.
Skull.



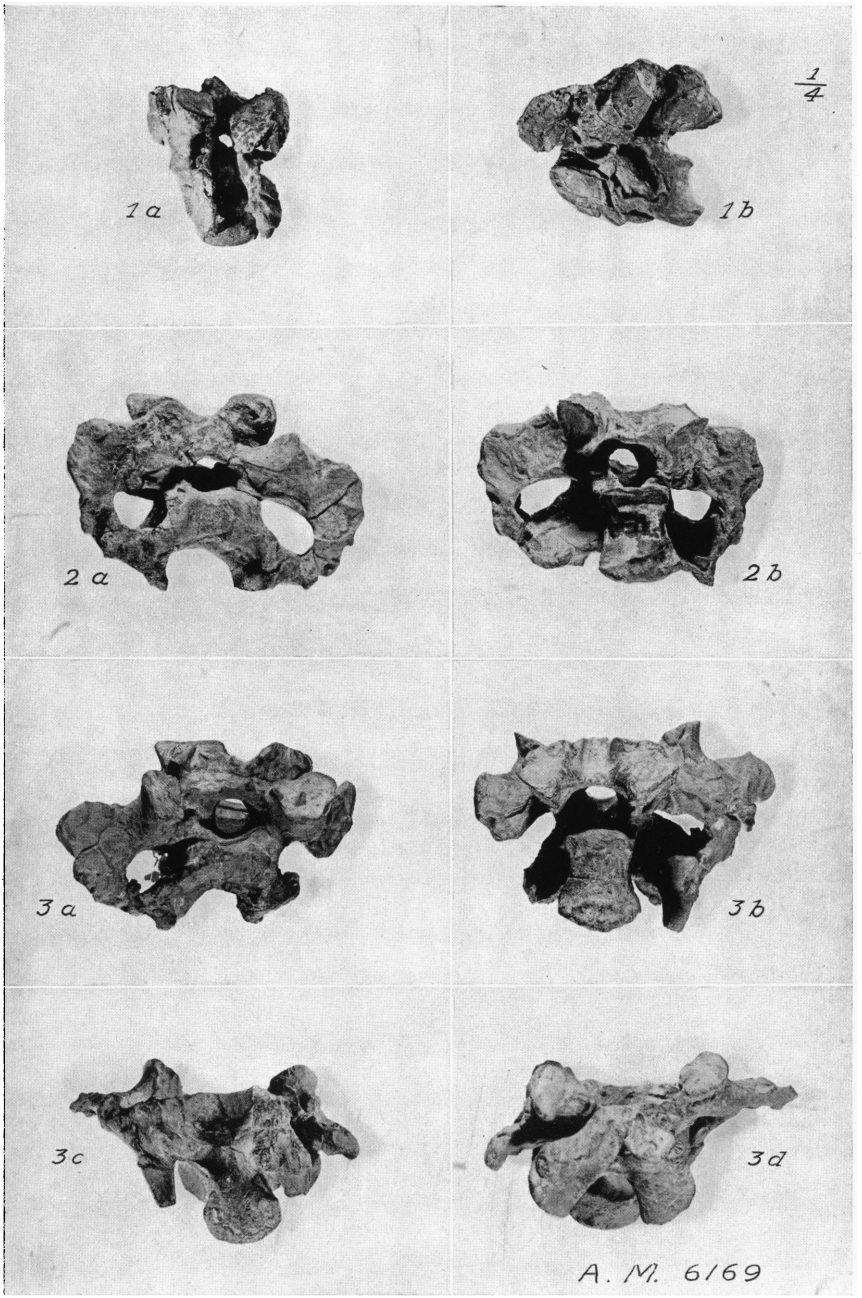
DIATRYMA STEINI.
Mandible.



DIATRYMA STEINI.
Occiput, quadrate, (?) pterygoid and atlas.



DIATRYMA STEINI.
Cervical vertebræ.



