

THE AUSTRALIAN DROMORNITHIDAE: A GROUP OF EXTINCT LARGE RATITES

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ABSTRACT: The Dromornithidae was a family of large ground birds, presumably ratite, that has a Miocene to Pleistocene (minimum age, 26,000 years B.P.) record in Australia. Five genera are now known, including *Dromornis*, *Genyornis*, *Ibandornis*, *Bullockornis*, and *Barawertornis*. The known forms range in size and agility from slightly larger than, and about as gracile as, the living emu, to truly gigantic, ponderous forms such as *Dromornis stirtoni* that rivaled or exceeded the size and proportions of the Malagassy elephant bird (*Aepyornis maximus*). Dromornithids and emus (Casuariidae) appear in the record simultaneously in the Miocene, the former ranging over most of Australia and reaching their greatest known diversity in the Miocene. Detailed osteological analyses of this group indicate that it is monophyletic, and more closely related to the Casuariidae, including emus, than to any other avian family.

The family Dromornithidae has been known for some time in Australia (Mitchell 1839), but because specimens were few and poorly preserved, little attention was given this group until recently. This paper presents a brief history of work on the dromornithids, familial and generic diagnoses, and hypotheses for phylogenetic relationships within the Dromornithidae as well as between the dromornithids and other avian families.

The first known reference to dromornithids lies in the oral traditions and art of the Aborigines. Tindale (1951) and Hall et al. (1951) noted traditions among the Tjapwurong tribe in western Victoria concerning "mihirung paringmal," or giant emus that supposedly lived "long ago when the volcanic hills [of the Western District of Victoria] were in a state of eruption." Some lava flows in this area are as young as 8000 years B.P. (Gill 1972). Temporal overlap of the dromornithids with Aborigines at about 26,000 years B.P. has recently been confirmed (Lancefield Swamp, Victoria; Gillespie et al. 1978), and younger records would not be surprising.

The first convincing evidence of a group of ratite birds distinct from the Casuariidae in Australia was the spectacular discovery in 1892 of partial skeletons in Pleistocene sediments of Lake Callabonna, South Australia. Newton (1893) reported this find, and subsequently Stirling (1896) and Stirling and Zietz (1896, 1900, 1905) described the Callabonna material as a new genus and species, *Genyornis newtoni*. Prior to this work all evidence of the extinct dromornithids, including the namesake of the family from Peak Downs in Queensland, *Dromornis australis* (Owen 1872, 1874), consisted of isolated and often fragmentary specimens. All of the specimens came from localities restricted to the eastern half of Australia.

Information on the Dromornithidae remained sparse until

the middle of the twentieth century. Several expeditions into central and northern Australia in the mid-1950's and thereafter led to the discovery of three new genera: *Barawertornis*, *Ibandornis* and *Bullockornis* (Rich 1979). Additional specimens of the previously known genera *Dromornis* and *Genyornis* were also recorded.

The dromornithids can now be delimited on the basis of the osteological material presently available, and meaningful comparisons with other ratite groups can be detailed. The trackways of probable dromornithids from southeastern Australia (Rich and Green 1974; Rich and Gill 1976) and a possible dromornithid egg from Pleistocene dune deposits in Western Australia offer negligible diagnostic data, however.

Abbreviations used are: AM, Australian Museum, Sydney; CPC, Commonwealth Palaeontological Collections, Bureau of Mineral Resources, Canberra; SIAM, American Museum of Natural History, Department of Vertebrate Paleontology Field Number, New York; UCMP, University of California, Museum of Paleontology, Berkeley.

DIAGNOSTIC FEATURES OF THE DROMORNITHIDAE

The dromornithids comprise a group of medium-sized to truly gigantic ground birds that were endemic to Australia from at least the Miocene until the late Pleistocene, perhaps as late as the Holocene. The smallest form, *Barawertornis tedfordi*, was about the size of the living ostrich or slightly smaller. The largest, *Dromornis stirtoni*, equaled or possibly exceeded the weight of any bird previously known (Fig. 1), including *Aepyornis maximus*, but was surpassed in height by the moas of New Zealand. Limb proportions vary from the massive-limbed *Dromornis stirtoni*, to the moderately slender, elongate-limbed *Genyornis*, to the extremely gracile-limbed *Ibandornis lawsoni*. *Barawertornis* is restricted to the early

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A



B



C



D



E



F



G



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K



N



L



M



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P

Miocene, *Bullockornis* to the late Miocene, *Ilbandornis* to the late Miocene or early Pliocene, *Dromornis* to the late Miocene and Pliocene, while *Genyornis* is restricted to the Pleistocene. The stratigraphic distribution of the dromornithids is summarized in Figure 2, and Figure 3 shows their geographic distribution.

The dromornithids were ratites in the *classic* sense, in that they lacked a true keel on the sternum. No palatal region of the skull is known, however, and allocation of this group to the palaeognathous birds is based entirely upon the similarities of their postcranial skeletons to those of emus and cassowaries. Vertebrae are also relatively rare elements, and in no specimen is a complete vertebral series known. The dromornithids can be characterized from their known elements by the following combination of characters: (1) sternum more elongate than broad with costal area occupying 60 percent of the lateral margin; (2) sternal notches lacking; (3) articulation of sternum with scapulocoracoid restricted to far lateral margins of anterior border of sternum; (4) glenoid facet of scapulocoracoid and entire wing greatly reduced, decidedly more than in ostriches and rheas; (5) humerus lacking well defined articular surfaces; (6) radius and ulna fused at several points along their shafts; (7) carpometacarpus lacking intermetacarpal space and with only one phalangeal articulation; (8) synsacrum of moderate width, not broad as in moas and aepyornithids; (9) synsacrum with articulation of hindlimb about midway between anterior and posterior ends, in contrast to condition in struthionids, where this articulation lies forward of midpoint, and in apterygids, where it lies posterior to midpoint; (10) pubes, ischia, and ilia subequal in posterior extension; (11) pubes not fused as in struthionids; (12) pubes fuse with ischium and in turn with ilium in adult specimens to produce elongate ilioischiatric fenestra and short ischiopubic fenestra, a condition found elsewhere within the ratites only in aepyornithids; (13) femur with trochanter projecting about same distance proximad of shaft as head; (14) femur with external condyle moderately exceeding internal condyle in distal extension, but not as disproportionately as in rheas and ostriches; (15) femur lacking massive muscle scars in popliteal area, thus differing from the femora of moas and aepyornithids; (16) femur with internal condyle with distalmost extension occurring anterior to condylar midpoint, approaching elliptical shape with major axis forming acute angle with posterior margin of shaft (semicircular in shape in emus, elephant birds; distally flattened in rheas, ostriches); (17) femur with condyles of equal depth; (18) tibiotarsus not decidedly mediolaterally compressed near proximal end; (19) tibiotarsus with inner cnemial crest extending far proximad to proximal articular surface; (20) tibiotarsus

with supratendinal bridge present, differing from those of all other ratites except moas, and tendinal canal centrally located; (21) tarsometatarsus with hypotarsal region broad and triangular in shape in proximal view, with two shallow hypotarsal canals located near medial and lateral boundaries of hypotarsus (this arrangement differs from the rectangular structure dissected by a single, deep canal found in moas and kiwis, the laterally offset hypotarsus of ostriches and rheas, and the low, rectangular hypotarsus of aepyornithids); (22) tarsometatarsus with single, prominent ridge extending most of length of posterior surface (this differs markedly from the short, double ridges in moas and kiwis, the short, narrow ridge in rheas and ostriches, and the absence of a ridge in aepyornithids); (23) tarsometatarsus without articulation for metatarsal I, indicating the absence of the first digit; (24) tarsometatarsus with three trochleae present, although internal trochlea often quite reduced; (25) pes with phalangeal count of 3-4-4, not the more characteristic ratite count of 3-4-5, and a tendency in at least the geologically younger forms (*Ilbandornis* and *Genyornis*) to develop blunted, hooflike unguals, rather than claws with a triangular or rounded cross section.

RELATIONSHIPS OF THE DROMORNITHIDAE TO OTHER AVIAN FAMILIES

In a recent paper (Rich 1979) I used three different methods of analysis in an attempt to determine the relationship of the Dromornithidae to the remaining ratites. Although I distinctly favor Method I, other methods that have frequently been used in phylogenetic analysis were explored to determine if all methods resulted in similar conclusions. In the first method a phenetic analysis based on the postcranial skeleton was performed initially to determine the family most closely related to the ratites, and their probable nearest relatives, the tinamous (*Tinamidae*) (Bock 1963). Then—using the definition that primitiveness was defined by common occurrence of a character in both the ratites and their nearest sibling group, the tinamous—an analysis to determine whether a character was primitive or derived was performed (see Rich 1979 for the data input for all analyses, and detailed tables summarizing the results).

The second method involved surveying all of the ratites and defining as primitive the most commonly occurring state for each character. Those characters that occurred rarely within the ratites were considered derived or advanced. Theoretically, this method would help to determine phyletic branching, where a derived character or suite of characters is held by three or less families. Derived characters that appeared early

Figure 1. A selection of diagnostic bones of Dromornithidae from mid- to late Cenozoic deposits of Australia. Femora of: (a) *Barawertornis tedfordi*, CPC 7341 (Type), Riversleigh, Queensland, Miocene (distal width 87 mm); (B–C) *Bullockornis planei*, CPC 13844 (Type) and CPC 13845 respectively, Bullock Creek, Northern Territory, Miocene (distal widths 160 mm and >152 mm); (D) *Dromornis stirtoni*, CPC 13851 (Type), Alcoota, Northern Territory, Late Miocene or early Pliocene (distal width 202 mm); (E) *Ilbandornis woodburnei*, CPC 13850 (Type) Alcoota, Northern Territory, late Miocene or early Pliocene (distal width 112 mm); (F) *Dromornis australis*, AM F10950, Peak Downs, Queensland, probably Pliocene (distal width 120 mm); (G) *Genyornis newtoni*, SIAM 61, proximal right humerus, Lake Callabonna, South Australia, Pleistocene (depth from external to internal tuberosity 25 mm); (H–K) *Ilbandornis* sp., UCMP 67038, characteristic ungual phalanx of pes, Alcoota, Northern Territory, late Miocene or early Pliocene (total length 28 mm); (L–M) *Dromornis stirtoni*, UCMP 113049, sternum, Alcoota, Northern Territory, late Miocene or early Pliocene (maximum width across sternocoracoidal processes approx. 225 mm); (N) *Dromornis stirtoni*, UCMP 113050, scapulocoracoid, Alcoota, Northern Territory, late Miocene or early Pliocene (total length >239 mm); (O) *Ilbandornis lawsoni*, UCMP 70118, proximal view of left tibiotarsus, Alcoota, Northern Territory, late Miocene or early Pliocene (maximum depth about 88 mm); and (P) *Ilbandornis* sp., UCMP 70649, distal end, right tibiotarsus, Alcoota, Northern Territory, late Miocene or early Pliocene (distal width 76 mm).