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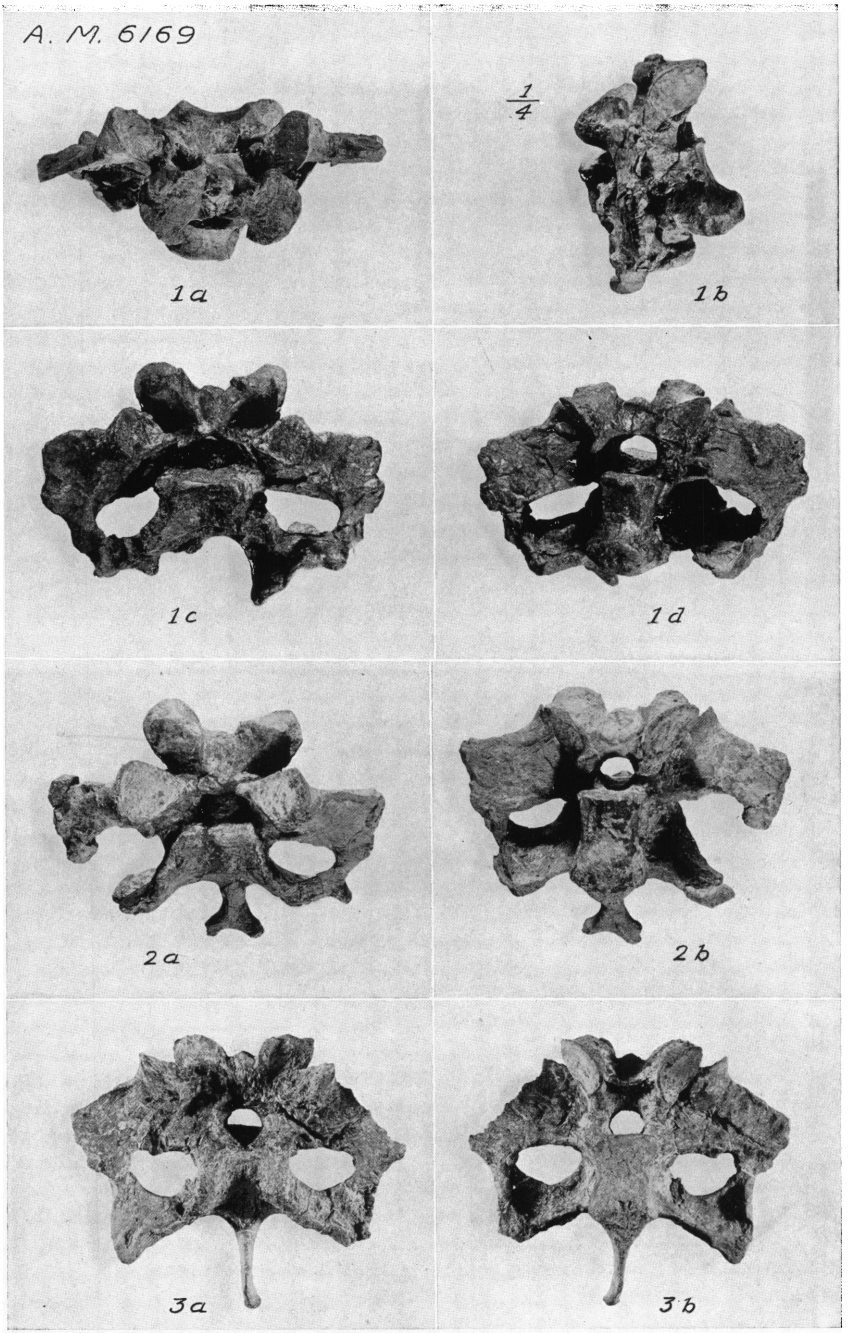
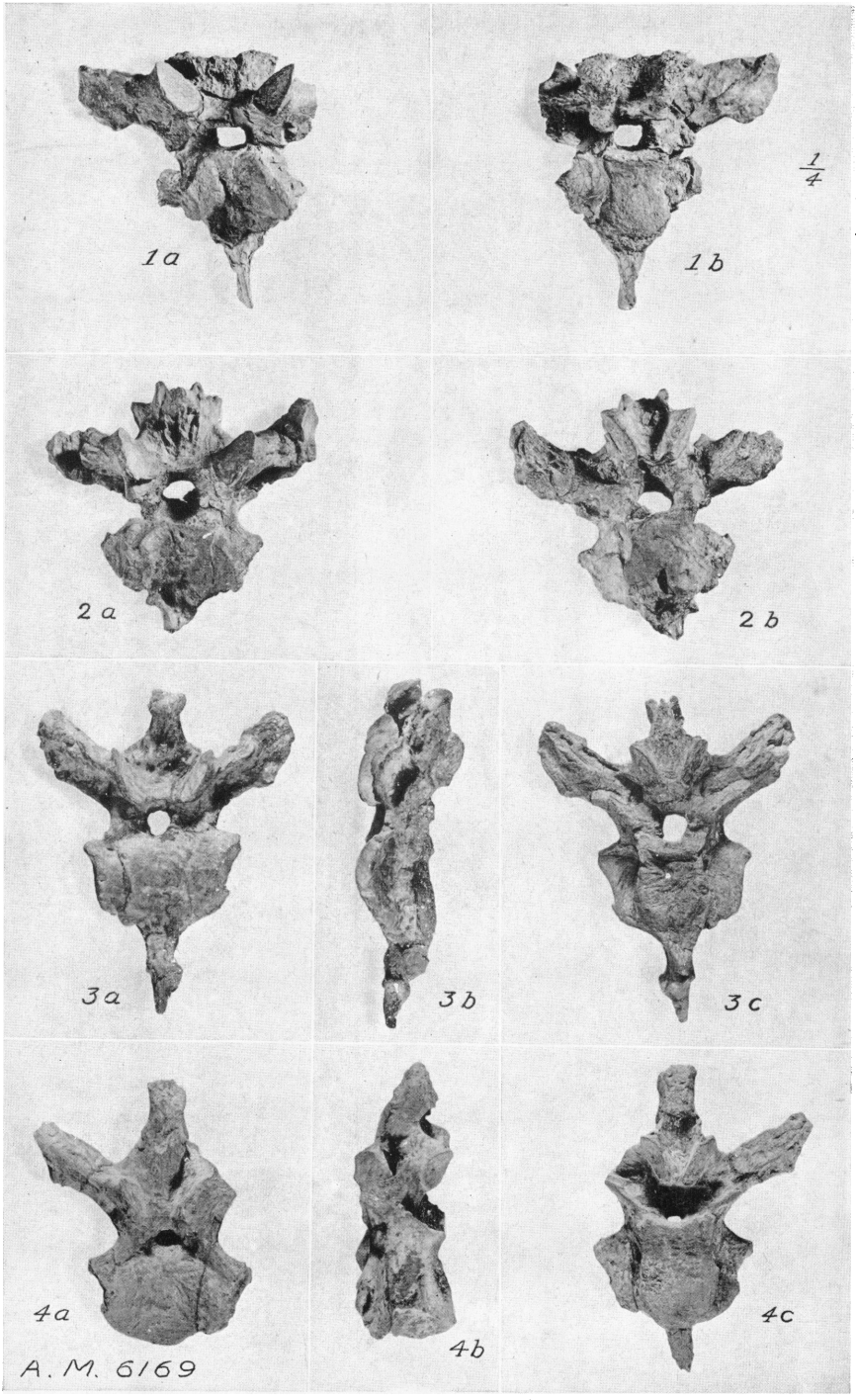
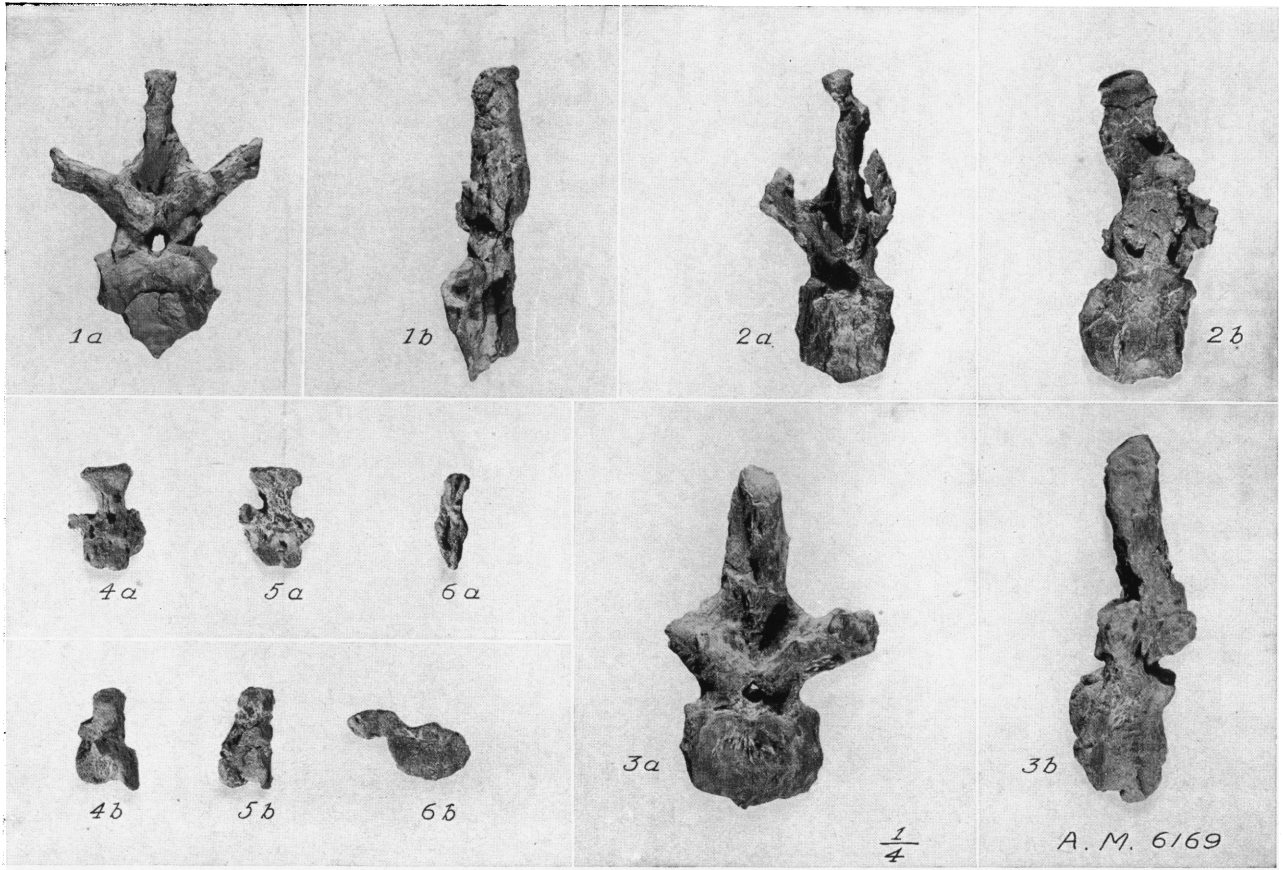
Cervical vertebræ.