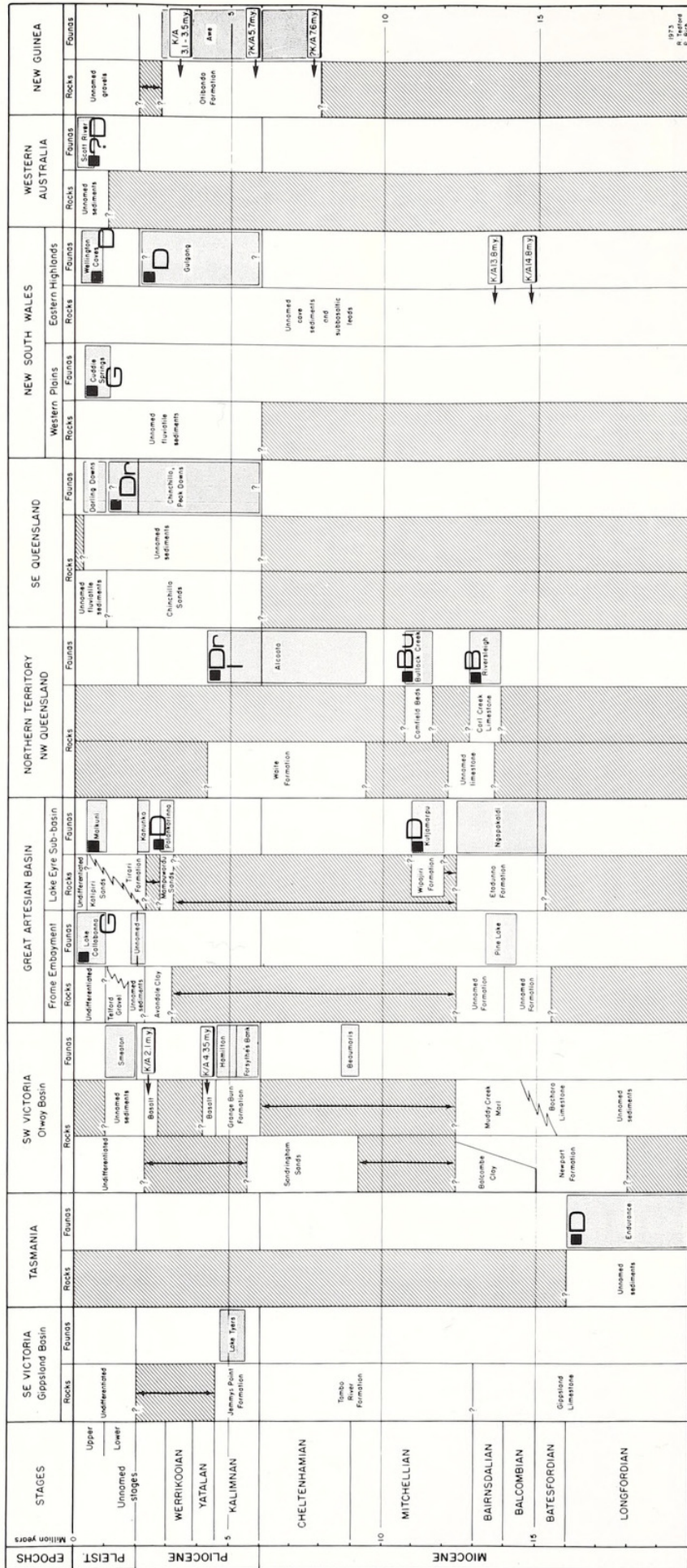


Figure 2. Stratigraphic distribution of the Dromornithidae in Australian Cenozoic deposits. Black squares represent occurrences of most dromornithid material. B, *Barawertornis*; Bu, *Bullockornis*; Dr, *Dromornithidae*; D, *Dromornithidae*; G, *Genyornis*; I, *Ibandornis*. Modified from Rich (1979).



Figure 3. Geographic distribution of the Dromornithidae in Australia. Δ , Pleistocene; \blacktriangle , Pliocene; \blacksquare , Miocene localities. Same abbreviations for generic names as in Fig. 2. (1) Diamantina River, D; (2) Warburton River, D; (3) Lancefield, D; (4) Cooper Creek, D; (5) Lake Callabonna, G; (6) Brother's Island, Pt. Lincoln, G; (7) Cuddie Springs, G; (8) Riversleigh, B; (9) Bullock Creek, Bu; (10) Canadian Lead (Gulgong, Mudgee), D; (11) Endurance Pit, South Mt. Cameron, D; (12) Wellington Caves, D; (13) Lake Ngapakaldi, D; (14) Snake Dam Locality, D; (15) Baldina Creek, G; (16) Normanville (Salt Creek), G; (17) Alcoota, Dr and I; (18) Big Cave (Naracoorte), D; (19) Penola, D; (20) Mt. Gambier, D; (21) Peake Downs, Dr; (22) Lake Palankarinna, D; (23) Scott River, ? D; (24) Mammoth Cave, D; (25) Thornbindah, D.

in the history of ratites, however, and thus possibly were possessed by a large number of the members of this group, would be misinterpreted by this method.

The third method involved an initial phenetic analysis of 56 characters (chosen because they could be used to diagnose the Dromornithidae; Rich 1979). The 56 characters studied were summed for each ratite group regardless of their polarity (primitive or advanced (=derived)), in essence a strictly numerical taxonomic approach. Only the sternum, synsacrum, and hindlimb elements were considered because of the lack of information about other elements of various fossil groups, and because of the near or total loss of the forelimb in the Dinornithidae-Emeidae lineage as well as its marked reduction in other ratites.

The primary purpose of using the three different methods was the determination of the avian group most closely related to the Dromornithidae. Thus, relationships between the re-

maining ratite groups are only briefly mentioned in the following discussion.

The analysis using Method I indicates that the Dromornithidae share decidedly more derived characters (19 of the 56 studied) with the Casuariidae (including emus) than with any other ratite family, but that the two families share few primitive characters (7) (see Table 1). The Casuariidae and the Dromornithidae show a large number of derived characters within the ratites, with 33 and 38 (respectively) of the 56 characters derived rather than primitive. The Struthionidae and Rheidae have nearly the same number of derived characters (37 and 33, respectively), but the Aepyornithidae, Apterygidae, Dinornithidae-Emeidae have fewer derived characters (30, 23, and 22, respectively). Among the 19 derived characters shared between the Casuariidae and Dromornithidae are four unique to these two groups. These are: (1) synsacrum with ilium, ischium, and pubis all protruding about the same dis-

Table 1. Number of characters of the sternum, synsacrum, and hind-limb shared by the ratites and their sibling group, the Tinamidae. Method I approach.

a. Shared derived characters (determined by lack of occurrence in the Tinamidae).