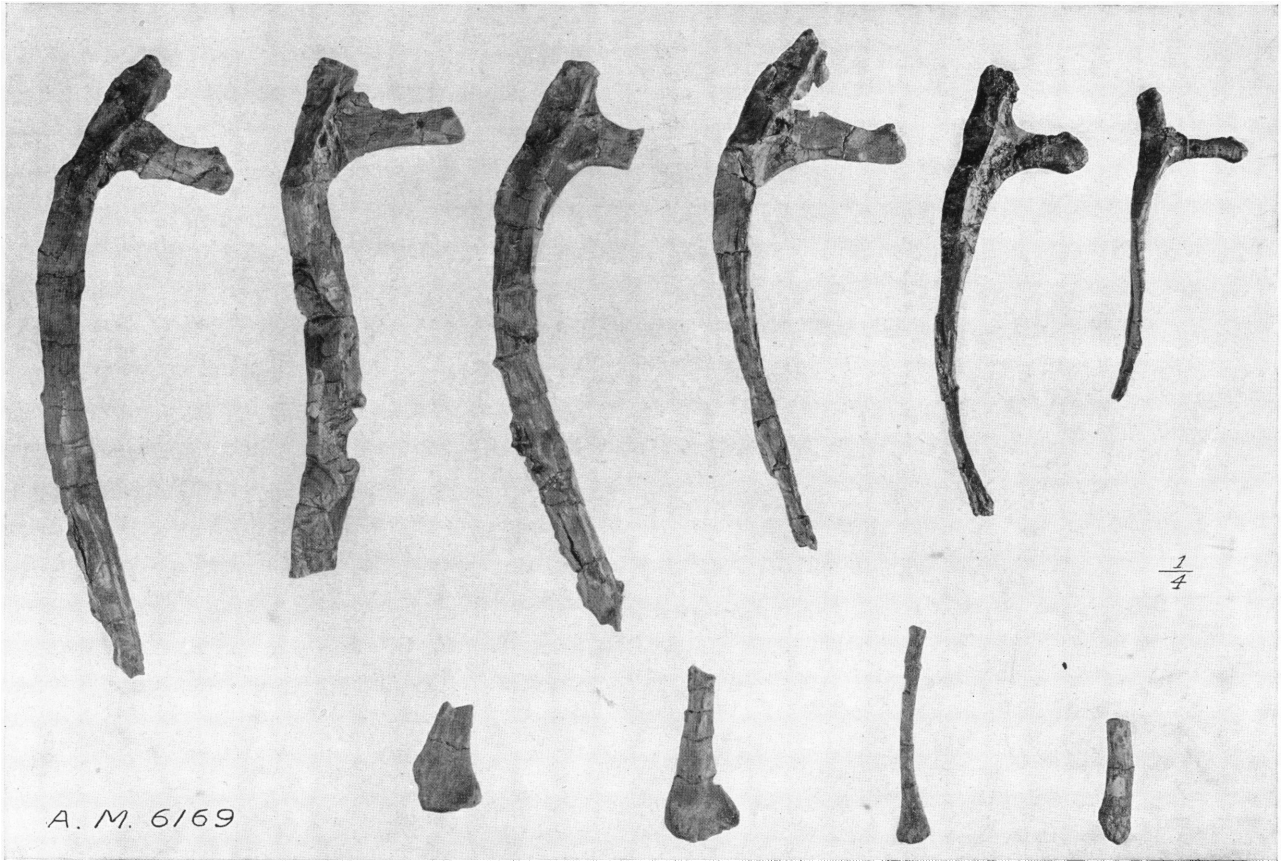
DIATRYMA STEINI.
Cervical vertebræ.



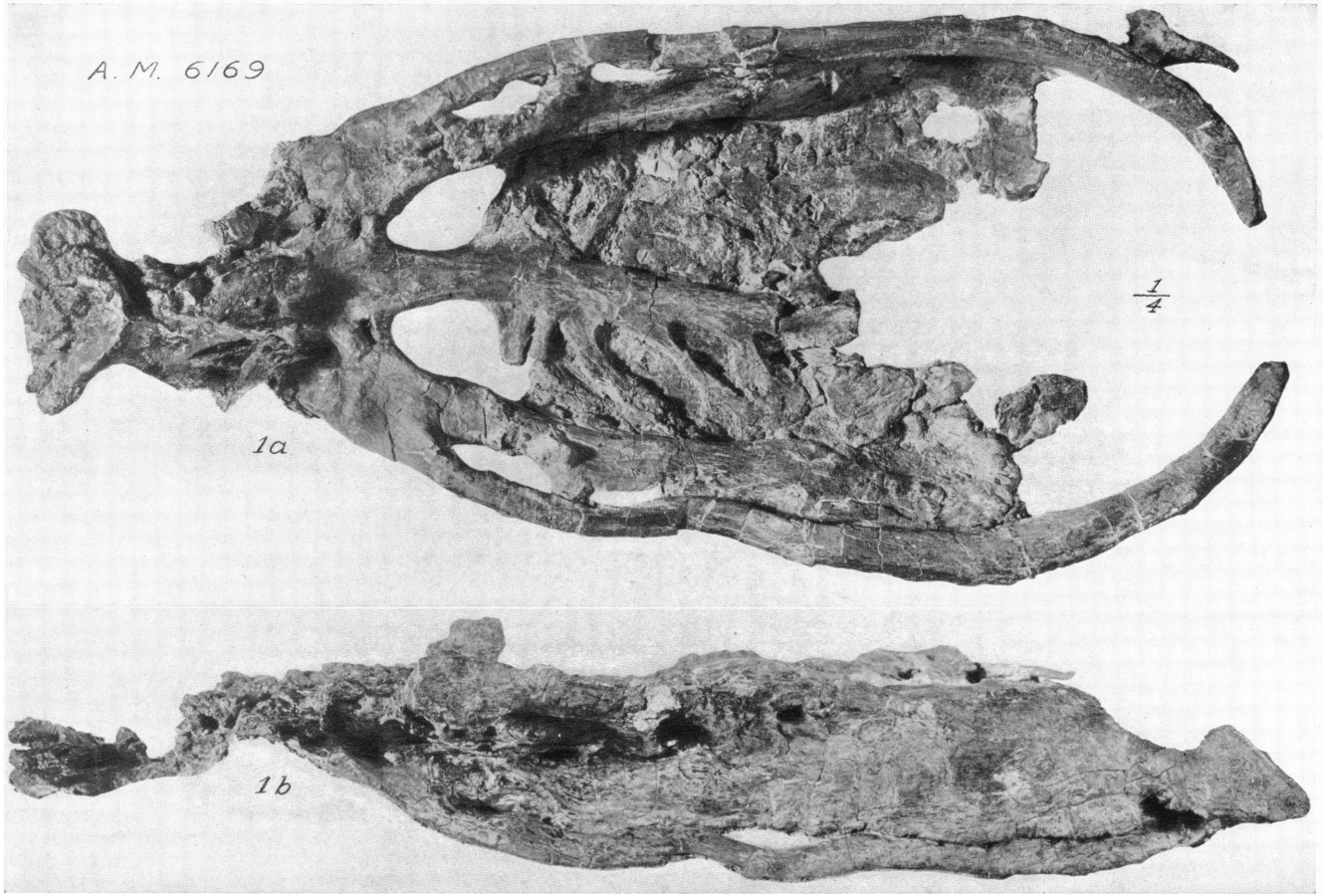
DIATRYMA STEINI.
Dorsal vertebræ.