	Struthionidae	Rheidae	Casuariidae	Dromornithidae	Aepyornithidae	Apterygidae	Dinornithidae-Emeidae
Struthionidae	—	—	—	—	—	—	—
Rheidae	26	—	—	—	—	—	—
Casuariidae	16	18	—	—	—	—	—
Dromornithidae	8	11	19	—	—	—	—
Aepyornithidae	13	11	13	12	—	—	—
Apterygidae	9	12	13	9	10	—	—
Dinornithidae-Emeidae	10	10	9	10	11	9	—

b. Shared primitive characters (determined by common occurrence in both ratites and Tinamidae).

	Struthionidae	Rheidae	Casuariidae	Dromornithidae	Aepyornithidae	Apterygidae	Dinornithidae-Emeidae
Struthionidae	—	—	—	—	—	—	—
Rheidae	13	—	—	—	—	—	—
Casuariidae	8	15	—	—	—	—	—
Dromornithidae	4	8	7	—	—	—	—
Aepyornithidae	7	10	13	7	—	—	—
Apterygidae	9	18	20	9	17	—	—
Dinornithidae-Emeidae	12	17	19	13	20	29	—

tance posteriad; (2) femur with internal condyle triangular, or elliptical closely approaching triangularity, with apex forming distalmost projection of condyle; (3) tibiotarsus with inner cnemial crest extending far proximad of proximal articular surface; and (4) tarsometatarsus with hypotarsus and intercotylar prominence extending about equal distances proximad to proximal articular surfaces. The remaining 15 derived characters shared between Casuariidae and Dromornithidae are likewise shared with at least one and often more ratite groups.

For each group of ratites, the following number of the 56 characters mentioned above for Method III were present in the derived condition using the Method I approach: Struthionidae 37; Rheidae 33; Casuariidae 33; Dromornithidae 38; Aepyornithidae 30; Apterygidae 23; Dinornithidae-Emeidae 22.

Thus, the analysis of Method I indicates that the Dromornithidae are most closely related to the Casuariidae. A single, common ancestral stock could have given rise to each of these two groups, and two separate colonizations within Australia-New Guinea are not necessary to account for their presence. The Australian ratites appear decidedly distinct from the New Zealand moas and kiwis (which form a close-knit osteological group) and are apparently the most primitive of all the ratite groups. The Casuariidae, but not the Dromornithidae, in turn share a large number of derived characters with the Struthion-

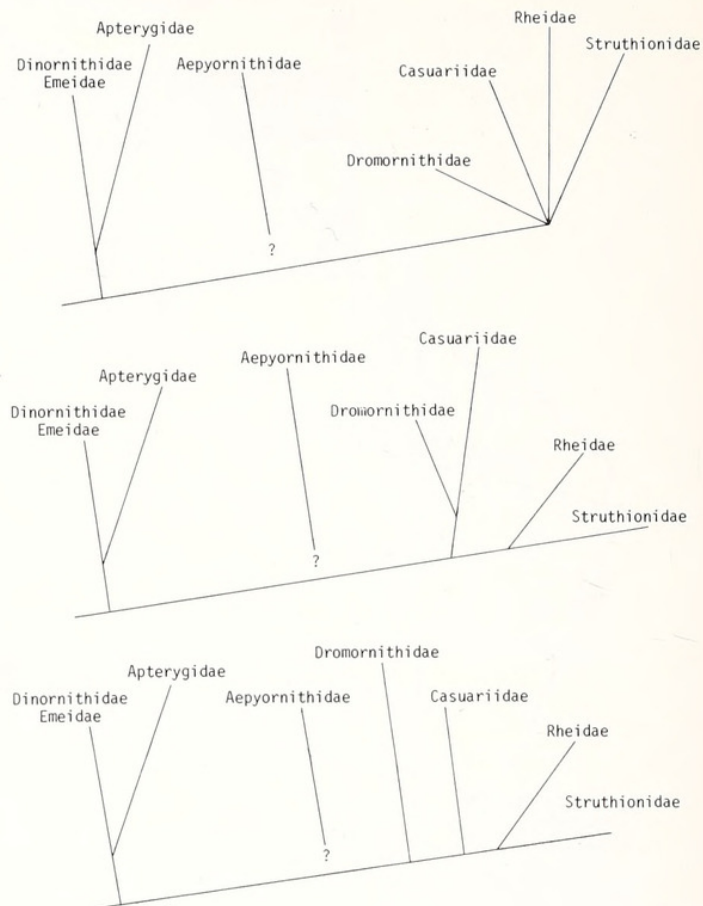


Figure 4. Phylogenetic hypotheses expressing possible interrelationships of the ratites.

idae (16 and 8, respectively) and Rheidae (18 and 11, respectively), which are quite closely related to one another (sharing 26 derived characters). Without further, more expanded analysis, however, it is difficult to determine how many of the characters shared by the Struthionidae-Rheidae and the Casuariidae are the result of convergent evolution. Three phyletic hypotheses are suggested (Fig. 4) based on the Method I approach.

The Method II approach, i.e., using commonality of a char-

Table 2. Number of derived characters (determined by commonality of occurrence within the ratites) of the sternum, synsacrum, and hind-limb shared by several ratite groups. Method II approach.

	Struthionidae	Rheidae	Casuariidae	Dromornithidae	Aepyornithidae	Apterygidae	Dinornithidae-Emeidae
Struthionidae	—	—	—	—	—	—	—
Rheidae	9	—	—	—	—	—	—
Casuariidae	2	2	—	—	—	—	—
Dromornithidae	1	2	7	—	—	—	—
Aepyornithidae	4	1	3	6	—	—	—
Apterygidae	1	0	2	1	1	—	—
Dinornithidae-Emeidae	3	2	1	7	4	8	—

Table 3. Number of unweighted characters of the 56 studied by Rich (1979) that are shared by the various ratite groups. Method III approach.