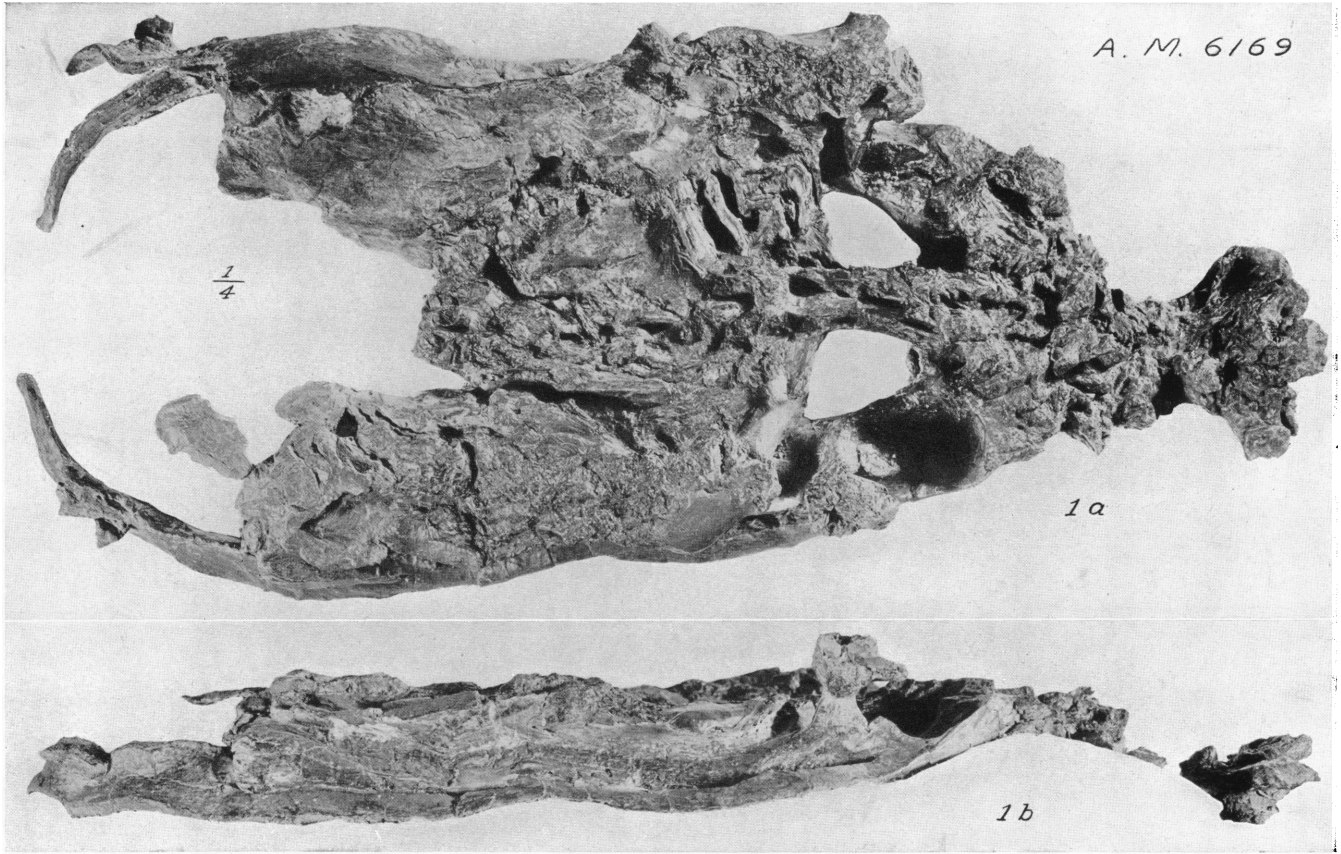
DIATRYMA STEINI.
Dorsal and caudal vertebræ.



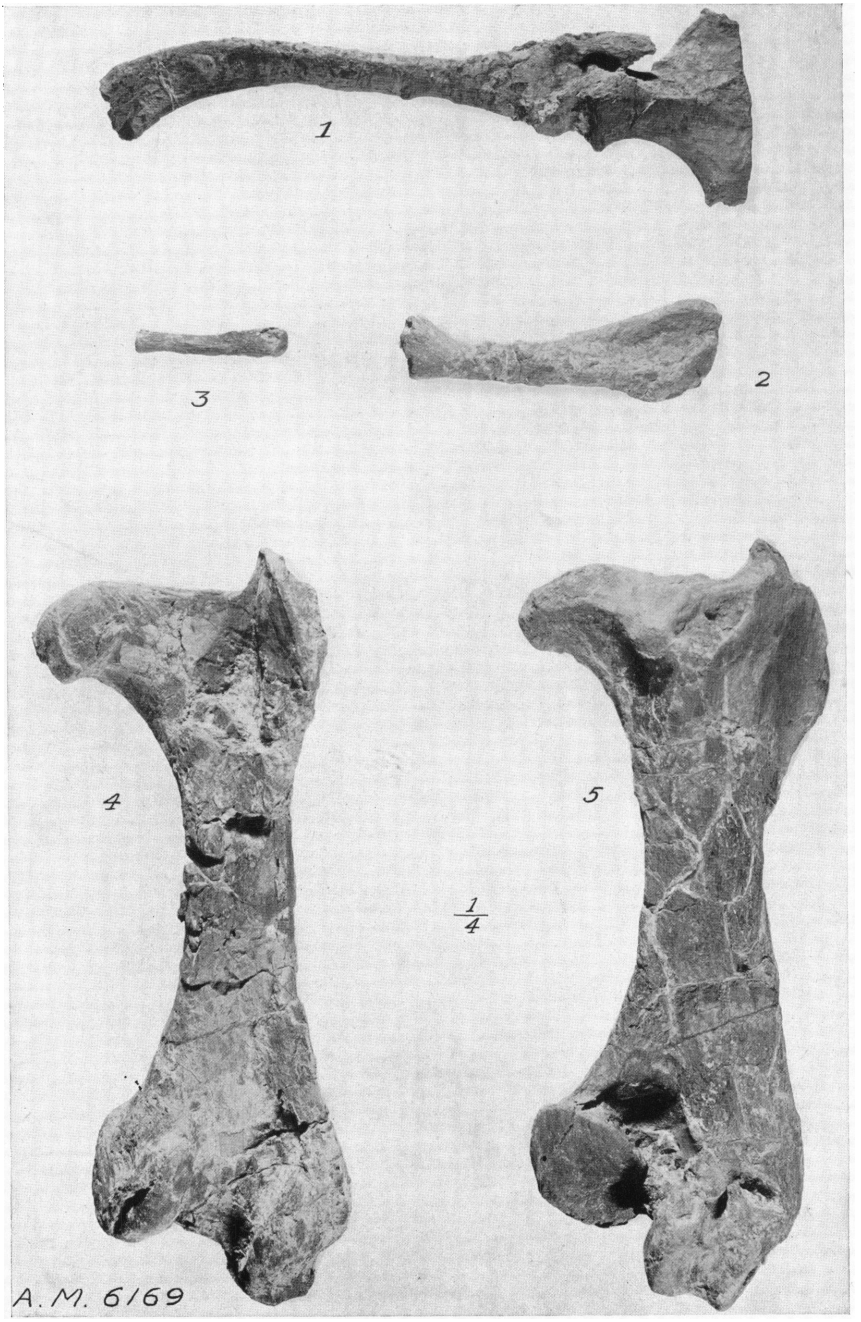
DIATRYMA STEINI.
Dorsal and sternal ribs.



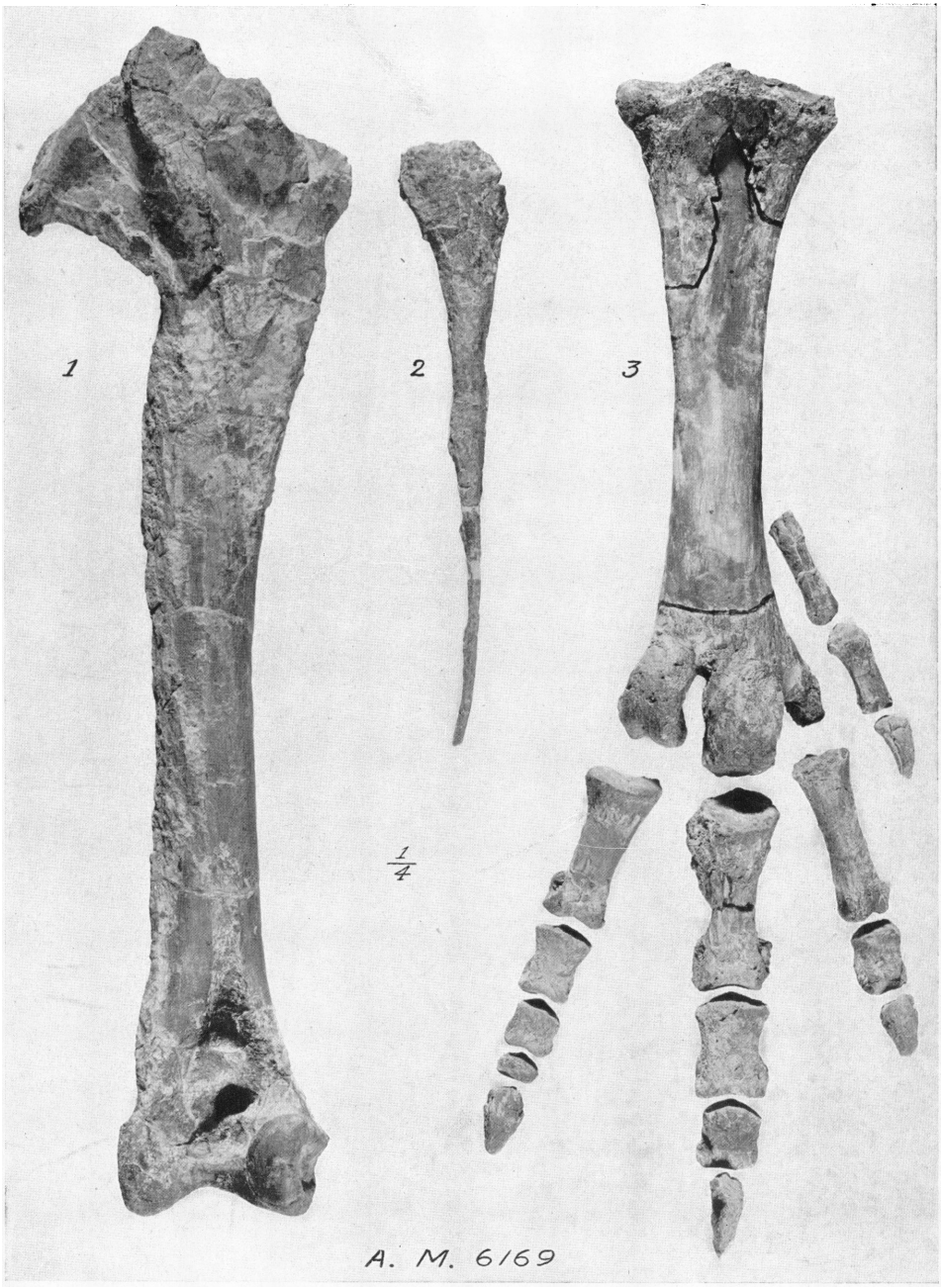
Diatryma steini.