	Struthionidae	Rheidae	Casuariidae	Dromornithidae	Aepyornithidae	Apterygidae	Dinornithidae-Emeidae
Struthionidae	—	—	—	—	—	—	—
Rheidae	39	—	—	—	—	—	—
Casuariidae	24	33	—	—	—	—	—
Dromornithidae	12	19	26	—	—	—	—
Aepyornithidae	20	21	26	19	—	—	—
Apterygidae	18	30	33	18	27	—	—
Dinornithidae-Emeidae	22	27	28	23	31	38	—

acter within the ratites to indicate primitiveness and rarity to indicate a derived or advanced condition, reinforced many of the conclusions reached in the Method I analysis, although not all were in agreement. The Dromornithidae shared the greatest number of derived characters (7) with both the Casuariidae and the Dinornithidae-Emeidae, but only one with the Apterygidae (see Table 2). The suggested similarity between moas and dromornithids can perhaps be accounted for by size and functional similarities, a result of convergent evolution. Using Method II, casuariids clearly share far more characters considered to be derived with dromornithids than with any other ratite group, and the relationship between the moas and kiwis of New Zealand is strongly supported.

Method III, the numerical taxonomic approach, also reinforced several of the relationships suggested by the two previous methods, but obscured or contradicted others (Table 3). The Dromornithidae still shared more characters (26) with the Casuariidae, but the Casuariidae shared more characters with the Rheidae (33) and the Apterygidae (33) than with any other ratite group. Method III suggests that the Struthionidae and Rheidae are more similar to one another than to any other ratite group (sharing 39 characters), as are the moas and kiwis (sharing 38 characters). The Aepyornithidae share the most characters with the Dinornithidae.

GENERIC RELATIONSHIPS WITHIN THE DROMORNITHIDAE

As illustrated above, three different types of phylogenetic analysis suggest that the Dromornithidae share the greatest number of similarities with the Casuariidae (Fig. 4). Because of this, I also evaluated the characters of the latter group when I considered intra-dromornithid relationships.

In my analyses, a character was considered to be primitive within the family Dromornithidae if it was shared by both the dromornithids and the casuariids, or in some cases if it frequently occurred in a wide range of avian families. Additionally, a second criterion used in some analyses was to assume a character to be primitive within the dromornithids if it was the more common state in this group. All of these methods of determining the polarity of a character, i.e., whether primitive or advanced, have been discussed in numerous publications

(Kluge and Farris 1969; Kluge 1971; Schaeffer et al. 1972; Hecht 1976). Time was *not* a factor that influenced determination of whether a character was primitive or advanced. In fact, one of the oldest occurring dromornithids, *Bullockornis*, appears to be one of the most specialized in the family. Once the primitive or advanced nature of each character or character complex was estimated, a phylogeny was derived based upon the minimum number of alterations to a primitive morphotype needed to produce the five genera and eight species known for the family. Analysis was restricted to the femur and tarsometatarsus because these are the only elements represented for all of the dromornithid genera, and most species. In Figure 5, 21 characters of these two elements are tabulated for each of the dromornithid genera as well as *Dromaius*, a casuariid genus. The phylogeny implied in Figures 5 and 6 resulted from analyses using the following two approaches.

First, an analysis of the dromornithid complex using commonality of occurrence within the Dromornithidae as an indicator of primitiveness was performed. The results are summarized in the following paragraphs (see Figs. 7 and 8 for illustrations of the femur, tibiotarsus, and tarsometatarsus).

Barawertornis, the oldest known dromornithid from Miocene sediments in the Northern Territory, is the most primitive and the smallest known member of the family, having 14 of the 21 characters summarized in Figure 5 in the primitive state. This genus is presumably specialized over the postulated primitive morphotype for the Dromornithidae in that on the femur, the internal condyle is broader than the external (char. 22),¹ the fibular condyle protrudes only moderately laterad (char. 15), the popliteal area is deep (char. 14); and, on the tarsometatarsus, trochleae II and IV are subequal in distal extension (char. 9).

The remaining dromornithids, including *Dromornis*, *Ilbandornis*, *Genyornis*, and *Bullockornis*, are derived with respect to *Barawertornis* because on the femur, the neck is not decidedly constricted (char. 3), the internal condyle has a decidedly elliptical shape (char. 18); and on the tarsometatarsus, trochlea II is moderately to highly reduced (char. 11).

Within the above lineage it is evident that *Dromornis*, *Ilbandornis*, and *Genyornis* are closely related and form a natural grouping separate from *Bullockornis*. Shared derived characters for this former lineage include the femur with the medial surface of the internal condyle decidedly ridged (char. 19), and the fibular condyle extending as far or nearly as far posteriad as the internal condyle (char. 26); and the tarsometatarsus with trochlea III moderately to decidedly broader than trochlea IV (char. 16).

Although decidedly more derived than *Barawertornis*, the *Dromornis*-*Ilbandornis*-*Genyornis* lineage, even if its most specialized member (*Genyornis*) is considered, does not possess as many derived characters within the Dromornithidae as does *Bullockornis* (12 out of 21, *Genyornis*; 14 out of 21, *Bullockornis*).

Bullockornis, with two species, is characterized by having the following derived characters: femur with shaft deep (char. 10), long axis of the external condyle nearly in line with the

¹ Character numbers refer to those cited by Rich (1979) in a detailed analysis of the Dromornithidae. Of the 200 characters analyzed, only a few were actually useful in the final phylogenetic analyses.