Pelvis, ventral and left side views.



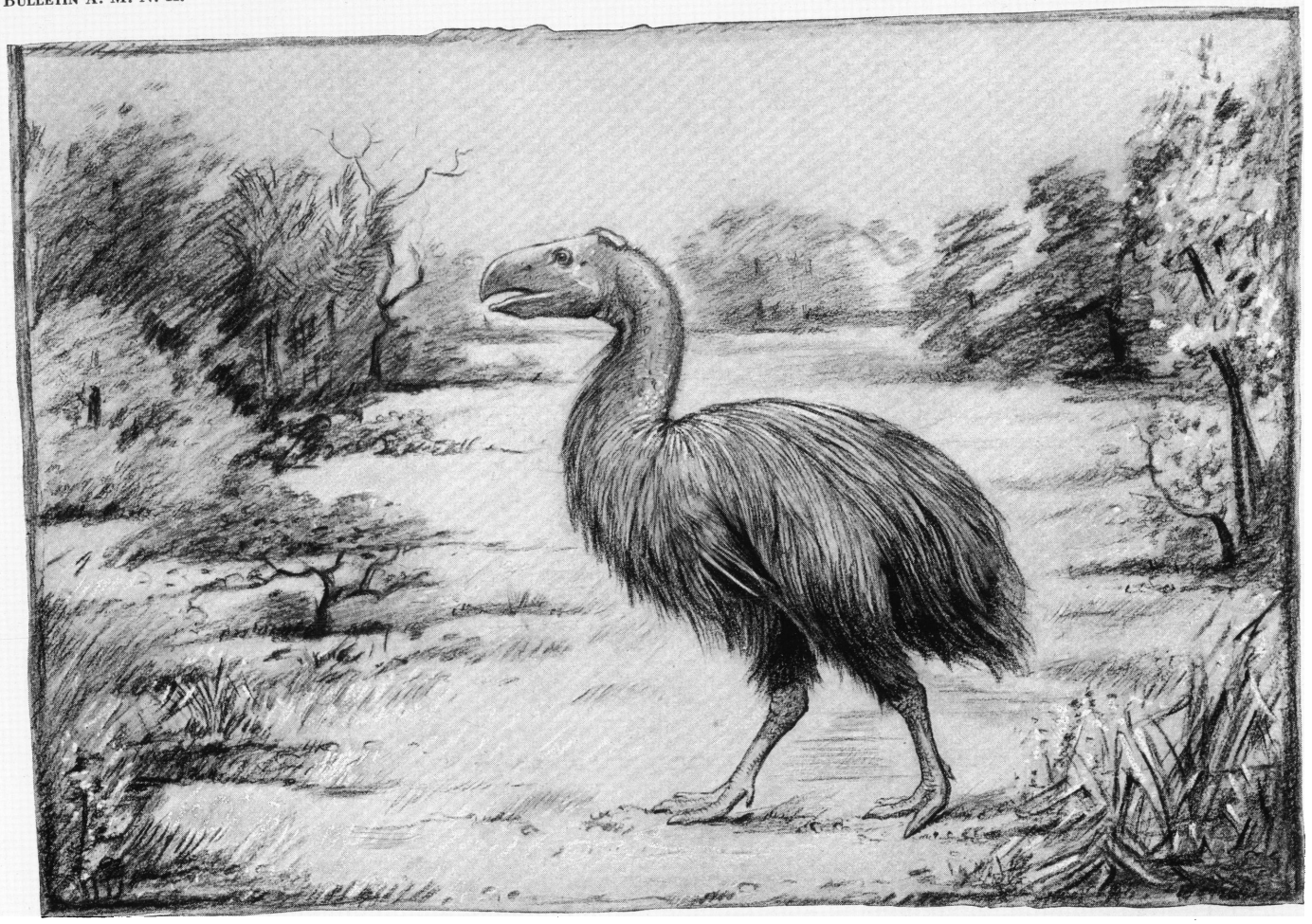
DIATRYMA STEINI.
Pelvis, dorsal and right side views.



DIATRYMA STEINI.
Shoulder girdle, humerus, (?) radius and femora.



Diatryma steini.
Tibia, fibula and pes.



Restoration of Diatryma steini. $\times \frac{1}{25}$.