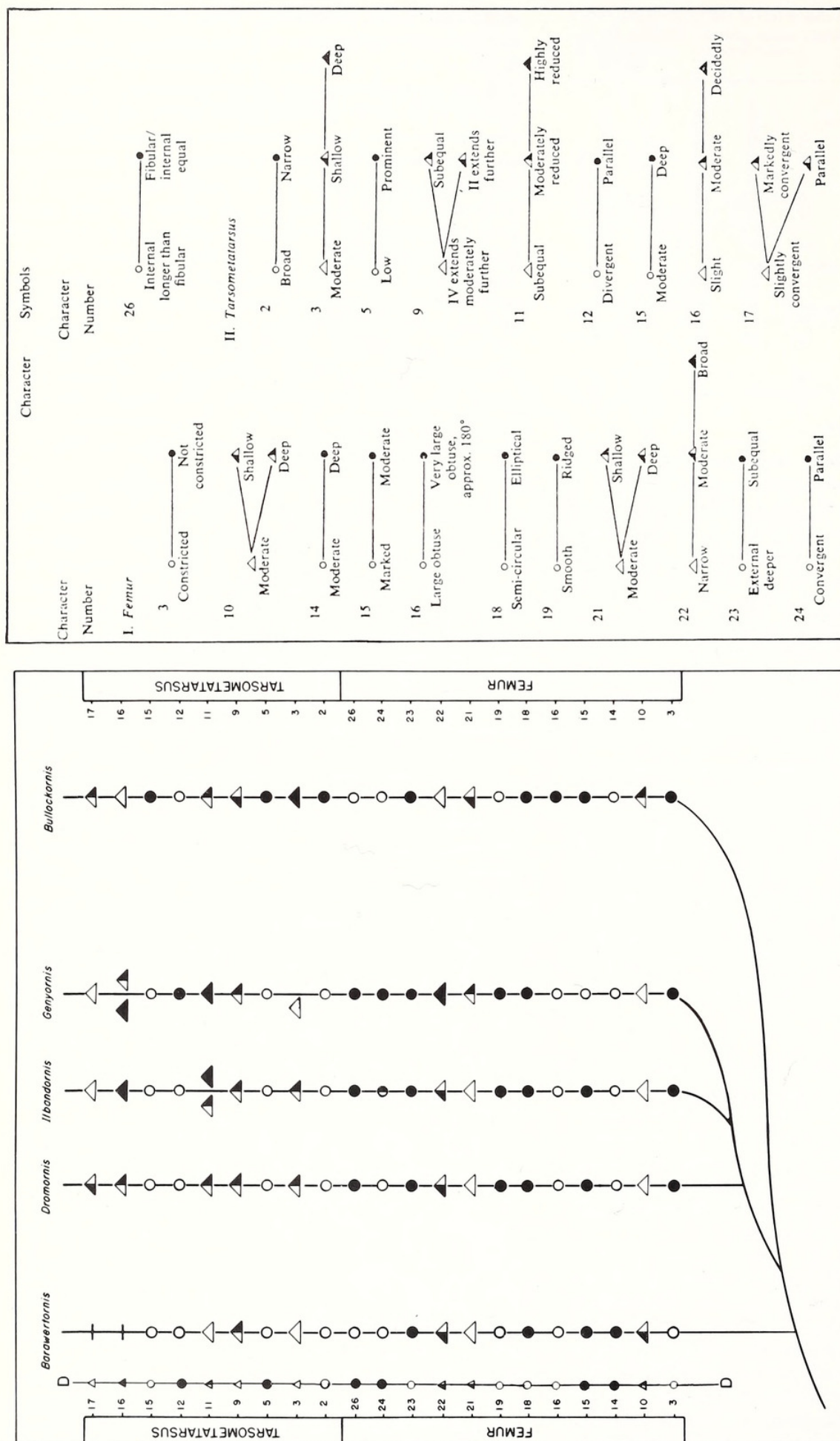


Figure 5. Distribution of characters used in constructing phylogenetic hypotheses for the Dromornithidae, based on the hindlimb. Character numbers refer to those used by Rich (1979); only a few of those analyzed were useful for phylogenetic interpretation. D, *Dromornis* (Casuariidae). Femur characters evaluated include: (3) degree of narrowing at neck, (10) degree of anteroposterior impression of shaft, (14) depth of popliteal area, (15) degree of lateral protrusion of fibular condyle, (16) angle formed between proximodistal axis of external condyle and long axis of shaft, (18) shape of internal condyle, (19) nature of distal one-fourth of internal shaft surface and internal condyle, (21) degree of anteroposterior compression of condyles with respect to width of distal end, (22) width of external condyle with respect to internal, (23) comparative depths of internal and external condyles, (24) degree of anterior convergence of long axis of condyles, (26) comparative posterior extension of fibular and internal condyles. Tarsometatarsus characters evaluated include: (2) width of intertrochlear space between trochleae III and IV, (3) depth of shaft, (5) prominence of subhypotarsal ridge, (9) comparative extension distad of trochlea II and IV, (11) reduction of trochlea II with respect to III and IV, (12) relative orientation of medial and lateral margins of trochlea II, (15) depth of trochlea III, (16) width of trochlea III with respect to width of trochlea IV at their anteroposterior midpoints, (17) degree of posterior convergence of lateral and medial margins of trochlea III.

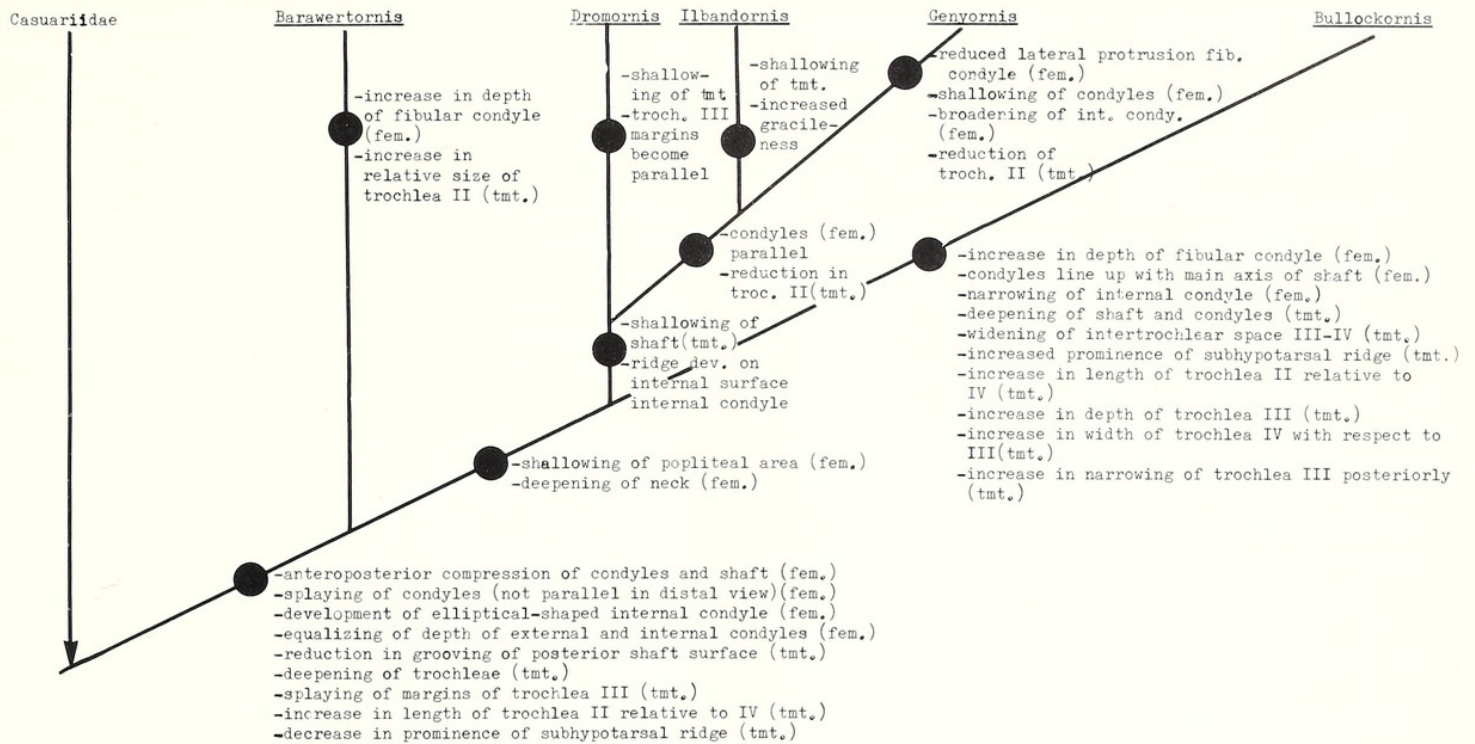


Figure 6. Phylogenetic hypothesis expressing possible interrelationships of the genera of dromornithids. Major changes occurring from most primitive (*Barawertornis*) to most advanced genera are enumerated.

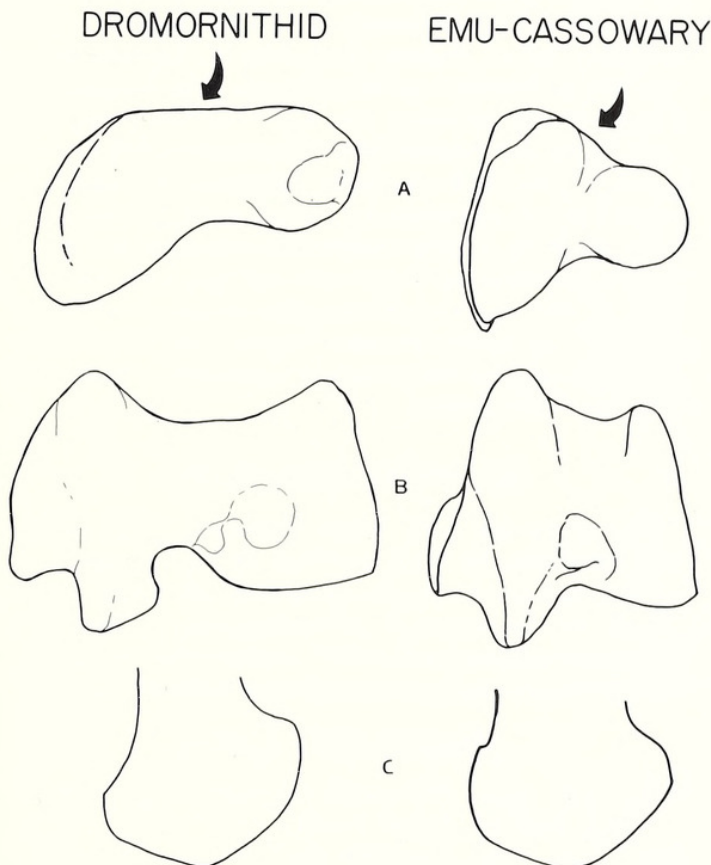


Figure 7. Comparison of femora of Dromornithidae and Casuariidae. A, proximal view; B, distal view; C, medial views.

long axis of the shaft (char. 16), and the internal and external condyles nearly subequal in depth (char. 23); tarsometatarsus with intertrochlear space between trochleae III and IV broad (char. 2), the subhypotarsal ridge prominent (char. 5), trochlea III extremely deep (char. 15), and the medial and lateral margins of trochlea III markedly convergent posteriorly (char. 17).

The second analytical approach used the common occurrence of a character state within the nearest sibling group, the Casuariidae, to indicate the primitive state of a character and produced the results described below.

Barawertornis has the greatest number of characters in a primitive state (11), even though two could not be evaluated, and *Bullockornis* the least (5). This reinforces the interpretation of the previous analysis. The following trends for the dromornithids are suggested by this analysis. In the femur there is a broadening of the neck region, and overall antero-posterior compression of shaft and distal end (*Bullockornis* may well be primitive in having a deep shaft, contrary to the suggestion of the previous analysis, or the deep condition is secondarily derived), a shallowing of popliteal area, an increase in lateral protrusion of external condyle, a decrease in twisting of condyles away from long axis of shaft, the development of an elliptical internal condyle (viewed medially), a broadening and narrowing of the internal condyle relative to width of external condyle, an increase in depth of external condyle so it becomes subequal in depth to internal condyle, and, in distal view, the long axes of condyles become parallel.

In the tarsometatarsus there is a decrease in the relative separation of trochleae III and IV, a deepening of shaft, a decrease in prominence of subhypotarsal ridge, an increase in distal extension of trochlea II, a reduction in size of trochlea II and thus in size of second digit, an increase in depth of trochlea III, and an increase in width of trochlea IV with

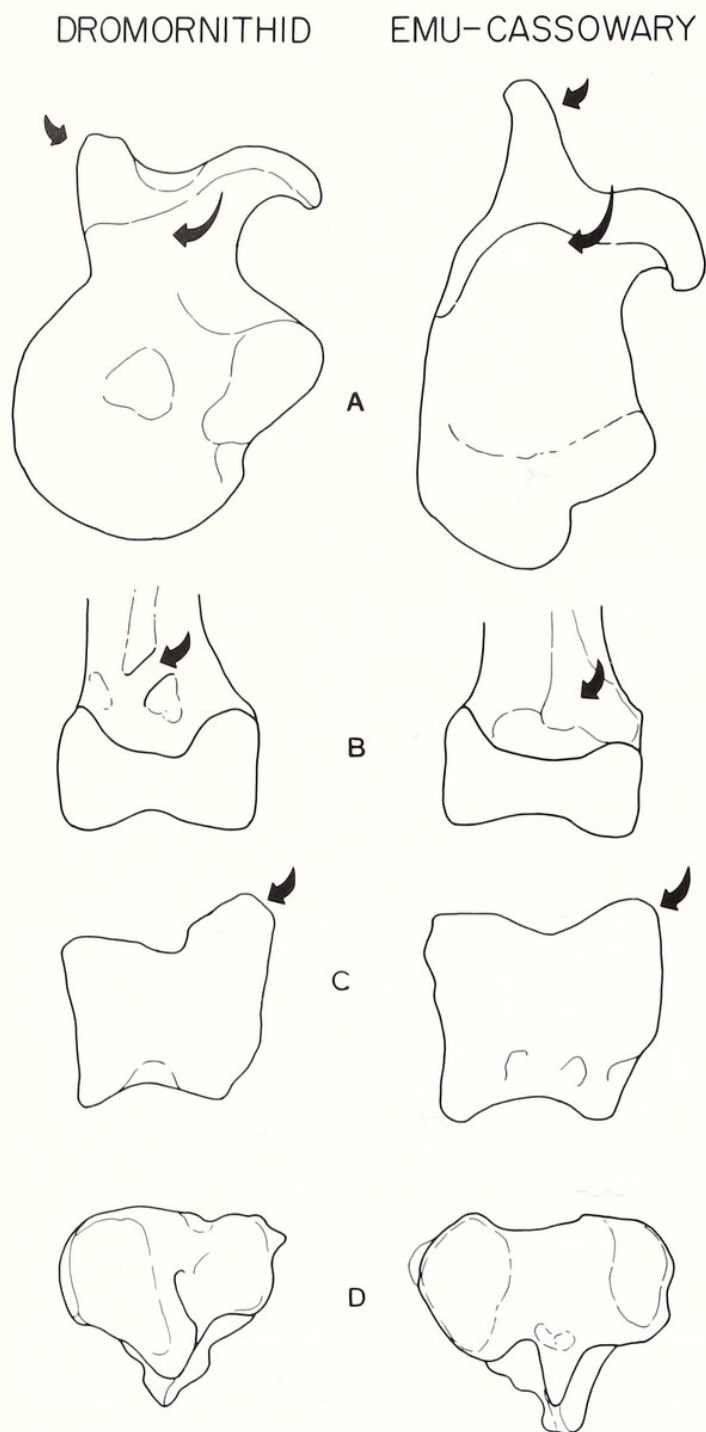


Figure 8. Comparison of tibiotarsi (A-C), and tarsometatarsi (D) of Dromornithidae and Casuariidae. A, D, proximal views; B, anterior views; C, distal views.

respect to trochlea III, and thus an equalization in the size of the two digits.

Other trends that occur at some time within the dromornithid lineage (but just when and in which genera is difficult to determine because of the lack of complete enough specimens of some genera) after it diverged from the cassowary and emu lineage include: (1) deepening and strengthening of the lower jaw, (2) deepening of the atlas vertebra, (3) flattening of the sternum and reduction in area of scapulocoracoid contact, as well as slight overall reduction in size of scapulocoracoid (the scapula and coracoid become more in line with one another),

(4) equalization of overall dimensions of radius and ulna, and lengthening of both relative to humerus, (5) decrease in depth of synsacrum dorsal to acetabulum and an increase in depth of pubic bar, (6) increase in mediolateral compression of cnemial crests and a decrease in depth of internal cnemial crest of tibiotarsus, (7) development of a supratendinal bridge on tibiotarsus (or retention from ancestral stock that gave rise to both Casuariidae and Dromornithidae), (8) increase in depth of internal condyle on tibiotarsus, and (9) development of hoof-like ungual phalanges on digits and loss of one phalanx in digit IV, resulting in a phalangeal formula for the pes of 3-4-4.

SUMMARY

The family Dromornithidae is composed of five genera and eight species of extinct ground birds restricted to the middle and late Cenozoic of Australia (Figs. 2 and 3). Although some forms were only slightly larger than their closest relatives, the emus and cassowaries, one form may have exceeded the weight of the largest known bird, *Aepyornis maximus* of Madagascar.

The history of the dromornithids extends back only into the Miocene, but the presence of four genera in the Miocene indicates that the group had its origins much earlier. The fossil record for most Cenozoic vertebrates in Australia is poorly known before the Miocene because of a lack of known older localities, a result of the geology of the Australian continent and the inaccessibility of certain areas that have paleontological promise.

The use of three different methods of phylogenetic analysis consistently suggested that the Dromornithidae were most closely related to the only other Australian ratite group, the Casuariidae. The dromornithids are quite distinct from the moas (Dinornithidae-Emeidae) of New Zealand and probably originated from a common stock with the Casuariidae, and possibly the Rheidae and Struthionidae. The ancestral form may have been advanced over that which gave rise to the moas, kiwis, and elephant birds. It is conceivable that a single ancestral stock on the Australian landmass could have given rise to both the casuariids and dromornithids, and two invasions are not an absolute requirement to account for the Australian ratite diversity. If such an event took place during the early to mid-Cretaceous, the ancestral form could conceivably have flown or walked between Australia and the remaining southern continents when tenuous connections still existed between these land masses.

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